Patrones de diversidad, distribución y dominancia de plantas leñosas en los bosques montanos del Parque Nacional Madidi, Bolivia

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Tesis doctoral

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REAL JARDÍN BOTÁNICO CSIC

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Introducción general

Los bosques tropicales de los Andes son ecosistemas de excepcional interés porque presentan (a) una alta riqueza de especies, (b) un alto nivel de endemismo, y (c) un alto número de especies amenazadas. Estos tres criterios son clave para optimizar la conservación de la biodiversidad a escala global y solo se simultanean en menos del 0,2% de la superficie terrestre (Orme et al. 2005). Distintos procesos explican por qué se encuentra aquí una gran parte de la biodiversidad del continente americano, que afectan tanto a la génesis de la diversidad (Rull 2011, Swenson et al. 2012) como a su mantenimiento (Distler et al. 2009, Jiménez et al. 2009). El evento reciente más importante para la actual diversidad de especies es el levantamiento de los Andes, que supuso la creación de nuevas y extensas áreas abiertas a la colonización vegetal. El mismo proceso tectónico que levantó los Andes, causó el cierre del istmo de Panamá hace unos 3,5 millones de años, casi inmediatamente seguido de una época glacial (Bartoli et al. 2005), lo que provocó en un breve lapso de tiempo una masiva migración de especies desde Norteamérica hacia Sudamérica (Hoorn et al. 2010). La colonización de los Andes, tanto desde Norteamérica a lo largo de las cadenas montañosas, como desde la llanura amazónica por parte de los taxones que superaron el filtro abiótico impuesto por la altitud, constituyen los fundamentos de la biodiversidad andina (Antonelli et al. 2009, Herzog et al. 2012, Hughes et al. 2013). Por otro lado, la erosión y sedimentación en la vertiente oriental de los Andes (húmeda y lluviosa), combinado con la alternancia de valles y series de cadenas de montañas, son causa de un mosaico muy diverso de suelos en los Andes, y de un gradiente edáfico longitudinal importante en la Amazonía (Pitman et al. 2008, Hoorn et al. 2010, Antonelli y Sanmartín 2011). En suma, el mapa andino es el de un paisaje abrupto y variado, donde la dispersión de especies es dificultosa y errática (Young 1995, 2012, Young et al. 2002) y donde existen fuertes gradientes de precipitación y temperatura, lo que hace que, los suelos tengan un carácter muy heterogéneo. Todo ello favorece la existencia de poblaciones aisladas entre sí, lo que ha provocado una intensa especiación desde hace ~2 millones de años (Antonelli et al. 2009, Pennington y Dick 2010, Rull 2011).

El paisaje ecológico y humano, así como el funcionamiento de la ecorregión, están sufriendo en la actualidad importantes cambios bióticos y abióticos (Herzog et al. 2012, Swenson et al. 2012). Algunos de estos procesos se ven acentuados por la natural vulnerabilidad de los bosques tropicales andinos en diversos aspectos. Por una parte, los mismos procesos que han causado el alto grado de endemismo en estas regiones montañosas confieren también al ecosistema una especial fragilidad en cuanto a la posibilidad de extinciones locales de especies, muchas de ellas con escasas poblaciones y/o de distribución muy limitada. Otra fuente de fragilidad importante del ecosistema son las fuertes pendientes que lo hacen más vulnerable que otros bosques tropicales a las construcciones de caminos, parcelas agrícolas y tala maderera, debido a la fuerte erosión que estas actividades provocan. Finalmente, varios estudios han mostrado que los ecosistemas tropicales a alta altitud experimentarán un cambio climático más acelerado que los de tierras bajas (Doumenge et al. 1995, Pounds et al. 1999, Foster 2001, Laurance et al. 2011, Larsen et al. 2012). Por tanto los bosques andinos tropicales son zonas críticas en cuanto a la adaptación del ser humano al cambio climático, además de un laboratorio natural para estudiar sus efectos ecológicos.

A pesar de su importancia global y de su rápida transformación en diferentes regiones y países, hasta el momento existe muy poca información (especialmente cuantitativa) de este tipo de ecosistemas, sobre lo cual han alertado recientemente varios grupos de investigación (*e.g.,* Bruijnzeel et al. 2010, Jones et al. 2011, Martin et al. 2011, Swenson et al. 2012). De hecho, para bosques como los estudiados en esta tesis, *a priori* se desconoce si un bosque de un localidad dada será florísticamente similar o muy diferente a otros bosques relativamente cercanos, si las especies que dominan en un determinado lugar o a una determinada altitud también lo hacen en regiones adyacentes, o si los bosques estarán dominados (o no) por un conjunto común de especies a una determinada escala. La escasez de estudios anteriores se debe a razones fundamentalmente logísticas, debido a las dificultades que entraña el estudio de estos bosques. El trabajo de campo es lento y costoso debido a lo abrupto del terreno, a la dificultosa accesibilidad (sin ríos navegables, sin demasiados caminos), a la baja densidad de población que conlleva la dificultad para encontrar ayudantes de campo locales, y a las condiciones climáticas más duras que en los cercanos bosques tropicales de tierras bajas. Esto ha lastrado históricamente el conocimiento de los bosques montanos respecto a los bosques amazónicos, mientras que éstos últimos han experimentado un gran avance en su conocimiento biológico durante las últimas décadas. La presente tesis pretende integrar el conocimiento existente en la Amazonía en un sistema más complejo que abarca tanto Andes como Amazonía, y el ecotono que une ambas ecorregiones.

MARCO TEÓRICO: DIVERSIDAD, DISTRIBUCIÓN Y DOMINANCIA DE PLANTAS LEÑOSAS

El marco conceptual en el que nos situamos maneja tres hipótesis complementarias que intentan explicar los patrones de distribución y biodiversidad en los bosques tropicales. La primera de ellas es la *hipótesis de la oligarquía*, que en sentido amplio sostiene que los bosques tropicales están compuestos por un pequeño grupo de especies (oligarquías) que son a la vez frecuentes en una región, abundantes localmente, y que dominan en los diferentes hábitats presentes (Pitman et al. 2001, Macía y Svenning 2005). Las otras dos hipótesis intentan explicar el recambio de especies invocando a dos mecanismos muy diferentes. En primer lugar, la *hipótesis del determinismo ambiental* mantiene que la mayor parte de las especies se distribuyen en función del ambiente y por tanto, existen relaciones entre la composición florística y las variables ambientales (*e.g.,* Tuomisto et al. 2003a, b, c). Por el contrario, la *teoría neutra de la biodiversidad y biogeografía* afirma que las especies son indiferentes al ambiente y se distribuyen al azar, aunque exista autocorrelación espacial por limitaciones en la dispersión (Hubbell 2001). Estas hipótesis no son excluyentes entre sí.

Dominancia e hipótesis de la oligarquía

Cualquier aproximación al estudio de la composición florística de un bosque, incluyendo una aproximación meramente descriptiva, pasa por definir y caracterizar sus taxones dominantes, ya que es fundamental para comprender el esqueleto del ecosistema y además están implicados en múltiples interacciones bióticas (Vázquez y Gaston 2004, Gaston 2010). La hipótesis de la oligarquía sostiene que los bosques tropicales, al igual que los templados, pueden caracterizarse por un limitado número de especies que representan la mayor parte de los individuos. Sostiene además que las especies dominantes a escalas locales lo hacen también a escalas más amplias, regionales o incluso continentales (Pitman et al. 2001, 2013). La hipótesis está estrechamente relacionada con la correlación positiva entre abundancia local y amplitud del rango de distribución de las especies, uno de los patrones macroecológicos mejor documentados (Gaston et al. 2000). La originalidad de la hipótesis de Pitman y colaboradores radica en ofrecer una visión complementaria al concepto de bosque tropical como un sistema extremadamente heterogéneo e impredecible, lleno de especies raras o desconocidas, imperante en el ámbito académico hasta hace una década.

La hipótesis de la oligarquía está muy centrada en los patrones y menos en los mecanismos. Sin embargo, asociadas a ella hay al menos tres hipótesis complementarias que intentan explicar la existencia de oligarquías desde un punto de vista mecanístico (Pitman et al. 2013): (1) las especies oligárquicas soportan un rango más amplio de condiciones ambientales que las especies raras (Brown 1984); (2) las especies oligárquicas tienen capacidad de dispersión a larga distancia (Ruokolainen y Vormisto 2000); (3) las especies oligárquicas pueden reclutar individuos juveniles en proximidad de los individuos adultos (*e.g.,* Comita et al. 2010), evadiendo de algún modo las dinámicas Janzen-Connell que promueven la coexistencia de muchas especies a escalas locales (Janzen 1970, Connell 1971).

A pesar de que los procesos subyacentes son rara vez explorados, la hipótesis de la oligarquía ha recibido amplio apoyo empírico en muy diferentes tipos de bosques tropicales, aunque casi siempre a escalas del orden de 10.000 km^2 y bajo condiciones ambientales relativamente homogéneas (Pitman et al. 2013).

Recambio de especies: procesos determinísticos **vs.** *procesos neutros*

Conocer cómo y por qué cambia la composición florística de un bosque a lo largo del espacio (recambio de especies, o diversidad beta) es una de las principales cuestiones en ecología y biogeografía (Condit et al. 2002, Duivenvoorden et al. 2002, Tuomisto 2010, Anderson et al. 2011, Kraft et al. 2011). La mayor parte de las teorías que intentan explicar la alta diversidad existente en los bosques tropicales se apoyan hasta cierto punto en la dicotomía entre procesos de reparto de nicho y los procesos espaciales neutros (Potts et al. 2002, Jabot et al. 2008, Legendre et al. 2009, Vergnon et al. 2009, Tuomisto et al. 2012). Ambas teorías apelan a mecanismos muy diferentes; sin embargo, estudios recientes los consideran procesos complementarios más que procesos antagónicos (Gravel et al. 2006, Herault 2007, Adler et al. 2007, Halley e Iwasa 2012).

Respecto al papel del ambiente sobre la distribución de las plantas, los estudios previos en bosques tropicales sugieren que el suelo podría reflejar la mayor parte de la información relevante para las plantas en bosques tropicales a escalas locales (John et al. 2007, Jones et al. 2008), intermedias (Costa et al. 2005, Bohlman et al. 2008, Andersen et al. 2010, 2012, Damasco et al. 2013), y regionales (Tuomisto et al. 2003a, Duivenvoorden et al. 2005, Macía et al. 2007, Guèze et al. 2013). Esto podría deberse a que el suelo refleja muchas de las grandes fuerzas que dan forma a los ecosistemas: está influenciado por la geología (tipo de roca dominante), por la topografía (*e.g.,* ladera *vs.* fondo de valle) y por variables macroclimáticas, microclimáticas y biológicas. Sin embargo, parece que existe también una tendencia a que la vegetación responda a factores macroclimáticos a escalas regionales y continentales, mientras que los factores edáficos son más determinantes a escalas locales (Siefert et al. 2012).

La teoría neutra de la biodiversidad y biogeografía (Hubbell 2001) propone que el espacio, y no el ambiente, es lo único relevante. Tiene, en esencia, una única asunción: todas las especies tienen las mismas tasas per cápita de muerte, de nacimiento, de dispersión y de especiación. Sería largo presentar aquí en detalle la controversia que ha despertado esta teoría. Muchos investigadores la consideran un modelo nulo válido y altamente parsimonioso frente al cual otros modelos más complejos deberían demostrar su superioridad (Hubbell 2005, 2006, 2008, Alonso et al. 2006, Rosindell et al. 2011). Otros investigadores, en cambio, la critican fundamentalmente por modelizar ecosistemas basándose en premisas falsas (*se sabe* las especies *no* son indiferentes al ambiente) (McGill 2003, Nee y Stone 2003, Ricklefs 2006, Ricklefs y Renner 2012). En cualquier caso, la teoría neutra ha supuesto un renovado interés en los procesos de dispersión, las dinámicas de metapoblaciones y otros procesos fundamentalmente aleatorios que ocurren a diferentes escalas en comunidades naturales (Chave 2008).

ZONA DE ESTUDIO: REGIÓN MADIDI

La región Madidi ocupa unos 40.000 km^2 entre los Andes y la Amazonía, en el noroeste de Bolivia cerca de la frontera con Perú (Fig. 1.1). Esta región constituye uno de los gradientes altitudinales forestales continuos más extensos del mundo y se estima que podrían existir hasta 12.000 especies de plantas vasculares (Cornejo-Mejía et al. 2011, Friedman-Rudovsky 2012). Evidentemente, documentar y analizar la riqueza florística de la región es una tarea titánica. Los mayores avances sin duda han sido realizados durante la última década por parte del denominado "Proyecto Madidi", una alianza entre el Herbario Nacional de Bolivia, Missouri Botanical Garden, Real Jardín Botánico de Madrid (entre los años 2000-2008) y la Universidad Autónoma de Madrid (desde el año 2009). La presente tesis es fruto de una colaboración estrecha con esta red de trabajo.

Datos empleados, colaboración con el Proyecto Madidi

El núcleo del presente trabajo es el estudio del bosque tropical montano, entre 1200 y 3100 m de altitud (Fig. 1.2). En conjunto, se midieron e identificaron 18.876 individuos pertenecientes a 877 especies en las 54 parcelas de 0,1 ha inventariadas (ver Apéndices 1 y 2, con las especies inventariadas y las características de las parcelas, respectivamente). Todas las especies fueron colectadas al menos una vez, lo que supuso 3100 colecciones botánicas, cada una de ellas con 1-8 duplicados. Si se suman todas las expediciones realizadas más los viajes exploratorios previos, se dedicaron más de 200 días de campo a inventariar este tipo de bosque durante la realización de la tesis. Todas las colecciones botánicas, tras ser prensadas, secadas y etiquetadas, fueron determinadas en el Herbario Nacional de Bolivia. Para cada parcela se obtuvo además una muestra compuesta de suelo superficial (0–15 cm) para buscar relaciones entre vegetación y suelos. Todas las muestras de suelos se analizaron a lo largo de unos seis meses, en el Departamento de Geología y Geoquímica de la Universidad Autónoma de Madrid (UAM), en colaboración con la Dra. Victoria Cala (Apéndice 3). Los datos florísticos obtenidos han sido empleados en todos los capítulos de esta tesis. Los datos edáficos han sido empleados en los capítulos 5 y 7.

Sin embargo, buena parte de las hipótesis que hemos manejado son aplicables no solo a bosque montano, sino también a otros bosques tropicales. Para lograr resultados del mayor alcance posible se han establecido diversas colaboraciones con los otros investigadores bolivianos y estadounidenses que han trabajado en la región de manera coordinada dentro del proyecto Madidi. Dichos investigadores han recopilado datos no solo de bosque montano sino también de bosques amazónicos y de bosques tropicales secos adyacentes. La incorporación de sus datos al presente trabajo ha sido posible gracias al uso de procedimientos estandarizados para el inventario florístico y los análisis de suelos, así como a la homogeneización taxonómica realizada.

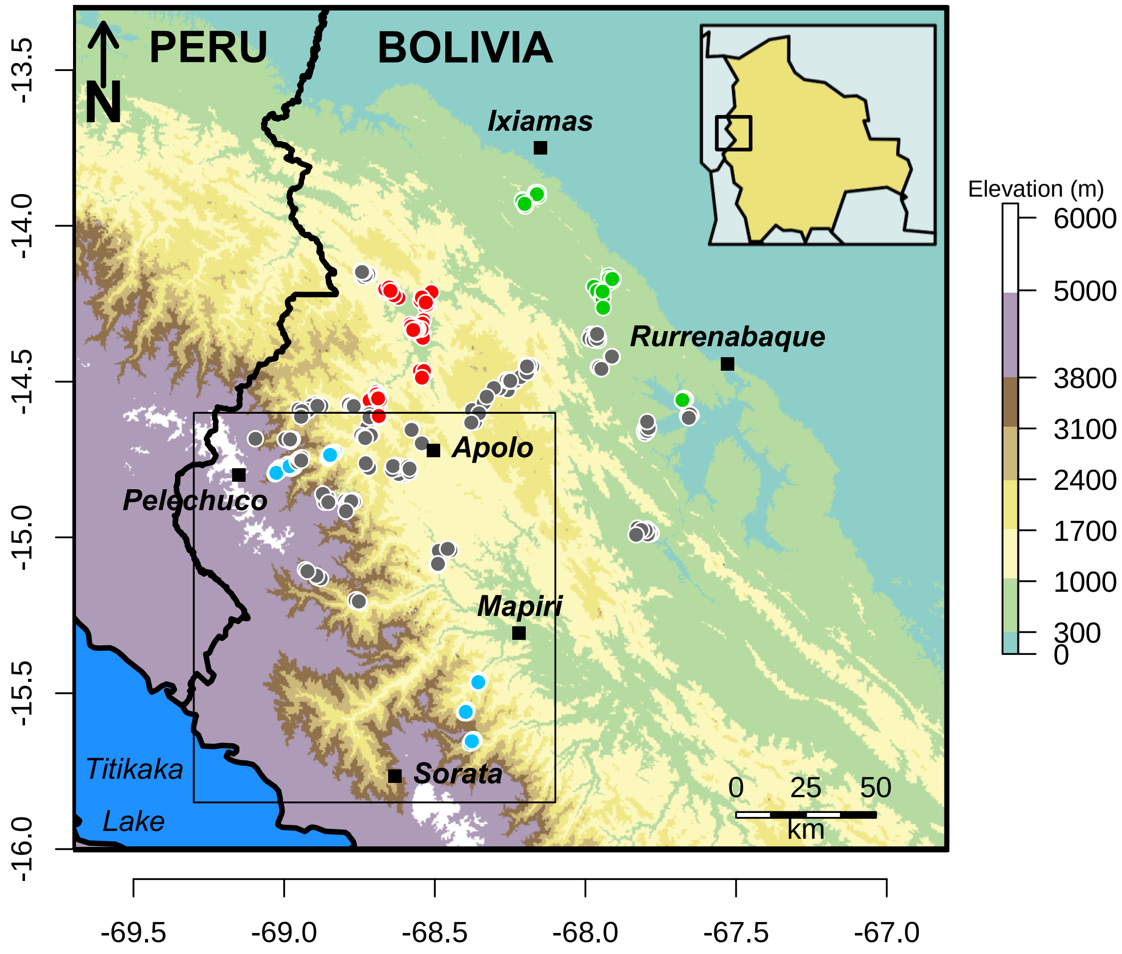

Figura 1.1. Localización de las 407 parcelas inventariadas en la región Madidi, en la transición entre los Andes y la Amazonía al noroeste de Bolivia. Los círculos azules corresponden a las 54 parcelas de bosque montano inventariadas por Gabriel Arellano (ver Fig. 1.2.). Los círculos verdes corresponden a las 44 parcelas de bosque amazónico inventariadas por Manuel J. Macía. Los círculos rojos corresponden a las parcelas de bosque seco inventariadas por el Proyecto Madidi. Los círculos grises corresponden a otras parcelas inventariadas por el Proyecto Madidi en bosque andinos y amazónicos a distintas altitudes. El recuadro indica la zona representada en la Fig. 1.2.

Figure 1.1. Location of the 407 inventoried plots in the Madidi region, in the transition between Andes and Amazonia in western Bolivia. Blue circles represent 54 plots of montane forest inventoried by Gabriel Arellano (see Fig. 1.2). Green circles represent 44 plots of Amazonian forest inventoried by Manuel J. Macía. Red circles represent dry forest plots inventoried by the Madidi Project. Grey circles represent wet forests plots inventoried by the Madidi Project at different elevations. The rectangle indicates the area represented in Fig. 1.2.

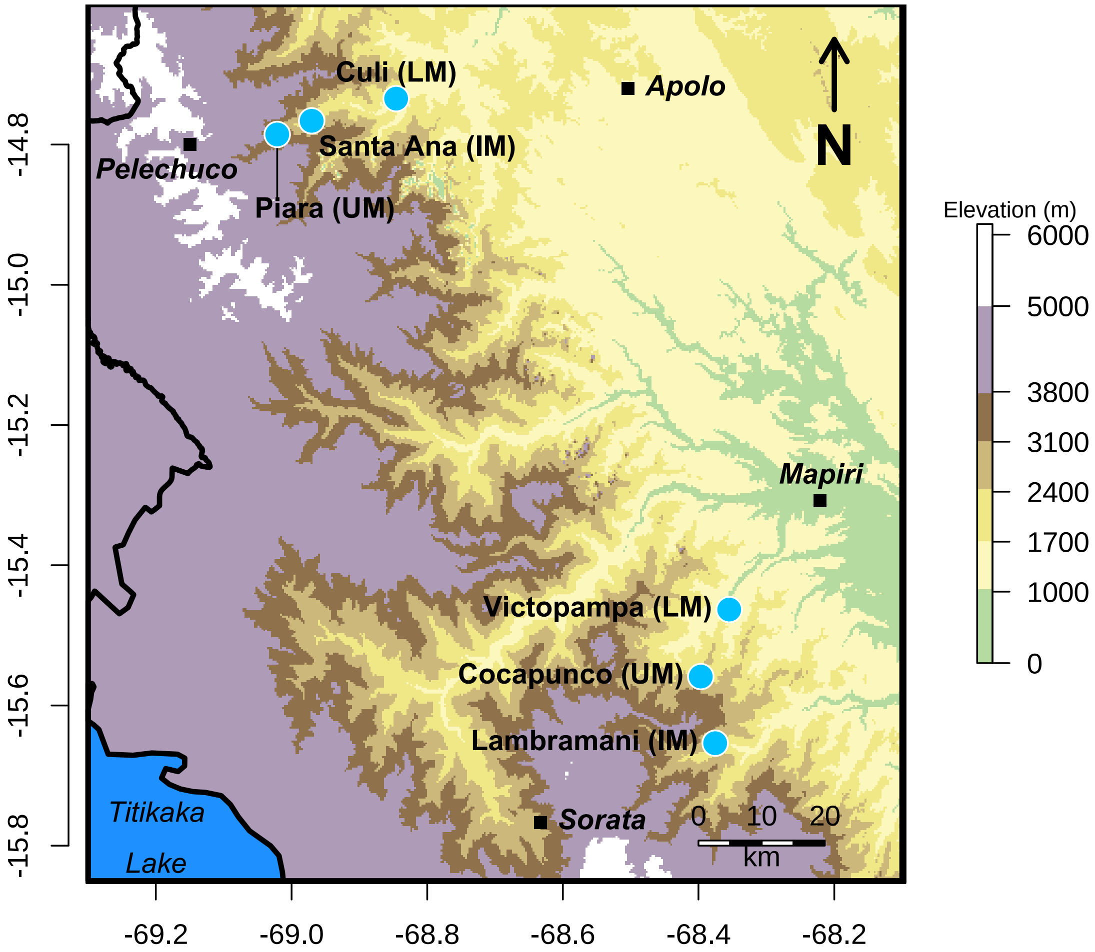

Figura 1.2. Localización de los seis sitios inventariados por Gabriel Arellano en las provincias de Franz-Tamayo y Larecaja. Cada sitio contiene nueve parcelas, y se disponen en tres diferentes altitudes: bosque montano bajo (LM, 1200–1500 m), bosque montano intermedio (IM, 2000–2300 m), y bosque montano alto (UM, 2800–3100 m).

Figure 1.2. Location of the six sites inventoried by Gabriel Arellano in the Franz-Tamayo and Larecaja Provinces. Each site contains nine plots, and are disposed at three different elevations: lower montane forest (LM, 1200–1500 m), intermediate montane forest (IM, 2000–2300 m), and upper montane forest (UM, 2800–3100 m).

En primer lugar, al conjunto de datos de bosque montano obtenidos durante mi trabajo de campo se añadió el conjunto de datos de bosque amazónico del Madidi obtenido por Manuel J. Macía, consistente en 44 parcelas de 0,1 ha. Todos los datos florísticos de estas 98 parcelas fueron empleados en los capítulos 4 a 7. Los datos edáficos de estos dos inventarios son totalmente comparables porque se analizaron siguiendo la misma metodología y en el mismo laboratorio de la UAM bajo la dirección de la Dra. Cala. Estos datos se emplearon para los capítulos 5 y 7. Las 54 + 44 parcelas suman >30.000 individuos, y >1500 especies.

En segundo lugar, para testar algunas hipótesis se decidió utilizar un gradiente altitudinal lo más amplio posible. Para ello, se añadieron las parcelas de 0,1 ha obtenidas por investigadores del Proyecto Madidi. Por tanto, a los datos de las 98 parcelas descritas anteriormente, se sumaron 309 parcelas para los capítulos 4 y 6 (datos florísticos), y 300 parcelas para el capítulo 7 (datos florísticos y edáficos). El set de datos completo, de unas 400 parcelas, suma >120.000 individuos y >2500 especies.

ESTRUCTURA Y OBJETIVOS DE LA TESIS

Esta tesis es un compendio de manuscritos, escritos a modo de artículos, de los que algunos están en revisión en revistas internacionales y otros permanecen únicamente como manuscritos, sin haberse enviado a ninguna revista. Debido a esta estructura, se encontrarán algunas reiteraciones en los capítulos, referente a la zona de estudio, los métodos y algunas de las hipótesis analizadas, que espero no sean excesivas.

CAPÍTULO 1: *Introducción general* a la memoria de tesis doctoral.

CAPÍTULO 2: *A standard protocol for woody plant inventories and soil characterization using 0.1-ha plots in tropical forests*. Se presenta una propuesta de protocolo con el método de inventario de campo desarrollado y los procedimientos para el análisis de las muestras de suelos. Este capítulo corresponde a un manuscrito que se re-enviará a *Biotropica* una vez que se hayan incorporado los comentarios de los revisores.

Los siguientes cuatro capítulos se pueden agrupar en un bloque que responde al objetivo general de conocer los patrones y mecanismos de dominancia de las plantas leñosas en los distintos tipos de bosque tropical (montano, amazónico y seco) y a diferentes escalas:

CAPÍTULO 3: *Local and regional dominance of woody plants along an elevational gradient in a tropical montane forest of northwestern Bolivia*. El objetivo específico de este capítulo ha sido documentar qué taxones dominan sobre otros a diferentes escalas en el bosque tropical montano de la región Madidi. Este capítulo corresponde a un artículo que actualmente se encuentra pendiente de la aceptación final en *Plant Ecology*, tras ser evaluado con revisiones menores.

CAPÍTULO 4: *Commonness patterns and the size of the species pool along a tropical elevational gradient: insights using a new quantitative tool*. El objetivo específico de este capítulo ha sido examinar la relación entre el número de especies, el número de especies dominantes y la intensidad de esa dominancia a diferentes escalas en los bosques montanos, secos, y amazónicos de la región Madidi. El capítulo corresponde a un artículo que está pendiente de la aceptación final en *Ecography*, tras ser evaluado con revisiones menores.

CAPÍTULO 5: *Niche breadth of oligarchic species in Amazonian and Andean rainforests*. El objetivo específico de este capítulo ha sido comprobar si existe alguna relación entre la amplitud de nicho y el grado de dominancia de las especies en los bosques montanos y amazónicos de la región Madidi. El capítulo corresponde a un manuscrito pendiente de enviar a *Journal of Biogeography*.

CAPÍTULO 6: *Potential determinants of rarity and commonness of woody plants in different types of tropical forests*. El objetivo específico de este capítulo ha sido comprobar si distintas características morfológicas de las especies (altura máxima, diámetro máximo, número de tallos y hábito) influyen en sus patrones de rareza y dominancia a distintas escalas en distintos tipos de bosque de la región Madidi. El capítulo corresponde a un manuscrito pendiente de enviar a *Ecology*.

Por otro lado, en el CAPÍTULO 7 titulado *Disentangling species turnover of woody plants in a tropical forest: from local to regional scales*, se ha abordado el objetivo de conocer los patrones y mecanismos generales que determinan el recambio de especies en bosques tropicales a diferentes escalas. En concreto se plantean dos objetivos específicos: (a) analizar el efecto relativo del espacio y el ambiente sobre el cambio de especies a distintas escalas en la región Madidi; y (b) estimar el efecto relativo del clima y el suelo sobre este recambio de especies a distintas escalas en la región Madidi. El capítulo corresponde a un manuscrito pendiente de enviar a *Global Ecology and Biogeography*.

Finalmente, en el CAPÍTULO 8 se incluyen unas consideraciones generales, con las principales conclusiones alcanzadas durante la investigación.

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CAPÍTULO 2

A standard protocol for woody plant inventories and soil characterization using 0.1-ha plots in tropical forests

Este capítulo se ha desarrollado en colaboración con V. Cala, A. F. Fuentes, L. Cayola, P. M. Jørgensen y M. J. Macía. Forma parte de un artículo pendiente de reenviarse a *Biotropica*, tras incorporar los comentarios sugeridos por los revisores.

ABSTRACT

Aim: To present a standard protocol for the ecofloristic assessment of tropical forests, including woody plant inventories and soil characterization.

Standard proposed: We present a two-level protocol to inventory woody plants using 0.1-ha plots. (1) The plot-level protocol offers specific recommendations on the size and shape of a plot, the taxa to include in the inventories, the minimum stem diameter cut-offs, the evaluation of multiple stems and height estimation. Additionally, we make a number of recommendations on soil sampling and analysis, a key issue requiring standardization in ecofloristic assessment research. (2) The site-level protocol specifies the procedures for establishing several plots within an area or habitat. It gives recommendations for the amount and placement of plots needed to obtain sufficient floristic data.

Conclusions: The use of both uniform woody plant inventories and laboratory soil analysis methods will facilitate data sharing and improve the understanding of large-scale biological patterns in tropical forests.

Keywords methods; floristic assessment; lianas; method standardization; plant biodiversity; tropical trees.

INTRODUCTION

The use of open data in ecology is a stimulating current trend involving great opportunities and challenges, including the standardization of methods and the development of robust metadata (Reichman et al. 2011). In the past few decades, the ecofloristic study of tropical forests has increasingly used standardized methods that allow the comparison of data among different research groups and investigated sites (Condit 1995, Condit et al. 2002, Malhi et al. 2002). Three types of quantitative samples are commonly used: (1) very large plots of 20–50 ha, primarily used by the Center for Tropical Forest Science (CTFS); (2) large plots (1 ha); and (3) small plots or transects (0.1 ha). The 20–50 ha plots are unusual not only because of their size but also because they include all woody plant stems whose diameter at breast height (dbh) is 1 cm or more (Table 2.1). The number of individuals included in such a plot may exceed 300,000 stems in the canopy and understory. The cost of establishing and continuously monitoring these plots is high. Plots of 1 ha usually have a dbh cut-off of 10 cm, *i.e.*, their focus is primarily on canopy trees, and the establishment and monitoring costs are moderate (Phillips et al. 2003a). Because the investment in time and money for large and very large plots is high to moderate, the spatial scale studied in these cases is often reduced to one or a few plots per site. Transects of 0.1 ha were first used by A. H. Gentry in the Neotropics during the 1980's, when he established a standard cut-off at 2.5 cm dbh, thereby including information on the canopy and understory plants (Gentry 1982, 1988). The objective of Gentry's transect method was to obtain alpha-diversity measures quickly, efficiently and inexpensively. Given the potentially high diversity that researchers often encounter in tropical forests, 0.1-ha transects may also be used for studies on a particular family or taxon (*e.g.,* Arecaceae, Melastomataceae, Pteridophyta).

Small 0.1-ha plots that also use a dbh cut-off of 2.5 cm represent an extension of Gentry's transects and are the focus of this protocol. Because these plots require less effort to install, it is possible to incorporate a larger amount of geographical and environmental variation than that obtained from larger plots (Table 2.1). In the case of 0.1-ha plots, more than 90 percent of the studies have been focused on ecofloristic assessments that consider most stems. In contrast, only approximately 50 percent of the studies of 1-ha plots, which consider only large trees, are focused on ecofloristic assessment (Phillips et al. 2003a).

Table 2.1. Summarized comparison of the four classical approaches to inventory woody plants in tropical forests.

Attributes	20−50-ha plots	1-ha plots	0.1-ha plots	0.1-ha transects
Size	500 × 500 m, 500 × 1000 m	100 × 100 m	20 × 50 m	2 × 500 m
Life forms	Woody plants with dbh ≥ 1 cm	Woody plants with dbh ≥ 10 cm (canopy trees and few lianas)	Woody plants with dbh ≥ 2.5 cm (canopy and understorey trees, and lianas)	Mostly understorey plants. Usually certain taxa only (*e.g.,* palms, ferns and fern allied, melastomes)
Field and monetary effort	Very high	High for the establishment and first inventory, intermediate for the next census	Low for the establishment, low or intermediate for the inventory (depending on habitats)	Low for the establishment, low or intermediate for the inventory (depending on taxa inventoried)
Efficiency	Very long-term	Permanent	Temporary	Temporary
Study forest dynamics	Suitable	Suitable	Unsuitable	Unsuitable
Internal floristic and edaphic heterogeneity	High	Intermediate	Low	High
Samples per site	One	One or few	Several	Several
Site species turnover	Within the sample	Within the sample and between samples (usually not studied)	Between samples	Within the sample and between samples
Proportion of site diversity inventoried	Intermediate	Low (but dependent of the number of replica)	High	High

The selection of the most appropriate sampling protocol will depend on the type of data needed to address the research questions. If the aim is to gather baseline data on the composition of local or regional diversity, smaller samples would be preferable because they require less effort and time. Moreover, the number of replicates can be increased to obtain more reliable results (Table 2.1). If identifications can be homogenized across a series of transects/plots, this approach is also highly effective for studying beta-diversity or species turnover rates along gradients (Phillips et al. 2003a, Macía et al. 2007, Guèze et al. 2013). Very large plots require months for installation and require continuous maintenance. The installation of large plots requires one to two weeks, whereas small plots require one to three days. The monetary costs in the three cases are proportional to the time invested.

The amount of information available about the characteristics of an established plot has varied substantially. These characteristics include the precise coordinates of the plot, compass directions, elevation and exposure. Too often, large-scale analyses of a multitude of plots are hampered by differences among plots in the information available and by the accuracy with which this information has been collected and preserved. Meta-analysis has, therefore, defaulted to the lowest common denominator to allow the inclusion of as many plots as possible. Specifically, few cases have been documented in which soil samples have been collected, although this information is essential to further understand key relationships between environmental conditions and forest vegetation (Table 2.2).

Moreover, the long-term value and the utility of any ecological data to be used in large-scale analysis depend on the availability of suitable and adequate metadata, *i.e.*, descriptive information describing the data content, context, quality, structure and accessibility (Fegraus et al. 2005).

The aim of this paper is to propose a standard protocol to be used in ecofloristic assessments of tropical forests for studies of both canopy and understory woody plants in 0.1-ha plots, including soil sampling. We believe that a standard protocol is needed to perform further comparisons at different geographical scales.

We propose a protocol at two spatial levels: (1) a plot-level protocol that sets the standards for the measurements and observations that should be taken in a homogeneous 0.1-ha plot and (2) a site-level protocol that proposes the sampling of the habitat heterogeneity of a given site by locating several plots in all recognized forest types.

Table 2.2. Bibliographical results found on relations between soil characteristics and floristic composition in tropical forests based on papers published during the last decade with at least two citations per year from a search in ISI Web of Knowledge. The scale is expressed in km of extent.

Reference	Forest type, country	Life form or group of plants	Scale	Relevant soil characteristics
Andersen et al. (2010)	Lower montane, Panama	Palms	13	N, cation availability, Al
Brearley et al. (2004)	Old secondary, Indonesia	Trees	<2	Soils only differ in Ca content
Costa et al. (2009)	Amazonian, Brazil	Palms	10	Clay content (canopy), clay and base contents (understorey)
Dezzeo et al. (2004)	Different vegation types in Gran Sabana, Venezuela	Vegetation types	<2	Soil irrelevant
Duque et al. (2002)	Amazonian, Colombia	Understorey and canopy trees	50	Texture, Ca, Mg, K, Na, P, C, N
Fine et al. (2005)	Amazonian, Ecuador and Peru	Burseraceae	1500	Soil type, color, texture, ammonium, nitrate and total N
Galindo-Jaimes et al. (2002)	*Pinus* dominated forests, Mexico	Trees	5	pH, P, organic matter, cation exchange capacity, N
Hemp (2005)	All types of forest from 800 to 3300 m at Mt. Kilimanjaro, Tanzania	All	50	Soil temperature, soil acidity
Homeier et al. (2010)	Montane, Ecuador	Trees	5	pH, total contents of Mg, K, Ca, N and P
Ibarra-Manriquez and Martinez-Ramos (2002)	Lowland and lower montane, Mexico	Lianas	10	Soil type, pH, P, N, drainage
Jones et al. (2008a)	Lowland, Costa Rica	Ferns	2.5	Soil type, Ca, Mg, pH, P, C, N

Table 2.2 (continued).

Reference	Forest type, country	Life form or group of plants	Scale	Relevant soil characteristics
Jones et al. (2008b)	Lowland, Costa Rica	Ferns	2.5	Ca, Mg, Al, K, pH, Mn, P, C
Laurance et al. (2006)	Amazonian, Brazil	Succesional trees	70	Soil irrelevant
Normand et al. (2006)	Terrace and floodplain, Peru	Palms	145	Soil irrelevant
Phillips et al. (2003b)	Amazonian, Peru	Trees	100	Ca, Mg, K, Na, Al, drainage
Potts et al. (2002)	Lowland, Borneo	Trees	500	Mg, K, Fe, Al
Poulsen et al. (2006)	Amazonian, Ecuador	Trees	0.1	Al, cation content (Ca), texture
Sarmiento et al. (2003)	Secondary paramo vegetation, Venezuela	All	50	pH, Ca, Mg, K
Sesnie et al. (2009)	Lowland and lower montane, Costa Rica	Trees and palms	80	Trees and palms: texture, C. Only palms: Ca, Mg, total acidity, pH, texture.
Thessler et al. (2005)	Amazonian, Ecuador	Ferns and melastomacs	30	Soil cation content
Toledo et al. (2011)	Lowland, Bolivia	Trees	1000	Soil fertility and soil texture
Tuomisto et al. (2002)	Amazonian, Ecuador	Ferns and melastomacs	25	Cation content
Tuomisto et al. (2003a)	Amazonian, Ecuador	Ferns and melastomacs	25	Satellite image bands (correlated with topography and soil fertility)
Tuomisto et al. (2003b)	Amazonian, Peru	Ferns and melastomacs	43	Exchangeable bases, texture
Tuomisto et al. (2003c)	*Terra firme*; Colombia, Ecuador and Peru	Ferns and melastomacs	1400	Cation content
Vormisto et al. (2004)	Amazonian, Ecuador and Peru	Palms	200	Cation content, texture
White and Hood (2004)	Dry forest, Mexico	Trees	200	Soil depth, % rock, pH, soil organic matter

PLOT-LEVEL PROTOCOL

The objective of a 0.1-ha plot is to study a forest that is relatively homogeneous in physiography and structure. For the study of old-growth forests, no plot should include large gaps or clear indications of any anthropogenic or natural disturbance. The variability within an area is studied through the establishment of different 0.1-ha plots that can represent several forest types or successional stages. In Amazonian forests, for example, each plot at a site could be established in *terra firme*, floodplain or swamp forest, but no plot should be located in the transition between two habitats.

We measure all woody plant stems rooting within the limits of the plot and with a dbh ≥ 2.5 cm, regardless of taxon or habit. These plant stems include trees, palms, tree ferns, lianas, woody hemiepiphytes and woody grasses. Certain hemiepiphytes (*e.g., Ficus*) have large woody aerial roots that function as stems and are indistinguishable from them. In such cases, we measure these structures as stems. Other woody structures, such as the large woody petioles of certain acaulescent palms, are easily recognizable and have a function that is clearly different. For this reason, they should not be inventoried. Herbaceous taxa are always excluded even if they reach a dbh ≥ 2.5 cm (*e.g.,* Zingiberaceae or hemiepiphytic Araceae).

In the following six subchapters, we present the standards to be used for the woody plant inventory: (1) plot shape and distance measurements, (2) plot description data, (3) measurements of dbh, (4) multiple stems, (5) stem height, (6) soil sampling and laboratory analysis and (7) plot metadata and data storage.

(1) Plot shape and distance measurements

The plot shape should be 50 × 20 m, avoiding other shapes or transect-like plots (*e.g.,* 10 × 100 m) to obtain maximum internal homogeneity. Only in exceptional situations, such as sampling on ridges, can the plot have this transect-like shape to fulfill the intra-plot homogeneity requirement. However, this decision may limit the opportunities for comparison with other plots. The plot will be divided into ten 10 × 10 m subplots to facilitate the inventory.

If a plot is established on a slope, the plot orientation (longest side) should follow the contour line as far as possible, and all distance measurements should be performed in the horizontal plane rather than following the slope of the terrain, following recommendations for large plots (Dallmeier 1992, Condit 1998). Deviations from this standard will under- or overestimate the area and, consequently, the number of individuals for the given 0.1-ha size, resulting in different measurements of alpha-diversity and forest composition. To minimize the effort and time required for plot measurement, especially in terrain with steep slopes, we suggest the use in the field of a table of corrected distances calculated from the following formula:

$$TD = HD\sqrt{1 + \left({}^{S_{per}}/_{100}\right)^2}$$

where TD is the distance along the terrain, HD the horizontal distance, and S_{per} the slope expressed in precentage.

For plots with a slope of less than 10 percent, the measuring tape can be held horizontally (a change of 2 m in height in a horizontal distance of 20 m). The error committed if the distances measured are not horizontal is <1 percent on a slope of 10 percent, 10 percent on a slope of 45 percent and >40 percent on a slope of 100 percent.

(2) Plot description data

This category of data includes general information on the plot that should always be recorded to allow future meta-analyses. These data should include the precise geographical coordinates, compass directions, elevation, exposure and the degree of the slope. It is advisable to record any other relevant qualitative information, such as topographic position (*e.g.,* ridge, valley, slope), forest type, habitat particularities, the presence of disturbance (quantified), or indications that allow the exact plot position to be located. Given that any meta-analysis is limited to the lowest common denominator, plot description data should be collected systematically and carefully for each plot.

(3) Measurements of dbh

All individuals rooting within the plot and with a dbh ≥ 2.5 cm should be measured at 130 cm from the rooting point (see Brokaw and Thompson [2000] for a review). Irregular trunks (*e.g.,* buttresses, swellings) are measured at a representative normal part of the trunk, usually above the "deformity" but as close as possible to 130 cm (Condit 1998, Phillips et al. 2002). Many exceptions are encountered in the field; see Condit (1998), Chapter 2.2 for an overview and solutions.

In the case of lianas, because a cut-off of 2.5 cm dbh does not provide a detailed assessment of diversity, those interested in making a detailed study of this life form should measure lianas with a dbh ≥ 1 cm at 130 cm from the rooting point (Gerwing et al. 2006, Schnitzer et al. 2008).

Hemiepiphytes are rare and scarce in most inventories. Given their odd structure, we suggest measuring the dbh at 130 cm from the rooting point without distinguishing roots and stems because this distinction is, most likely, impossible in the field. For these individuals, at least an estimate of the dbh at 130 cm from the point where a regular stem begins would also be advisable. Lianas and hemiepiphytes should be analyzed as different life forms. A specific protocol to sample hemiepiphytes is still needed.

(4) Multiple stems

Multiple stems of the same individual (rooting at the same point) should be considered as one individual, as ecofloristic assessment is based on individuals and not on stems. This distinction is a key issue in community assembly because different stems do not function biologically as different individuals in terms of many key ecological processes, such as niche partitioning and dispersal processes. Branches below 130 cm are considered multiple stems. Two stems connected underground must show a reasonably obvious connection to be inventoried as one individual. In the case of clonal species, two stems within 1 m of each other can be considered the same individual (Condit 1998), but different rules may be established in the field, depending on the biology of the species.

The inclusion of woody stems with dbh <2.5 cm in practice makes no substantial differences in terms of the basal area, although it may be of interest to some researchers because these smaller stems may provide a considerable amount of information for structural and community analysis. In any case, records should be kept of each stem separately. However, for further analyses where one dbh measure is necessary for a multistemmed individual, the final dbh can be calculated as follows (Macía 2008, 2011):

$$DBH = \sqrt{\sum dbh_i{}^2}$$

where DBH is the final dbh for the multiple stems of one individual, and dbh_i is the dbh of each measured stem, i, of one individual.

(5) Stem height

We propose to estimate the total height of each stem. If cost and time permit, an accurate measure of height can be obtained based on the protocols for the permanent plots inventoried by RAINFOR and CTFS (Chave et al. 2005). Height is rarely used in ecofloristic assessments, but it may be necessary to describe the forest structure, characterize species traits or estimate the aboveground biomass.

(6) Soil sampling and laboratory analysis

The wide array of possible soil sampling and laboratory analysis methods makes it virtually impossible to find two research groups using the same method. Therefore, it is difficult to establish generalizations across research sites about the relationship between soil variables and community composition (Sollins 1998), a key point in ecofloristic assessment and forest ecology (Phillips et al. 2003a, Chave 2008).

The superficial rooting zone holds the most relevant edaphic information. We therefore recommend sampling a superficial composite soil sample from a soil depth of 0−15 cm. In this upper layer, slightly decomposed organic material (*e.g.,* leaves, flowers, seeds) must not be sampled. The composite sample consists of a mixture of five subsamples collected in the center of five subplots arranged in a zig-zag pattern to obtain a full picture of the soil variability within the plot. These five points are located as far apart as possible and are, at the same time, well within the borders of the plot. The soil samples should be air-dried and protected from the rain and direct sunlight. After drying, they should be sifted through a 2-mm sieve.

We propose the following order of relevance for the analysis of different soil properties relative to floristic composition in forests. Our proposal is based on a review performed in the ISI Web of Knowledge for "soil" and "tropical forest" and "floristic composition" over the past decade. We found a total of 27 papers with at least two citations per year, representing more than 85 percent of the citations (Table 2.2). According to their results, the most influential soil properties are as follows: (1) base content (Ca, Mg, K, Na); (2) C and N; (3) pH; (4) texture; (5) P; (6) Al; and (7) micronutrients.

For determination of available Al and soil nutrients (*i.e.*, P, Ca, K, Mg, Na, Cu, Zn, Fe, Mn, Ni, Co) we recommend the use of the Mehlich-3 extraction method (Mehlich 1984) and ICP (inductively coupled plasma) spectrometry. The Mehlich-3 method is widely used for the extraction of plant-available nutrients and Al over a wide pH range (from acid to calcareous soils), and it is widely agreed that a trade-off exists in terms of laboratory time requirements, financial costs, effort and the extractability of critical elements such as P and Al (Mehlich 1984). ICP spectrometry is a normalized and rapid technique that is routinely used to measure nutrient concentrations and that allows the simultaneous measurement of multiple variables (Chave 2008).

For these reasons, we recommend the use of Mehlich-3 extraction and ICP spectrometry for the determination of available fractions of macronutrients (Ca, Mg, K and P), micronutrients (Cu, Zn, Fe, Mn and Na) and other elements, such as Al.

All data obtained from Mehlich-3 extractions refer to extractable nutrients that are presumably used by plants on a short-term basis. Total concentrations of nutrients in soils are considered of lower biological importance but could also represent an interesting topic to study because total concentrations may reflect the long-term availability of nutrients (Paoli et al. 2006). If information on total concentrations is needed, we suggest an ICP evaluation of extracts after *aqua regia* digestion, which releases the so-called biologically relevant fraction of elements (Ure 1995, Reeuwijk 2002).

The N in soil occurs in two principal forms: inorganic N (fixed ammonium, interchangeable ammonium, nitrate, nitrite and gases) and organic N. Inorganic N is commonly less than two percent of the total N in surface soils (Harmsen and Kolenbrander 1965) and may be difficult to study in a standardized way. Interchangeable ammonium and nitrate are particularly unstable in soils, and concentrations change in a few hours after sampling; several days of air-drying should stabilize and minimize their already-low concentrations (Turner and Romero 2009). The traditional and manual Kjeldahl method (Reeuwijk 2002) is the most frequently used method to measure the organic N content plus the inorganic ammonium content, a measurement that represents a pseudo-total N content. Furthermore, the alternative use of auto-analyzers allows the determination of the total amount of N and C through total combustion and the measurement of the resultant gases. In the case of N, these results are comparable to the results of the Kjeldahl method.

In the case of C, the traditional method to determine organic C content has been the simple and rapid Walkley and Black method (Walkley and Black 1974). However, this procedure results in the incomplete oxidation of the organic C and requires the application of a correction factor (usually 1.33) to adjust the recovery of organic C, thus representing a compromise approach (Reeuwijk 2002). Because the auto-analyzers also measure the inorganic C content, whereas the Walkley and Black method indirectly measures only the organic C content, the comparisons between the two methods are not straightforward. Moreover, in terms of ease of use, the amount of soil sample needed, data precision and direct comparability, the automated methods are preferred to the manual methods (Schumacher 2002). For these reasons, we recommend the use of an auto-analyzer to determine the total content of N and C.

Finally, we recommend that pH be measured in a 1:2.5 soil:water suspension (Reeuwijk 2002). To analyze soil texture, we recommend the hydrometer method following H_2O_2 oxidation of organic matter and dispersion with hexametaphosphate (Day 1965).

(7) Plot metadata and data storage

Metadata constitutes a technical description of the database fields and the measurement methods. It can take several forms, but it is often represented as a table that indicates the field name, how the observation or measurement was performed and the units in which the information is presented. It may also include references to more extensive descriptions, as in the case of soil analysis methods. We recommend that a basic document of this type be developed for any dataset or series of plots and that it be stored together with the data to maximize its value. Researchers may take advantage of well-developed tools, such as the Ecological Metadata Language, and other standards for metadata creation and storage (Fegraus et al. 2005).

Safeguarding the collected data and making them available for others is also a strong recommendation. Several existing networks are interested in incorporating quantitative inventories in general. Rainfor, Salvias, BIEN, and Tropicos® are examples of such networks. Depositing data in such networks does not necessarily mean that the data are immediately publicly available. However, it is clearly the desire of these networks that such data should eventually become available for large-scale meta-analysis.

SITE-LEVEL PROTOCOL

We define a site as a group of 0.1-ha plots covering the environmental heterogeneity of a small geographical region. It is necessary to obtain a clear idea of the environmental heterogeneity at a site to establish a plan for the placement of plots within the site.

Ideally, a site provides sufficient floristic information to reach approximate saturation on a species accumulation curve. In species-rich forests, it is well-known that new and uncommon species will be added with each new plot inventoried within a given site. In practice, therefore, a site will never reach an asymptote (Ugland et al. 2003, Chao et al. 2009, Gotelli and Colwell 2010). Nevertheless, all common species at the site should be recorded, and a tendency for the number of new species added with each new plot to be as small as possible should be distinct and obvious.

The first parameter to consider in the establishment of a site is the topography of the overall landscape. If a site is relatively flat (*e.g.,* Amazonian rain forests), we suggest that plots be established at a minimum distance of 500 m apart within a circular area of 40 km^2. In tropical rain forests, the floristic composition of a small area can be described by obtaining data from at least 2000 individuals (Condit et al. 1998). This value is normally exceeded in an inventory of 10 0.1-ha plots (Macía 2008). Five hundred meters is an arbitrary distance chosen to meet the assumption of floristic independence between plots (Duivenvoorden et al. 2005, Duque et al. 2005, Macía 2008).

If the landscape has significant topographic variation (*e.g.,* montane forests), we suggest establishing 10 0.1-ha plots within a maximum altitudinal range of 300 m and using a 300-m horizontal distance as the minimum inter-plot distance. The shape of the site will depend on the topography, which strongly influences the field design. The 300-m inter-plot distance is also arbitrary but is a minimum threshold based on the rapid shift in floristic composition, structure, and edaphic variables with increasing geographical distance in montane forests (Gentry 1995, Webster 1995).

The geographical delimitation of a site is a key point relative to the development of an efficient floristic assessment of the area of interest. The researcher needs to determine the adequate distance used to separate two or more sites as a function of the diversity of the ecoregion, changes in physiographic, edaphic or environmental conditions and, at the same time, as a function of the research objectives.

Our recommendation of ten 0.1-ha plots for species-rich tropical rainforest may be reduced if a reliable estimate of alpha-diversity and composition of a relative species-poor forest is the only goal of the study, as would be the case for montane or swamp forests. However, our recommendation is to follow the same protocol to further perform comparisons across different regions. Moreover, this protocol could be applied for the inventory of *any* forest, although species-rich tropical forests serve as a model involving the greatest possible complexity and field effort.

Acknowledgments

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CAPÍTULO 3

Local and regional dominance of woody plants along an elevational gradient in a tropical montane forest of northwestern Bolivia

Este capítulo se ha desarrollado en colaboración con Manuel J. Macía. Una versión del mismo ha sido aceptada para su publicación en *Plant Ecology*, una vez se hayan incorporado las revisiones menores sugeridas por el editor de la revista.

ABSTRACT

The aim of this study was to investigate the dominance patterns of woody plants in a tropical montane forest of northwestern Bolivia and to understand underlying processes at the local and regional scales. We inventoried three elevation ranges: lower (1200–1500 m), intermediate (2000–2300 m), and upper montane forests (2800–3100 m). At each elevation, we inventoried two sites that were ~100 km apart. Specifically, we asked the following questions: (1) Are dominant taxa distributed locally, or are they also dominant at larger scales? and (2) Is the local importance of shared taxa congruent among sites at the same elevation range? We inventoried 18,876 woody plant individuals with a diameter at breast height ≥2.5 cm belonging to 877 species, 286 genera, and 100 families in 54 0.1-ha plots. A strong floristic congruence was found at the family and genus levels within and across elevations, but not at the species level. However, the pattern of species dominance for the whole study regions was similar to that reported for similar scales in the Amazonia: 10–15% of species accounted for 50–75% of individuals, although dominant species were not oligarchic across the whole elevational gradient due to the high environmental heterogeneity. Dominant taxa were shared to a larger degree between sites at the same elevational range than non-dominant taxa, indicating that oligarchy does not mean uniformity. Finally, the shared taxa exhibited similar importance between sites at the lower elevation range but dissimilar importance at the higher elevation range, reflecting an increase in the relative importance of local processes *vs.* regional processes with increasing elevation.

Keywords: altitudinal zonation, dispersal limitation, environmental filtering, oligarchy hypothesis, species turnover, tropical Andes.

INTRODUCTION

The knowledge of dominant taxa is essential to the understanding of any ecosystem because they account for the majority of individuals, biomass and energy flows (Vázquez and Gaston 2004, Gaston 2010). If dominant species are affected by human or natural disturbances, such as overexploitation or climatic changes, pronounced cascades of reductions and losses of other species could result because dominant species shape their environments and are involved in large numbers of biotic interactions (Gaston 2010). Tropical montane forests suffer some of the highest rates of habitat conversion of any tropical ecosystem and extreme fragility with regard to climate change (Doumenge et al. 1995, Pounds et al. 1999, Foster 2001, Laurance et al. 2011, Larsen et al. 2012). Unfortunately, the challenging terrain of this ecosystem and limited accessibility, resources and manpower have long hampered the study of its flora. To date, the understanding and conservation of this fragile ecosystem have relied on a few (quantitative) floristic inventories to shed light on ecological and biogeographical processes, including those of species dominance (*e.g.,* La Torre-Cuadros et al. 2007, Bruijnzeel et al. 2010, Jones et al. 2011, Martin et al. 2011).

Most tropical forest inventories have indicated that the floristic composition of a given locality tends to be a combination of a limited set of dominant species together with a large number of rare species (Hubbell and Foster 1986, Gaston 2012). Beyond the local scale, it has also been widely reported that the same set of locally dominant species tends to prevail over large areas, conforming to what has been called an "oligarchic pattern" (Pitman et al. 2001, 2013; Macía and Svenning 2005). The oligarchy hypothesis originally proposed that such a pattern applies for Amazonian *terra firme* forests, but many recent works have found the same pattern in other tropical forests at the regional scale (Bridgewater et al. 2004, Eilu et al. 2004, Paoli et al. 2006, Norden et al. 2009, Williams et al. 2010, Keppel et al. 2011, Jabot and Chave 2011). However, whether this hypothesis applies to tropical Andean forests at different scales remains poorly studied.

The goal of this study was to investigate the dominance patterns of woody plants in tropical montane forests of northwestern Bolivia and to understand which processes (local, occurring at extents <5 km, or regional, occurring at extents ~100 km) influences the observed patterns the most. We focused on three elevational ranges; at each elevation, we inventoried two sites approximately 100 km apart, to answer the following four research questions:

(1) Which are the dominant families, genera, and species in lower, intermediate and upper montane forests?

(2) Is the dominance of a taxon limited to the local scale (*i.e.*, to one site), or are such groups also dominant at larger scales (*i.e.*, at the two sites of the same elevation ~100 km apart) or in different habitats (*i.e.*, across different elevations)? The oligarchy hypothesis predicts that oligarchies are weak or may even be undetectable when the environmental heterogeneity in a given forest is too high (Pitman et al. 2013). Because montane forests are characterized by strong elevational gradients and rapid shifts in edaphic and micro-environmental variables at any elevation (Gentry 1995, Vitousek 1998, Gerold 2008), we would expect weak oligarchies at the regional scale and within the whole elevational gradient under study.

(3) Is the overlap of dominant taxa among sites similar to the overlap of non-dominant taxa? Oligarchic taxa tend to homogenize the floristic composition within the same habitat where conditions are relatively homogeneous, but at the regional scale, the plant community often exhibits high species turnover (Pitman et al. 1999, 2001; Macía and Svenning 2005; Macía 2011). If locally dominant taxa are both important at the regional scale and compatible with high floristic heterogeneity, we would expect greater overlap for dominant taxa than for non-dominant taxa.

(4) Is the local importance of shared taxa congruent among sites at the same elevation? Two alternative predictions arise from this question: (A) If local environmental conditions determine the local importance of taxa, a taxon will have the same importance across the landscape as long as the conditions are the same. Therefore, we would expect that taxa have the same importance in different sites at the same elevation. (B) If high landscape connectivity at the regional scale homogenizes the local abundances of taxa between different sites regardless of specific local conditions, we would expect similar taxon importance across different sites at lower elevations, but dissimilar importance across sites at higher elevations because of the lower landscape connectivity at such elevations (Wiens 2004, Kozak and Wiens 2006, Graham and Fine 2008).

METHODS

Sampling design and study area

Fieldwork was conducted in three elevational bands of northwestern montane forest in Bolivia (see Fig. 1.2). The bands had elevation ranges of 300 m and were separated by 500 m of elevation, as follows: lower montane forest at 1200–1500 m (LMF), intermediate montane forest at 2000–2300 m (IMF) and upper montane forest at 2800–3100 m (UMF). At each band we inventoried two sites; one was in Franz-Tamayo Province within the limits of Madidi National Park, and the other was ~100 km away in Larecaja Province, close to the Pilón-Lajas Biosphere Reserve. At LMF we conducted inventories in the sites of Culi (Franz-Tamayo Province) and Victopampa (Larecaja Province); at IMF we conducted inventories in the sites of Santa Ana (Franz-Tamayo Province) and Lambramani (Larecaja Province); and in UMF we conducted inventories in the sites of Piara (Franz-Tamayo Province) and Cocapunco (Larecaja Province). At each of the sites, we established nine 0.1-ha (20 × 50 m) plots with a minimum inter-plot distance of 250 m, for a total of 54 plots.

All studied sites were only accessible by foot and were from one to four days away from the nearest village. The vegetation at all sites was old-growth mature tropical rainforest with sporadic disturbances due to landslides, but there were no recent signs of human perturbation. Plots were installed to inventory internally homogeneous forests, but maximizing the within-site environmental variation. We avoided secondary forests, characterized by a high abundance of *Cecropia* trees, small bambusoids or vines and/or a lack of large trees. All plots had >2000 mm annual mean precipitation and a 2- to 3-month dry period (Ribera 1992, Navarro et al. 2004). The annual mean temperatures varied from 22 °C at the lowest elevation to 10 °C at the highest elevation. At all elevations, soils were acidic (pH < 5) and rich in organic matter in the top layer.

Data collection

All woody plant individuals rooted within the plot with at least one stem of diameter at breast height (dbh, measured at 130 cm from the ground) equal to or greater than 2.5 cm were measured. Multiple stems of the same individual were measured down to 1 cm dbh to more accurately measure the basal area of shrubs, a common life-form in montane forests. All individuals were identified or assigned to a morphospecies, all of which were collected at least once in a site. The full set of vouchers was deposited at LPB and a nearly complete set at MO (acronyms according to Thiers 2012). Less than 5% of individuals were excluded from the analysis because they were sterile specimens that could not be assigned to reliable morphospecies names. All data are available for query in the TROPICOS database (www.tropicos.org/PlotSearch.aspx?projectid=20).

Data analysis

We measured taxa dominance at site level. To do so, we calculated the Importance Value Index (IVI) at the species and genus levels (Curtis and McIntosh 1951) and the Family Importance Value Index (FIVI) (Mori et al. 1983). The sum of total IVI or FIVI values for species, genera and families is 300 at each site. We ranked the species, genera, and families in decreasing order of importance at each site based on the importance value index (IVI or FIVI). We defined "important taxa" as those whose values summed to 150 of the total of 300 for the IVI or FIVI. In this way, the number of important taxa decreases with decreasing diversity but remains at a constant proportion of importance at each site. Therefore, this category is directly comparable between sites with different floristic compositions, diversity and dominance patterns. Finally, to compare our inventories with earlier studies, we calculated the percentage of individuals represented by the top 10% and 15% of species.

For each pair of sites at the same elevation, we tested whether the important taxa were less than, more than, or equally floristically similar to the rest of the community. To do so, we compared all possible pairs of plots at different sites of the same elevation ($9 \times 9 = 81$ pairs of plots per elevational range). We did not compare plots within a site because the oligarchy hypothesis is intended to apply at larger scales. For each pair of plots, we calculated the proportion of shared important taxa between the two plots with the Jaccard similarity index (J_I). The same was repeated for the remaining taxa, obtaining the proportion of shared non-important taxa ($J_{\text{no-I}}$) for each pair of plots. Finally, for each elevational range and taxonomic level, we compared J_{I} and $J_{\text{no-I}}$ by performing Wilcoxon signed rank tests.

To analyze regional-scale congruence in the importance of shared taxa in the community, we conducted Pearson correlations between the importance of shared taxa at one site and their importance at another site at the same elevation. Importance values were log-transformed prior to the analysis to make the analysis more robust against the extreme importance of some taxa at some sites.

The significance level for all the analysis was established at 0.05. All calculations and analyses were performed with R (R Development Core Team and R Core Team 2012).

RESULTS

Floristic composition

We found a total of 877 species, 286 genera, and 100 families in the inventory of 18,876 individuals. At each site, 4–8 families were important (Table 3.1). Overall, Melastomataceae was the most important family among sites and across elevations, being the only family that was important at all sites. Sites at LMF shared as important families Euphorbiaceae, Lauraceae, Melastomataceae, Moraceae, and Rubiaceae. The same families, with the exception of Moraceae, were shared as important between the sites at IMF. At UMF, the important shared families were Clusiaceae, Cunoniaceae, and Melastomataceae. The abovementioned seven families (7% of the total number of identified families) accounted for 35% of species and 50% of individuals.

Table 3.1 Comparison of the important (bold) families of six study sites at three different elevations, as inventoried in 54 0.1-ha plots of tropical montane forest in the Franz-Tamayo and Larecaja Provinces, northwestern Bolivia. Families are ranked by mean FIVI. Cu.: Culi; Vi.: Victopampa; Sa.: Santa Ana; La.: Lambramani; Pi.: Piara; Co.:Cocapunco.

Family (number of species)	1200−1500 m		2000−2300 m		2800−3100 m		Mean FIVI
	Cu.	Vi.	Sa.	La.	Pi.	Co.	
Melastomataceae (94)	**37.25**	**22.78**	**24.66**	**37.64**	**22.87**	**33.39**	29.77
Rubiaceae (71)	**31.92**	**35.71**	**42.75**	**24.93**	8.00	5.09	24.73
Lauraceae (74)	**34.22**	**24.50**	**21.69**	**31.30**	8.01	12.06	21.96
Clusiaceae (17)	5.30	6.05	**24.82**	11.37	**17.92**	**44.17**	18.27
Cunoniaceae (18)	-	0.36	0.92	4.53	**27.74**	**62.14**	15.95
Chloranthaceae (6)	2.48	2.27	**22.52**	7.67	**31.20**	4.81	11.83
Asteraceae (50)	2.39	2.90	10.96	11.28	**34.08**	4.12	10.96
Moraceae (23)	**25.68**	**19.38**	7.60	10.08	1.74	-	10.75
Euphorbiaceae (13)	**12.67**	**10.72**	**17.27**	**11.89**	8.50	-	10.18
Cyatheaceae (13)	4.46	4.12	3.51	**36.71**	0.86	8.74	9.73
Primulaceae (12)	5.86	3.57	8.82	7.00	11.13	**16.56**	8.82
Ericaceae (16)	1.54	0.84	5.56	0.97	**20.52**	8.27	6.28
Myrtaceae (37)	8.19	**11.58**	5.99	5.57	3.30	-	5.77
Fabaceae (33)	8.66	**20.21**	1.29	0.82	1.83	-	5.47
Phyllanthaceae (8)	6.34	**11.25**	4.83	6.61	-	-	4.84
Meliaceae (9)	1.38	3.78	0.67	**18.58**	1.34	-	4.29
Monimiaceae (3)	**9.69**	0.97	2.27	2.35	-	-	2.55

At the generic level, floristic differences were more pronounced between sites and across elevations. *Miconia* was the only genus that was important at all elevations (Table 3.2). *Alchornea*, *Hieronyma*, *Ocotea,* and *Piper* were important at LMF and IMF, whereas *Clusia*, *Hedyosmum,* and *Clethra* were important at IMF and UMF. These eight genera (2.8% of the total) accounted for 18% of the species and 34% of the individuals. Another 38 genera were important in only one of the studied elevation ranges.

Table 3.2 Comparison of genera that were important (bold) in at least two of the six study sites at three different elevations, as inventoried in 54 0.1-ha plots of tropical montane forest in the Franz-Tamayo and Larecaja Provinces, northwestern Bolivia. Genera are ranked by mean IVI. Cu.: Culi; Vi.: Victopampa; Sa.: Santa Ana; La.: Lambramani; Pi.: Piara; Co.:Cocapunco.

Genus (number of species)	1200−1500 m		2000−2300 m		2800−3100 m		Mean IVI
	Cu.	Vi.	Sa.	La.	Pi.	Co.	
Clusia (11)	1.82	0.55	**25.64**	**10.72**	**20.21**	**47.33**	17.71
Miconia (70)	**22.32**	**11.19**	**17.91**	**18.81**	9.94	**25.87**	17.67
Weinmannia (18)	-	0.23	0.68	4.46	**27.67**	**55.59**	14.77
Hedyosmum (6)	3.12	3.16	**23.35**	**9.03**	**31.84**	5.16	12.61
Psychotria (17)	3.68	3.49	**35.30**	**6.62**	7.68	4.88	10.27
Ocotea (32)	**12.91**	**7.35**	**10.48**	**17.03**	2.73	5.31	9.30
Myrsine (7)	3.61	1.66	8.37	6.02	**12.63**	**16.81**	8.18
Clethra (9)	0.23	0.20	**14.82**	2.27	**13.70**	**14.33**	7.59
Alchornea (5)	**5.16**	3.13	**16.14**	**10.63**	9.00	-	7.34
Piper (21)	**7.63**	**8.71**	4.08	**9.01**	3.44	-	5.48
Hieronyma (5)	**6.02**	**8.30**	6.72	**7.10**	-	-	4.69
Tapirira (1)	**6.10**	**11.56**	-	-	-	-	2.94
Perebea (2)	**8.24**	**8.65**	-	-	-	-	2.82
Guatteria (5)	**6.21**	**6.51**	0.42	2.11	-	-	2.54
Pseudolmedia (3)	**7.05**	**5.49**	-	0.86	0.47	-	2.31
Inga (17)	**4.62**	**6.96**	0.83	1.22	-	-	2.27
Pourouma (5)	**7.22**	**6.25**	-	-	-	-	2.25
Schizocalyx (1)	**7.40**	**5.73**	-	-	-	-	2.19
Aparisthmium (1)	**5.81**	**7.04**	-	-	-	-	2.14
Protium (2)	**7.85**	**3.97**	-	-	-	-	1.97
Virola (6)	**4.34**	**5.38**	-	-	-	-	1.62

At the species level, we found a low overlap of important species between sites and across elevations. *Alchornea glandulosa* Poepp. was important at all LMF and IMF sites, and *Myrsine coriacea* (Sw.) R. Br. ex Roem. & Schult. was important at all IMF and UMF sites. Five other species (*Hedyosmum racemosum* (Ruiz & Pav.) G. Don, *Dendropanax* sp. nov. = G. Arellano 1271, *Topobea multiflora* (D. Don) Triana, *Piper* *bolivianum* C. DC. and *Hieronyma* vel sp. nov. = G. Arellano 658) were important at 2–3 sites at LMF and IMF. The species *Hedyosmum angustifolium* (Ruiz & Pav.) Solms was important at the IMF and UMF sites in Franz-Tamayo Province. These eight species (0.9% of the total) comprised 7.7% of the individuals. The remaining important species (104; 11.9% of the total) were restricted to one elevational range and accounted for 55.5% of all individuals. Overall, the 10% of species with the highest abundances accounted for 64% of all individuals, and the top 15% most abundant species accounted for 74% of all individuals.

Overlap of important taxa vs. *non-important taxa*

When pairs of plots at different sites within the same elevational range were compared, we found that the overlap between important taxa was greater than the overlap for non-important taxa (Fig. 3.1). In all cases, the results were highly statistically significant ($P < 0.001$).

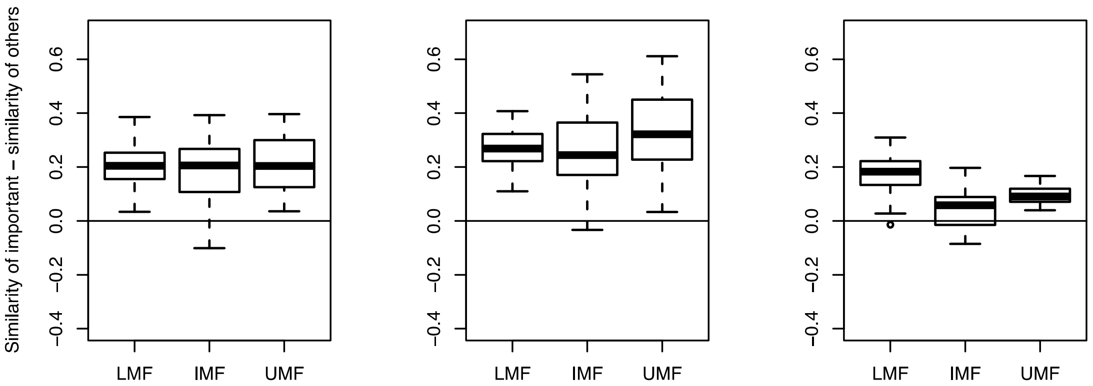

Figure 3.1. Differences between the overlap of important taxa and the overlap of non-important taxa, calculated between pairs of plots of different sites within the same elevation range in 54 0.1-ha plots of tropical montane forests in northwestern Bolivia: lower montane forest (LMF, 1200–1500 m); intermediate montane forest (IMF, 2000–2300 m); and upper montane forest (UMF, 2800–3100 m). The horizontal line at y = 0.

Correlations for the importance of taxa between sites

The correlation between the importance of shared taxa at one site and their importance at another site at the same elevation indicated that the strength of the correlation diminished at higher elevations and at lower taxonomic levels (Fig. 3.2). The correlation was positive and statistically significant in most cases, with the exception of genera and species between the two sites at UMF.

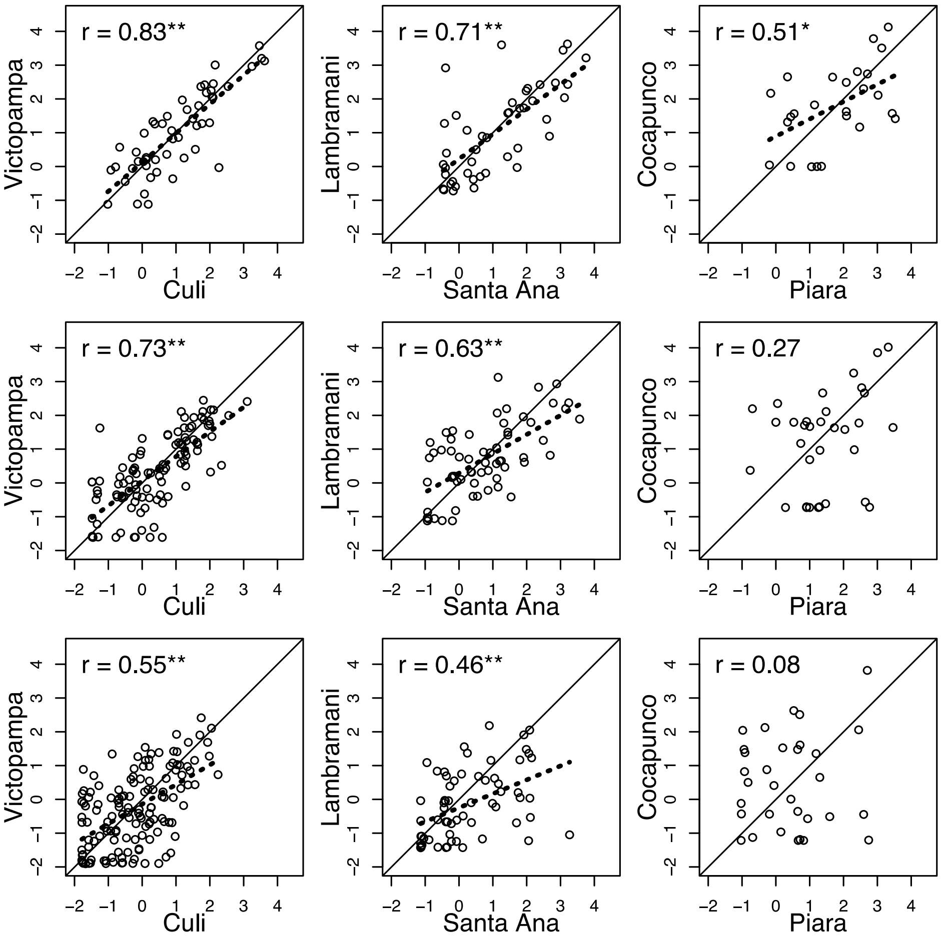

Figure 3.2. Results of Pearson correlations between the importance of taxa at one site and at another site at the same elevation, for three elevational ranges characterized by 54 0.1-ha plots of tropical montane forest in northwestern Bolivia: lower montane forest (LMF, 1200–1500 m); intermediate montane forest (IMF, 2000–2300 m); and upper montane forest (UMF, 2800–3100 m). Axes represent IVI or FIVI indexes on a logarithmic scale. The solid line (diagonal) represents the hypothesis that the importances of taxa are identical at the two sites, and the dashed line represents the observed relationship between importances at the two sites. Statistical significance: ** $P < 0.001$; * $P < 0.01$.

DISCUSSION

Floristic patterns

We found a strong floristic congruence between sites and across elevations at the family and genus levels. The paradigmatic dominant montane families in the Andes (Melastomataceae, Rubiaceae, and Lauraceae) previously reported to be among the most important taxa (*e.g.,* Gentry 1995, Fuentes 2005, La Torre-Cuadros et al. 2007, Macía and Fuertes 2008) were strongly represented in our study region. As expected, below 1500 m, we found a floristic composition with a high importance of Amazonian-originated taxa whose importance tends to diminish at intermediate elevations, such as Moraceae and a significant set of genera that are shared as important by the two sites at LMF but are important nowhere else (*e.g., Guatteria*, *Inga*, *Pourouma*, *Pseudolmedia*). This elevational filter of Amazonian-originated taxa continues above 2500 m, where only the most widespread Amazonian-originated families, such as Melastomataceae or Rubiaceae, co-occur with distinctive Andean taxa such as *Clusia*, *Weinmannia* or *Hedyosmum* (Beck et al. 1993, Gentry 1995, Webster 1995). This pattern is again in accordance with previous floristic studies in the Andes (Araujo-Murakami et al. 2005a, b, Fuentes 2005, Silman et al. 2005, La Torre-Cuadros et al. 2007, Feeley et al. 2011), whose results also indicate that the importance of a given family in Andean forests is due generally to one or a few genera, especially above 2000 m, where Melastomataceae owes its importance to *Miconia*, Rubiaceae to *Psychotria*, Lauraceae to *Ocotea*, Clusiaceae to *Clusia* and Cunoniaceae to *Weinmannia*,.

We found relatively few species that were important at more than one site, especially at the IMF and UMF sites, together with a very large pool of site-restricted species. Additionally, some of the most important species are endemic to Bolivia (*P. bolivianum*) or to the Madidi region (*Dendropanax* sp. nov. and *Hieronyma* vel sp. nov.). As tropical montane forests are full of uniqueness, we could not find strong floristic similarities at the species level to other floristic inventories in the Andes (*e.g.,* Smith and Killeen 1995, La Torre-Cuadros et al. 2007, Macía and Fuertes 2008, Ledo et al. 2012) or even to other inventories in the Madidi area (Araujo-Murakami et al. 2005c, Bascopé and Jørgensen 2005, Cabrera-Condarco 2005, Loza et al. 2010). Such high species heterogeneity is a common characteristic of many organisms in the Andes and is assumed to be a result of the relatively recent diversification during the Andean uplift caused by strong population isolation (Fjeldsa and Lovett 1997, Jetz et al. 2004, Parra-Olea et al. 2012). Unfortunately, this heterogeneity prevents understanding the main floristic patterns of the area using data at species-level, and therefore, the utilization of higher-taxon surrogates has been demonstrated to be a more useful tool, as previously indicated for Andean forests (Kessler and Bach 1999, La Torre-Cuadros et al. 2007).

Dominance across elevations

Sixty-four and 74% of the individuals belong to the most abundant 10 and 15% of the species, values almost equal to the numbers reported for oligarchic species in the lowlands of northwestern Amazonia. For example, in Yasuní, 48–63% of individuals belong to 10–11% of the recorded species (Macía 2011, Pitman et al. 2013); in Manu, 73% of the individuals belong to 15% of the species (Pitman et al. 2013); and in the Madidi lowlands, 62% of individuals belong to 11% of the species (Macía 2008). Thus, the overall pattern in montane forests appears to be similar to that of lowland forests.

However, if we look more carefully at the top 10–15% most abundant species, they cannot be qualified as 'true' oligarchic species because they are not clearly distributed among different habitats (in our case: elevations) (Ruokolainen and Vormisto 2000, Pitman et al. 2001, Bridgewater et al. 2004, Macía and Svenning 2005, Paoli et al. 2006). For instance, only *M. coriacea*, *A. glandulosa*, and six other species (<1% of all species) exhibit importance in two adjacent elevational ranges (500 m apart, with a maximum range of 1100 m), and these species only account for ~8% of all individuals. Moreover, most individuals belong to important species that are restricted to a single elevational range, and no species qualifies as oligarchic along the whole elevational gradient. This finding confirms the prediction that large-scale oligarchy is limited within very heterogeneous conditions (Tuomisto et al. 2003a, b; Vormisto et al. 2004; Macía and Svenning 2005; Réjou-Méchain et al. 2008; Toledo et al. 2011, 2012), although the data are compatible with the existence of strong oligarchies at smaller scales (Guevara Andino 2006; Honorio Coronado et al. 2009; Toledo et al. 2011, 2012).

Dominance within elevational ranges

The greater overlap of important taxa between different sites within the same elevation range compared with non-important taxa indicates that oligarchy does not lead to uniformity and that the dominant taxa at each site are not a random subset of the local pool of taxa, as predicted (Pitman et al. 2001, 2013). This also applies to the non-important taxa in the community: the local importance of any taxon at a given site is not random, as shown by the generally positive correlation between the importance of a given taxon at one site and its importance at the other sites in the same elevation range. However, the overlap of important species diminishes with elevation, becoming very weak or absent in the UMF. Although the UMF sites are only ~100 km apart and are environmentally and floristically alike, there is no clear relationship between the local importance of shared species, whereas such a relationship does exist in lowland species at greater scales (see Fig. 3 in Pitman et al. (2001) involving a 1400 km extent and Fig. 3 in Macía and Svenning (2005) involving a 1900 km extent). This is congruent with the prediction based on the decrease in landscape connectivity at higher elevations (Hubbell 2001, Chave 2008). Therefore, we find support for long distance dispersal as a major driver of dominance patterns that is at least as important as local environmental determinism in shaping the patterns of importance of taxa at regional scales (Ruokolainen and Vormisto 2000; Kristiansen et al. 2009, 2011).

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CAPÍTULO 4

Commonness patterns and the size of the species pool along a tropical elevational gradient: insights using a new quantitative tool

Este capítulo se ha desarrollado en colaboración con L. Cayola, I. Loza, V. Torrez y M. J. Macía. Una versión del mismo ha sido aceptada para su publicación en *Ecography*, una vez se hayan incorporado las revisiones menores sugeridas por el editor de la revista.

ABSTRACT

The goal of this study was a quantitative assessment of two-dimensional commonness in the lowland, dry, and montane tropical forests of the Madidi region (Bolivia). This region spans a large elevational and environmental gradient, with great diversity differences among sites. We aimed to explain commonness patterns at different scales based on elevation and differences in the size of the species pool and developed a measure of ecological commonness based on the *h* index of academic productivity and a criterion to separate common from uncommon species. With this approach, we calculated the 1) mean commonness of all species of the community; 2) proportion of common species of the community; and 3) mean commonness of the common species. The results showed that the commonness patterns in the Madidi region are strongly linked to the size of the species pool, independently of the environmental heterogeneity involved and the type of forest and spatial scale considered. Although these factors do not affect the general quality of the community, they do influence differences in commonness among species. Overall, we identified strong support for the oligarchy hypothesis, regardless of the strength of the pattern, and conclude that a quantitative approach to commonness could lead to great insights into community structure.

Keywords: *h* index, liana, oligarchy, Rabinowitz’s classification, rarity, relative abundance, spatial ecology, species dominance, tropical forests, woody plants

INTRODUCTION

Variations in species commonness and in the number of species across regions are central subjects of community ecology. Although the term "commonness" has different uses, here it refers only to a two-dimensional property of species that combines both local abundance and spatial distribution (Davidar et al. 2008, Kristiansen et al. 2009, Pitman et al. 2013); *i.e.*, common species are those with high local abundance *and* broad spatial distribution, and uncommon species are those with low local abundance *or* narrow spatial distribution (see Fig. 4.1). Within this context, little is known about commonness patterns in tropical forests and the causes for the observed differences between regions or along environmental gradients (Pitman et al. 2001, 2013, Vormisto et al. 2004, Macía and Svenning 2005).

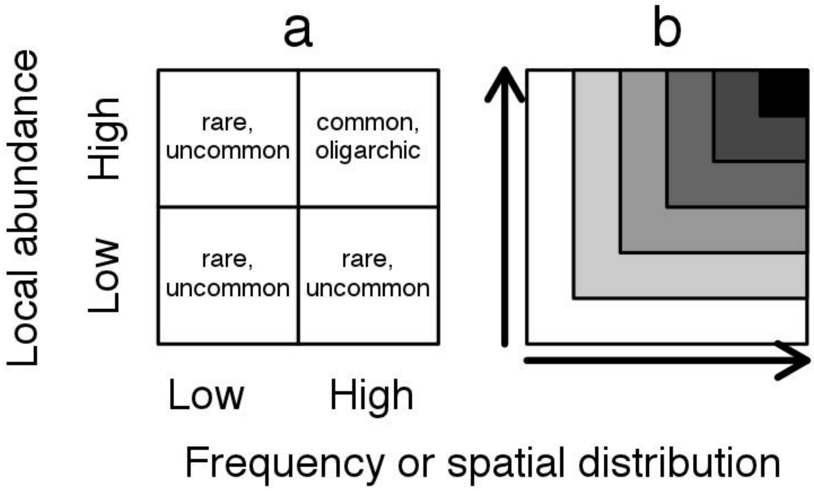

Figure 4.1. Categorical and quantitative approaches to two-dimensional commonness: (a) classification of species according to their local abundances and frequencies (Rabinowitz 1981, Rabinowitz et al. 1986, Pitman et al. 1999); and (b) quantitative approach to the same concept of commonness (present study); darker greys indicate greater commonness. Two-dimensional commonness differs from uni-dimensional commonness in combining simultaneously two criteria: common species are those that combine high local abundances with high frequency. Therefore, from this point of view, frequent but locally scarce species are not considered common, neither locally abundant but infrequent species.

Knowledge about common species is central to the understanding of ecosystems. Although common species are only a limited subset of the community, they account for the majority of individuals, biomass, and energy flows (Vázquez and Gaston 2004, Gaston 2010). Moreover, common species determine the spatial patterns of species distribution and biodiversity gradients even above that expected for their abundance (Lennon et al. 2003, Vázquez and Gaston 2004, Sizling et al. 2009, Pérez-Quesada and Brazeiro 2013). The two-dimensional approach to commonness is of great practical importance because it could shed light on the mapping of vast unvisited areas and large-scale planning of ecosystems management (Pitman et al. 2001, 2013, Gaston and Fuller 2008).

The delimitation and characterization of common species have received much attention in the context of the oligarchy hypothesis (Pitman et al. 2001), which suggests that Amazonian forests are dominated by a set of common species (*i.e.*, abundant and frequent species). This pattern is assumed to result from the ecological superiority of those dominant species, which seem to be qualitatively different species from the rest, and form a limited and definable set. Even though the hypothesis was proposed to describe *terra firme* Amazonian forests, many authors have found the same situation in other tropical communities in the Neotropics (Brewer and Webb 2002, Bridgewater et al. 2004, Svenning et al. 2004, Macía and Svenning 2005, Macía 2008, 2011, Norden et al. 2009, Williams et al. 2010), Asian Paleotropics (Paoli et al. 2006, Keppel et al. 2011), and African Paleotropics (Eilu et al. 2004, Jabot and Chave 2011). Pitman et al. (2001, 2013) predicted the pattern to be stronger at the local and intermediate scales and within relatively homogeneous habitats, but why it is such a generalized observation in many types of forests remains largely unclear.

With respect to the relationship between species commonness and the size of the species pool, many groups have reported that species richness and species dominance are negatively correlated (Bazzaz 1975, Huston 1979, Armesto and Pickett 1985, Hubbell 2001, He and Legendre 2002, Hurlbert 2004, Dornelas et al. 2011). Because the same number of individuals is allocated across more species, there will be fewer individuals per species. Therefore, we expect the size of the species pool to relate negatively with species average abundance and, consequently, with its average commonness. Pitman et al. (2001) followed the same reasoning to argue that the quantitative differences between tropical and strongly oligarchic temperate forests are only a consequence of the greater diversity in the tropics but that the overall pattern is qualitatively the same. This scenario would imply that the degree of dominance of common species is negatively related to the size of the species pool while the proportion of common species is independent of it.

The literature on two-dimensional commonness offers significant insights into community structure. However, the categorical approach employed so far (Fig. 4.1a) limits potential comparisons between different sets of taxa or different regions (Rabinowitz 1981, Rabinowitz et al. 1986, Ricklefs 2000). In contrast, here we propose to quantify commonness of species of a given community in a continuous way (Fig. 4.1b). This new approach does not allow distinction of different forms of rarity but greatly facilitates shifting from species-level to community-level questions about commonness.

To our knowledge, this study represents the first attempt to quantify and compare commonness patterns among lowland, dry, and montane tropical forests. We explored the relationships between commonness and the size of the species pool across different scales. First, we analyzed the variation of species commonness patterns with elevation and the size of the species pool at local scales (10 × 10 km). Second, we quantified commonness characteristics at larger scales, *i.e.*, (a) within large landscape units defined by the type of forest, and (b) for the whole Madidi region (200 × 200 km), which encompasses huge environmental variation. Finally, we tested whether the new methodological approach used here to quantify commonness in plant communities matches with the perspective on commonness of the oligarchy hypothesis (Pitman et al. 2001, 2013).

METHODS

Study region and floristic data

During the last 12 years, we carried out extensive standardized floristic inventories in the Madidi region, located on the eastern slopes of the Bolivian Andes, between latitude −12.43º and −15.72º and longitude −69.48º and −66.66º. It includes mature forests from the Amazon to the forest limit, *c.* 4000 m. We inventoried *c.* 122,000 plant individuals through the establishment of 407 plots of 0.1-ha (20 × 50 m), with a minimum inter-plot distance of 250 m. The study region contains many vegetation types (Navarro et al. 2004, Fuentes 2005), but for the present study the plots were classified into three broad forest types: (1) lowland forests (include Amazonian and pre-Andean *terra firme* forests); (2) semideciduous Andean forests ("dry forests" in the following), characterized by lack of precipitation for 4–5 months per year due to local rain shadow, with a prevalence of deciduous species (ranging from 650 to 1350 m in elevation); and (3) wet montane forests ("montane forests" in the following; includes different montane, Andean, sub-Andean, Yungas and *ceja de monte* formations). The assignment of plots to vegetation types was done in the field following the physiognomic and floristic indicators summarized by Navarro et al. (2004) and Fuentes (2005), who described in detail the vegetation types in the Madidi National Park and surrounding areas. Although almost exactly a threshold of 1000 m in elevation defines the limit between Amazonian and montane forests, four plots between 1000 and 1100 m were assigned to lowland forests, according to local environmental and floristic characteristics, and two plots between 900 and 1000 m were assigned to montane forests. Overall, 95 plots were inventoried in lowland forests, 82 in dry forests, and 230 in montane forests. These plots were dispersed over an area of roughly 110 × 110 km in lowland forests, 35 × 35 km in dry forests, and 130 × 130 km in montane forests.

Plots were installed to avoid big gaps or recent human disturbance. At each plot, we inventoried all woody plant individuals with a diameter equal or greater to 2.5 cm at 130 cm above ground. All species were collected at least once, except for a few well-known species like *Iriartea deltoidea* Ruiz & Pav. and *Socratea exorrhiza* (Mart.) H. Wendl. All individuals were identified to a valid species name or assigned to a morphospecies. Extensive taxonomic work was conducted during 2010 at the Herbario Nacional de Bolivia to ensure that all species and morphospecies names were standardized across all plots. Less than 3.5% of individuals were excluded from the analysis because they were sterile specimens that could not be assigned to a reliable morphospecies. All plot characteristics, floristic inventories, and voucher specimens are available to query in the TROPICOS database (www.tropicos.org/PlotSearch.aspx?projectid=20). Voucher specimens are kept in the LPB and MO herbaria (acronyms according to Thiers 2012).

Characterization of species commonness

We calculated species commonness based on a modified version of the *h* index, a widely known bibliometric tool to measure academic performance (Hirsch 2005). We assigned to each species a commonness proportional *h* index (h_p) when it was present in h_p percentage of plots with h_p percentage or more of the individuals in each of those plots. For example, a species with h_p = 10% is present in 10% of the plots and represents 10% or more of the individuals in those plots. The value of this index is not limited by sampling effort and varies within the interval 0–100%. This index cannot be obtained by using a single formula because it is the solution to the equation $h_p = f(h_p)$, where f could be any monotonically decreasing function. In practice, however, h_p is very easily obtained from the observed sequence of abundance values of the species (see Appendix A at the end of the chapter for the simple R code for its calculation). Because h_p measures properties in two dimensions with a single number, this index facilitates the integration of species-based information into the community level to explore commonness patterns, which is the focus of the present paper. Three community metrics are taken into account: (1) mean commonness of all species of the community; (2) proportion of common species of the community; (3) mean commonness of the common species, which is a measure of the strength of dominance shown by the common species.

Mean commonness at the local scale: measurement and determinants

To study the patterns at the local scale, we divided the study area with a regular grid of 10 × 10 km cells. Any cell containing five or more plots was considered a sampling unit. The elevation of a sampling unit was calculated as the mean elevation of the plots included. We calculated the mean h_p of all the species within a sampling unit.

To estimate the size of the species pool (*S*), defined as the total number of species within a sampling unit, we used the bootstrap estimator (Gotelli and Colwell 2010): $S = S_O + \Sigma\ (1-p_i)^N$; where S_O is the number of observed species within the sampling unit, p_i is the proportion of plots of a sampling unit where the species *i* is present, and *N* is the number of plots inventoried in the sampling unit.

To explain the observed pattern of mean commonness at the local scale, we conducted two simple linear regressions between the estimated size of the species pool and elevation as explanatory variables, and the mean h_p of the species of a sampling unit as the response variable. To assess the effect of one explanatory variable while controlling for the effect of the other, we conducted partial linear regressions. The statistical significance was estimated with a Monte Carlo test after 999 random permutations (Legendre 2008).

Delimitation of the set of common species

To obtain the group of common species in a community, we plotted a proportional commonness-rank curve to summarize the commonness profile of a community, ranking all species by their h_p indexes and, secondarily, by abundance (Fig. 4.2). The axes were scaled from 0 to 1 because we were interested in the *shape* of the curve less so in the absolute values (*i.e.*, the number of species or the commonness attained by the most common species). With a quantitative measure of commonness, common species are defined as those above a given threshold of commonness, which separates them from the rest. We defined that threshold as the *h* index of the proportional commonness-rank curve. Graphically, this is interpreted as the point where the diagonal (y = x) crosses the proportional commonness-rank curve (see Fig. 4.2). Given that this new coefficient is an *h* index of h_p indexes, we use the notation h_h. Unlike h_p, which measures attributes of the species, h_h measures a property of the community. For example, a community with $h_h = 0.10$ means that 10% of the observed species present h_p indexes above the 10th percentile. As in the case of h_p, this index cannot be obtained by using a single formula but is easily obtained from the observed sequence of h_p values of the species (see Appendix A). We propose the h_h criterion because it describes a characteristic of the community that does not depend on the number of species, *i.e.,* it responds to the steepness of a curve but not to the number of points that constitute such curve (see Fig. 4.2). Moreover, it is expressed formally as a proportion of species and therefore it is comparable among communities that differ in their number of species.

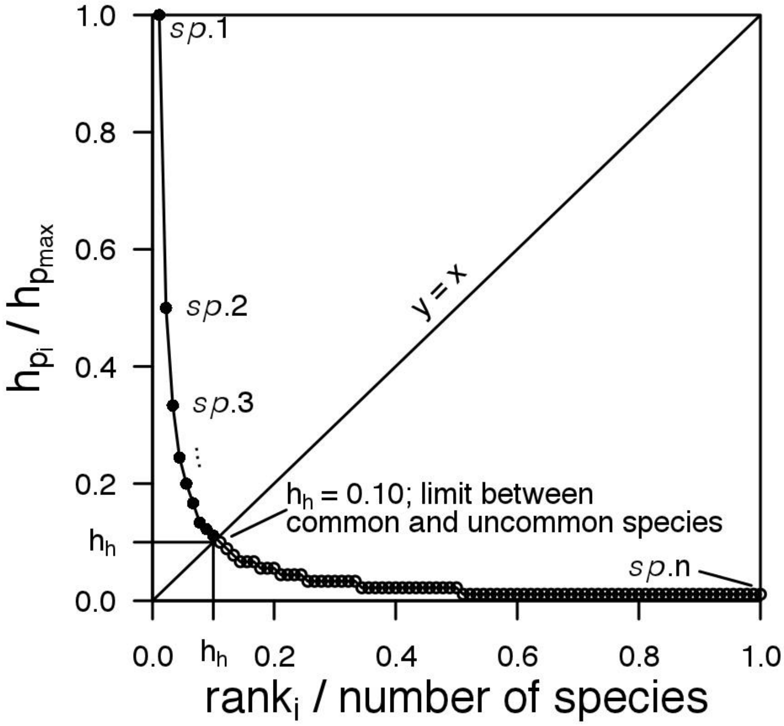

Figure 4.2. Example of a proportional commonness-rank curve and delimitation of common species of a community with the h_h criterion. The x-axis represents the proportional rank of a given species, ranked by h_p index. Because it is proportional, it varies within the range [0, 1], instead of [1, number of species]. The y-axis represents the ratio between the h_p index of a species and the h_p of the most common species. Because it is proportional, it varies within the range [0, 1] instead of [0, maximum h_p]. The point where the diagonal crosses the proportional commonness-rank curve is its h index (h_h), which is used in the present study as the threshold between common and uncommon species. The represented example community has $h_\mathrm{h} = 0.10$: 10% of the species are qualified as common.

Patterns of common species at the local scale

We delimited the set of common species within 10 × 10 km sampling units following the h_h criterion. Then we counted the number of common species and divided that by the size of the species pool to find the proportion of common species in the estimated size of the species pool. To know how common the common species were, we calculated their mean h_p.

To identify potential determinants of patterns of common species, we conducted four simple linear regressions, one for each combination of one response variable (proportion of common species and mean h_p of common species) with one explanatory variable (estimated size of the species pool and elevation). Finally, to explore the effect of one explanatory variable while controlling for the effect of the other, we conducted four partial linear regressions, one for each combination of one response variable with one explanatory variable. The statistical significance of the partial regressions was estimated with a Monte Carlo test after 999 random permutations (Legendre 2008).

Comparison between forest types and characterization of the region

To explore possible differences between lowland, dry, and montane tropical forests, we characterized each forest type on the basis of the mean h_{p} of their species, proportion of common species, and the mean h_{p} of its common species, following the same calculations as described above for the local-scale analysis. To characterize the whole Madidi region (200 × 200 km), all plots were considered together and all calculations repeated.

Comparison between h_h criterion and Pitman et al. (2001, 2013) perspective on commonness

To check how well h_{h} fits the original oligarchy concept, we extracted all of the plots below 500 m elevation and delimited the set of common species to be compared with those of Pitman et al. (2001, 2013). All of the calculations and analyses were done with R (R Development Core Team and R Core Team 2012). The level of significance for all analyses was 0.05.

RESULTS

Commonness at the local scale

The mean commonness of all species of the community at the local scale (10 × 10 km) ranged from 0 to 2.55% (mean = 0.58%). It increased significantly with elevation (adjusted $R^2 = 0.23$; $P = 0.002$), even when the effect of the species pool was partialled out ($R^2 = 0.12$; $P = 0.041$) (Table 4.1). It was also negatively related with the size of the species pool (adjusted $R^2 = 0.19$; $P = 0.006$) but was not statistically significant when the effect of the elevation was partialled out ($P = 0.106$).

The proportion of common species in the sampling units ranged from 0 to 21.0% of the species pool (mean = 5.14%) and was not related with pool size ($P = 0.183$), even when the effect of the elevation was partialled out ($P = 0.632$) (Table 4.1). We found a slight increase in the proportion of common species with elevation (adjusted $R^2 = 0.11$; $P = 0.031$), but it did not remain statistically significant when the effect of the size of the species pool was partialled out ($P = 0.087$).

The mean commonness of the common species varied between 4.62 and 20.0% (mean = 11.26%). It was negatively related with the size of the species pool (adjusted $R^2 = 0.20$; $P = 0.007$), even when the effect of the elevation was partialled out ($R^2 = 0.19$; $P = 0.014$). In contrast, it was not significantly related with the elevation ($P = 0.263$), even when the effect of the size of the species pool was partialled out ($P = 0.991$).

Table 4.1. Results of the simple and partial linear regressions between the size of the species pool and elevation using the h_p index for the three commonness metrics studied. Values are standardized coefficients in the regression. Significant results are shown in bold (***: $P < 0.001$; **: $P < 0.01$; * $P < 0.05$). S: size of the species pool; E: elevation; S | E; size of the species pool, elevation partialled out; E | S: elevation, size of the species pool partialled out.

	Mean h_p of all species	Proportion of common species	Mean h_p of common species
S	**−0.46** ($R^2_{adj} = 0.19$)**	−0.23 (**R^2_{adj}** = 0.03)	**−0.46** ($R^2_{adj} = 0.20$)**
E	**0.51** ($R^2_{adj} = 0.23$)**	**0.37* ($R^2_{adj} = 0.11$)**	0.20 (**R^2_{adj}** = 0.01)
S | E	−0.30 ($R^2 = 0.08$)	−0.10 ($R^2 = 0.01$)	**−0.46* ($R^2 = 0.19$)**
E | S	**0.38* ($R^2 = 0.12$)**	0.33 ($R^2 = 0.09$)	0.002 ($R^2 < 0.01$)

Commonness at larger scales

The three broad forest types showed contrasting characteristics of commonness patterns (Table 4.2). They could be ordered by their size of the species pool, with the montane having the largest species pool, followed by the lowland, and with the dry forest showing a very small species pool. In parallel, the montane forest had the lowest commonness of common species, followed by the lowland forests, while the dry forest showed very strong dominance of its common species. When all the community was considered, lowland and montane forests showed very similar mean commonness of species, but the dry forest was almost double that value. In contrast with these differences, the proportion of common species was similar among the three forest types (12–13%).

When the whole Madidi region was considered, the mean commonness and the commonness of the common species were lower than for the three forest types separately, but the proportion of common species was similar (14%) (Table 4.2).

Table 4.2. Community structure parameters for the lowland, dry, and montane forests and the whole Madidi region; h_p was the commonness index used.

Forest types	Mean h_p of all species (%)	Proportion of common species (%)	Mean h_p of common species (%)	Estimated number of species	Mean elevation (m)
Lowland	0.76	11.77	2.92	1232	498
Dry	1.47	11.81	5.26	457	940
Montane	0.80	12.66	2.58	1975	2052
All	0.69	13.92	2.07	2831	1465

When increasing the scale, the species were less common but more equally common (Fig. 4.3). This pattern was associated with a greater proportion of common species but with less difference in commonness between common and uncommon species.

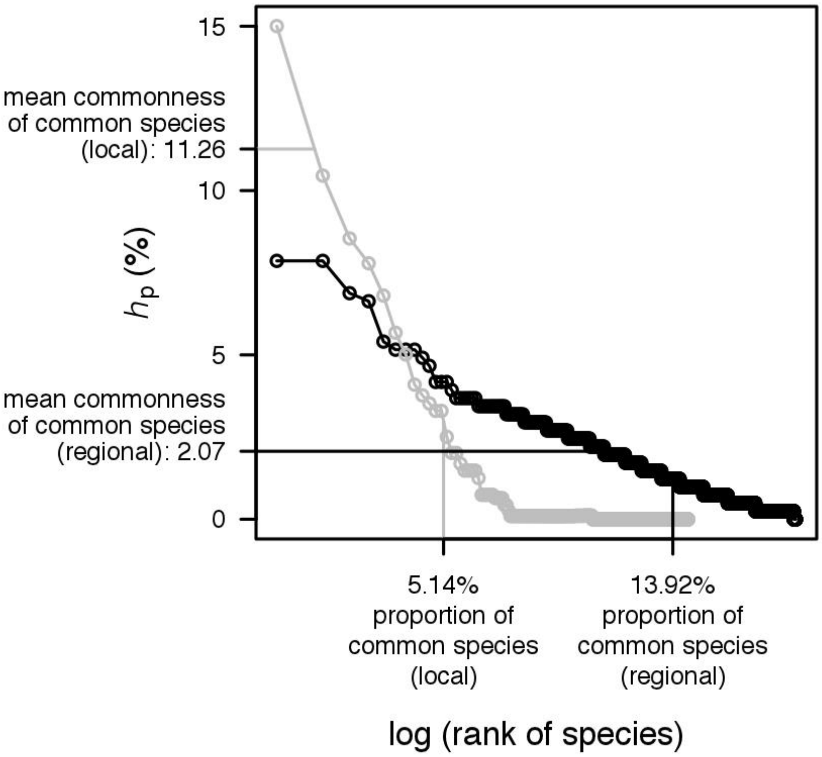

Figure 4.3. Across-scale comparison of the distribution of commonness between the whole Madidi region (in black) and mean values of 10 × 10 km sites within the region (in grey). The highlighted values correspond to the delimitation and characterization of the set of common species at local and regional scales.

Delimitation of the set of common species below 500 m

The subset of all plots below 500 m is a similar system to the Ecuadorean and Peruvian Amazonian forest where Pitman et al. (2001, 2013) developed the original oligarchy hypothesis. While they applied their expert criteria to separate oligarchic species from the rest, we applied the h_h criterion. We found a total of 122 common species (12.41% of the estimated species pool) below 500 m in 66 0.1-ha plots in the Madidi region (Appendix B, at the end of the chapter). Of these species, 108 were trees, and 14 were lianas. The selected species ranged from 2 species that were present in 10.61% of the plots as at least 10.61% of the individuals (*Iriartea deltoidea* and *Rinorea viridifolia* Rusby) to 47 species present in 1.52% of the plots as 1.52% of the individuals or more. The most common liana species was *Hebanthe occidentalis* (R.E. Fr.) Borsch & Pedersen (h_p = 3.03%).

DISCUSSION

Our main purpose was to perform a quantitative assessment of two-dimensional commonness along an extensive tropical elevational gradient. We also aimed to compare two spatial scales and different types of forests.

Commonness at local scales showed a clear elevational pattern with species being more common, on average, at higher elevations. There was also a negative relationship between the number of species and the degree of species dominance at local scales. These results agree with those of many previous researchers and are logically grounded in the allocation of the same amount of individuals across a different number of species, which affects the mean abundance and, consequently, mean commonness (Hubbell 2001, He and Legendre 2002, Hurlbert 2004, Dornelas et al. 2011). The same logic of the size of the species pool applies to the alpha-diversity, even within those sampling units with relatively similar plots and, therefore, relatively small pool of species. That means that, regardless the size of the species pool, the species within sampling units with high alpha-diversity will tend to present a lower proportion of individuals within each plot, and therefore their commonness (as measured by h_p) will decrease in average. If the elevation and alpha-diversity are correlated within our study region (a general pattern found in most Andean regions for different taxa; Kessler et al. 2001, Krömer et al. 2005, Kessler 2009, Laurance et al. 2011, Palin et al. 2011, Kluge and Kessler 2011, Karger et al. 2011), this could explain the relationship between elevation and mean commonness that the size of the species pool does not explain.

The elevational pattern has no exact parallel when the three forest types are considered at larger scales by elevation. Although the differences between lowland and montane forests were expected for the elevational ranges considered, the dry forest did not show intermediate characteristics as would be expected according to its elevation. In contrast, the size of the species pool seemed to be a more robust predictor of the differences between types of forest, particularly within the dry forest, with fewer but much more common species than the other two forest types. Some authors reporting the same pattern in other dry forests have suggested different ecological determinants of this stronger dominance, such as stronger competition, more frequent disturbance, or the presence of rare species more prone to local extinction due to isolation from other dry areas (Hubbell 1979, Pennington et al. 2009). All of these mechanisms could influence the commonness patterns by modifying the size of the species pool. Moreover, our results for lowland and montane forests suggest that the mechanisms shaping species commonness differences between sites are the same as those shaping continuous diversity changes along the elevational gradient (Karger et al. 2011, Kluge and Kessler 2011, Kraft et al. 2011, Sanders and Rahbek 2012). These results, added to those obtained at the local scale, suggest that the degree of dominance of species, far from being determined solely by local processes such as successful adaptation to local environmental conditions, could be largely driven by the evolutionary and historical processes that shape the species pool within a given area (Lessard et al. 2012b).

While the degree of species dominance seems to be largely driven by the species pool, we found presence of a dominant set of common species, *i.e.*, the so-called "oligarchic pattern" *sensu* Pitman et al. (2001, 2013), at all scales and types of forest with independence of the size of the species pool. The consistency of the oligarchic pattern at the large scales studied (types of forest and whole Madidi region) is noteworthy. In all cases, a limited and definable set of common species accounted for 11–14% of the species pool. These figures are strikingly similar to those underlying the original concept of oligarchy (10% in Yasuní and 15% in Manu). Moreover, other works directly addressing oligarchy with subjective expert criteria offer similar proportion of common species, with 119 oligarchic species out of 1087 (11%) reported in Yasuní (Macía 2011), 94 oligarchic species out of 877 (11%) reported in lowland Madidi (Macía 2008), 121 oligarchic species out of *c*. 1000 (12%) in Brazilian *cerrado* (Bridgewater et al. 2004) and 38 oligarchic species out of 311 (12%) in liana communities in Yasuní (Burnham 2002). Other researchers report contrasting results, ranging from 30% of common species (Eilu et al. 2004) to only one or few species, usually *Iriartea deltoidea* and *Socratea exorrhiza* in the Amazonia, and homologous dominant species in other tropical forests (Paoli et al. 2006, Norden et al. 2009, Jabot and Chave 2011). Unfortunately, comparisons with all these results are very limited because of the inherent subjectivity of the categorical or merely descriptive approaches to commonness (Ricklefs 2000). In general, our results coupled with those of others suggest a general dominance pattern at these scales; however, given the mentioned limitations, we do not intend to extrapolate beyond the comparison with the original oligarchy hypothesis.

The consistency of the oligarchic pattern at both scales is surprising because we analyzed data sets that were very different in number of species (<500 to >2500), elevational ranges (<300 to ~3600 m), and environmental heterogeneity (from relatively homogeneous patches within the same forest type to the huge environmental variation covered by the whole Madidi region). At first sight, this consistency does not support the assumption of oligarchies present only at limited environmental heterogeneity (Pitman et al. 2001, 2013), and hence contrasts with the conclusions of previous researchers who rejected the oligarchy hypothesis based on datasets covering great environmental heterogeneity (Tuomisto et al. 2003, Réjou-Méchain et al. 2008, Toledo et al. 2011, 2012). We acknowledge that the environmental heterogeneity covered by the whole Madidi region has an effect on the strength of the oligarchic pattern, probably weaker than any of the more homogeneous 10 × 10 km areas considered at the local scale (Fig. 4.3). However, the method employed here does not require addressing oligarchy with an all-or-nothing view, and allows quantifying oligarchic patterns that are not obvious under more subjective approaches. Overall, our results clearly indicate the existence of a definable set of dominant species under very different conditions and, at least, from the local to regional scale. Further study would be required of the patterns of oligarchic co-occurrence to distinguish a combination of habitat-characteristic oligarchies from the presence of true large-scale generalist oligarchies.

Overall, it is very unlikely that our conclusions are biased by the method employed. The strong similarities between our quantitative approach applied to forests below 500 m in the Bolivian Amazon and the expert criteria of Pitman et al. applied to forests in the Ecuadorean and Peruvian Amazon indicate that our method fits very well with the original concept of oligarchy. Similarities include the amount of species qualified as common in Madidi (12% of the estimated species pool *vs.* 10–15%) and the identities of these species, with 45 of our Madidi common species below 500 m shared as common in Yasuní or Manu or both, while Yasuní and Manu shared 42 of their regional sets of common species (Appendix B; Pitman et al. 2013). The type of individuals that we included in our inventory and that Pitman et al. did not (lianas, shrubs, and treelets) explains some minor differences. For example, we found several oligarchic *Piper* and Melastomataceae species, as well as several oligarchic liana species. Unfortunately, no comparable studies have addressed the dominance of treelets or shrubs in the Neotropics. However, our method seems to perform well for lianas, since 3/14 of our oligarchic liana species are also reported as oligarchic in Yasuní (Burnham 2002). Finally, these results indicate not only that the same pattern can be found in different regions, but also evidence large-scale dominance of certain species across different regions in northwestern Amazonia, at least when the same habitat is considered, for both trees and lianas (Burnham 2002, 2004, Pitman et al. 2013).

We have found that the commonness patterns in the Madidi region are strongly linked to the size of the species pool, independently of the elevational variability involved and the type of forest and spatial scale considered. Remarkably, these factors affect the inter-species differences in commonness but not the general quality of the community. Although previous researchers have rejected the oligarchy hypothesis (Tuomisto et al. 2003, Réjou-Méchain et al. 2008, Toledo et al. 2011, 2012), we believe that it reflects measurable properties of the community that can be considered continuously across different habitats or scales, regardless of the strength of the pattern. Moreover, our results show that the comprehension of dominance and commonness patterns, including the oligarchy hypothesis, improves by interpreting the patterns in light of the species pool influence, as happens with other important aspects of community structure such as alpha- and beta-diversity gradients (Ricklefs 1987, Kraft et al. 2011, Myers et al. 2013), among others (Lessard et al. 2012a, b). Finally, taking advantage of a quantitative approach to commonness could facilitate an understanding of the mechanisms creating commonness differences among species and shaping community commonness patterns at different scales.

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Appendix A. R functions to calculate h_p and h_h indexes, and obtain the list of common species, from a composition matrix *M* based on abundances, with one row per plot and one column per species.

```
    hp.function <- function(M) # two-dimensional commonness of
species
    {
     hp <- apply(M/rowSums(M), 2, function(x)
max((1:nrow(M)/nrow(M))[sort(x,
decreasing=T)>=(1:nrow(M)/nrow(M))]))
     hp [which(hp =="-Inf")] <- 0 # assigns hp=0 to very
uncommon species
     names(hp) <- colnames(M) # assigns the name of the species
     return(hp)
    }
```

```
    hh.function <- function(M) # observed proportion of common
species, and ordered list of common species
    {
     hp <- hp.function(M) # calculates hp indexes
     hh <- max(((1:ncol(M))/ncol(M))[(sort(hp,
decreasing=T)/max(hp)) >= ((1:ncol(M))/ncol(M))]) # calculates
hh index
     if(!is.na(hh)) a <- cbind(hp, colSums(M))
     if(!is.na(hh)) common <- rownames(a[order(-a[, 1], -a[,
2]), ])[1:(hh*ncol(M))] # names of common species (ordered by hp
indexes and total abundances)
     if(is.na(hh)) common <- NULL
     return(list(hh=hh, common=common)) # output with the hh
index of the community and the names of the common species
    }
```

Appendix B. List of common species below 500 m in the Madidi region (Bolivia). * after the h_p index indicates if the species also has been considered oligarchic in other regions in the Amazonia, according to Appendix 1 of Pitman, N. C. A. et al. 2013. Oligarchies in Amazonian tree communities: a ten-year review. - Ecography 36: 114–123; and, in the case of lianas, Table 3 of Burnham, R. J. 2002. Dominance, diversity and distribution of lianas in Yasuní, Ecuador: who is on top? - Journal of Tropical Ecology 18: 845–864.

Family	Species	h_p (%)
Amaranthaceae	*Hebanthe occidentalis* (R.E. Fr.) Borsch & Pedersen (liana)	3.03
Anacardiaceae	*Tapirira guianensis* Aubl.	1.52 *
Annonaceae	*Cremastosperma leiophyllum* (Diels) R.E. Fr.	3.03
	Duguetia hadrantha (Diels) R.E. Fr.	1.52
	Duguetia spixiana Mart.	4.55
	Mosannona parva Chatrou	3.03
	Oxandra aff. *acuminata* = M. J. Macía 5777	3.03
	Ruizodendron ovale (Ruiz & Pav.) R.E. Fr.	1.52 *
	Unonopsis floribunda Diels	1.52
Apocynaceae	*Forsteronia graciloides* Woodson (liana)	3.03
Araliaceae	*Dendropanax arboreus* (L.) Decne. & Planch.	1.52 *
Arecaceae	*Astrocaryum murumuru* Mart.	3.03 *
	Attalea phalerata Mart. ex Spreng.	1.52
	Bactris major Jacq.	4.55
	Chamaedorea angustisecta Burret	1.52
	Euterpe precatoria Mart.	4.55 *
	Iriartea deltoidea Ruiz & Pav.	10.61 *
	Mauritia flexuosa L. f.	4.55
	Oenocarpus mapora H. Karst.	3.03
	Socratea exorrhiza (Mart.) H. Wendl.	6.06 *
Bignoniaceae	*Cydista lilacina* A.H. Gentry (liana)	3.03
	Roentgenia bracteomana (K.Schum. ex Sprague) Urb. (liana)	1.52
	Xylophragma pratense (Bureau & K.Schum.) Sprague (liana)	3.03
Boraginaceae	*Cordia nodosa* Lam.	1.52
Burseraceae	*Protium amazonicum* (Cuatrec.) D.C. Daly	3.03 *
	Protium rhynchophyllum (Rusby) D.C. Daly	3.03
	Tetragastris altissima (Aubl.) Swart	3.03 *
Buxaceae	*Styloceras brokawii* A.H. Gentry & R.B. Foster	3.03
Cannabaceae	*Celtis iguanaea* (Jacq.) Sarg.	1.52
	Celtis schippii Standl.	4.55 *
Celastraceae	*Hippocratea volubilis* L. (liana)	3.03
	Cheiloclinium cognatum (Miers) A.C. Sm.	1.52
	Salacia impressifolia (Miers) A.C. Sm.	1.52
Chrysobalanaceae	*Hirtella bullata* Benth.	1.52
	Hirtella racemosa Lam.	6.06
	Licania brittoniana Fritsch	1.52
Clusiaceae	*Garcinia gardneriana* (Planch. & Triana) Zappi	1.52

Family	Species	h_p (%)
Clusiaceae	*Garcinia madruno* (Kunth) Hammel	4.55
Combretaceae	*Combretum laxum* Jacq. (liana)	1.52 *
	Terminalia amazonia (J.F. Gmel.) Exell	1.52 *
Cyatheaceae	*Cyathea amazonica* R.C. Moran	3.03
Dichapetalaceae	*Tapura juruana* (Ule) Rizzini	1.52
Elaeocarpaceae	*Sloanea fragrans* Rusby	1.52 *
	Sloanea guianensis (Aubl.) Benth.	3.03
Euphorbiaceae	*Mabea anadena* Pax & K. Hoffm.	1.52
Fabaceae	*Dalbergia frutescens* (Vell.) Britton (liana)	3.03
	Inga thibaudiana DC.	3.03 *
Hernandiaceae	*Sparattanthelium amazonum* Mart. (liana)	1.52
Lacistemataceae	*Lacistema aggregatum* (P.J. Bergius) Rusby	1.52
Lauraceae	*Aiouea grandifolia* van der Werff	1.52
	Aniba panurensis (Meisn.) Mez	1.52
	Nectandra pulverulenta Nees	1.52 *
Lecythidaceae	*Cariniana estrellensis* (Raddi) Kuntze	3.03
	Eschweilera andina (Rusby) J.F. Macbr.	1.52 *
Loganiaceae	*Strychnos asperula* Sprague & Sandwith (liana)	3.03
Malvaceae	*Byttneria pescapriifolia* Britton (liana)	3.03
	Pentaplaris davidsmithii Dorr & C. Bayer	6.06
	Quararibea wittii K. Schum. & Ulbr.	6.06 *
	Theobroma cacao L.	1.52 *
Melastomataceae	*Miconia centrodesma* Naudin	3.03
	Mouriri myrtilloides (Sw.) Poir.	3.03
	Tococa guianensis Aubl.	4.55
Meliaceae	*Guarea gomma* Pulle	3.03 *
	Guarea guidonia (L.) Sleumer	1.52
	Guarea kunthiana A. Juss.	3.03 *
	Guarea macrophylla Vahl	6.06 *
	Guarea pterorhachis Harms	1.52 *
	Trichilia pleeana (A. Juss.) C. DC.	3.03
Menispermaceae	*Abuta grandifolia* (Mart.) Sandwith	1.52
Monimiaceae	*Mollinedia ovata* Ruiz & Pav.	3.03
Moraceae	*Brosimum alicastrum* Sw.	3.03 *
	Clarisia biflora Ruiz & Pav.	1.52 *
	Naucleopsis krukovii (Standl.) C.C. Berg	3.03 *
	Poulsenia armata (Miq.) Standl.	1.52
	Pseudolmedia laevis (Ruiz & Pav.) J.F. Macbr.	4.55 *
	Pseudolmedia macrophylla Trécul	4.55 *
	Sorocea briquetii J.F. Macbr.	3.03 *
	Sorocea guilleminiana Gaudich.	3.03
Myristicaceae	*Otoba glycycarpa* (Ducke) W. Rodrigues & T.S. Jaramillo	3.03 *
	Otoba parvifolia (Markgr.) A.H. Gentry	3.03 *

Family	Species	h_p (%)
Myristicaceae	*Virola sebifera* Aubl.	1.52 *
Myrtaceae	*Calyptranthes lanceolata* O. Berg	3.03
	Eugenia florida DC.	1.52
	Myrciaria floribunda (H. West ex Willd.) O. Berg	1.52
Phyllanthaceae	*Hieronyma alchorneoides* Allemão	1.52
Piperaceae	*Piper glabratum* Kunth	4.55
	Piper heterophyllum Ruiz & Pav.	3.03
	Piper obliquum Ruiz & Pav.	4.55
	Piper reticulatum L.	3.03
Poaceae	*Guadua sarcocarpa* Londoño & P. M. Peterson	3.03
Polygonaceae	*Triplaris americana* L.	1.52
	Triplaris setosa Rusby	4.55
Primulaceae	*Stylogyne ambigua* (Mart.) Mez	3.03
	Stylogyne cauliflora (Mart. & Miq.) Mez	3.03
Putranjivaceae	*Drypetes amazonica* Steyerm.	3.03 *
Rubiaceae	*Uncaria guianensis* (Aubl.) J.F. Gmel. (liana)	3.03 *
	Uncaria tomentosa (Willd.) DC. (liana)	3.03
	Ixora peruviana (Spruce ex K. Schum.) Standl.	3.03
	Psychotria viridis Ruiz & Pav.	1.52
Rutaceae	*Erythrochiton fallax* Kallunki	1.52
Sabiaceae	*Meliosma herbertii* Rolfe	1.52 *
Salicaceae	*Casearia sylvestris* Sw.	1.52 *
	Hasseltia floribunda Kunth	1.52 *
	Lunania parviflora Spruce ex Benth.	3.03 *
Sapindaceae	*Allophylus floribundus* (Poepp.) Radlk.	3.03
Sapotaceae	*Pouteria bangii* (Rusby) T.D. Penn.	3.03
	Pouteria cladantha Sandwith	3.03
	Pouteria torta (Mart.) Radlk.	1.52 *
	Sarcaulus brasiliensis (A. DC.) Eyma	1.52
	Sarcaulus vel. sp. nov. Radlk. = E. J. Ticona 181	3.03
Siparunaceae	*Siparuna bifida* (Poepp. & Endl.) A. DC.	4.55
	Siparuna decipiens (Tul.) A. DC.	6.06 *
	Siparuna guianensis Aubl.	1.52
Ulmaceae	*Ampelocera edentula* Kuhlm.	1.52 *
Urticaceae	*Pourouma cecropiifolia* Mart.	1.52 *
	Pourouma minor Benoist	3.03 *
Verbenaceae	*Petrea maynensis* Huber (liana)	3.03 *
Violaceae	*Leonia crassa* L.B. Sm. & A. Fernández	3.03 *
	Leonia glycycarpa Ruiz & Pav.	6.06 *
	Rinorea apiculata Hekking	7.58 *
	Rinorea viridifolia Rusby	10.61 *
	Rinoreocarpus ulei (Melch.) Ducke	3.03 *

CAPÍTULO 5

Niche breadth of oligarchic species in Amazonian and Andean rainforests

Este capítulo se ha desarrollado en colaboración con V. Cala y M. J. Macía. Forma parte de un manuscrito pendiente de enviar a *Journal of Biogeography*.

ABSTRACT

Aim: To test the niche breadth hypothesis (NBH), which states that dominant species have broader environmental tolerances than rare species, focusing on oligarchic species distributions along the gradients of edaphic and climatic variables.

Location: Amazonian and Andean tropical rainforests along an ~3000 m elevation gradient, covering an area of 200 × 200 km in northwestern Bolivia.

Methods: All woody plants with a diameter at breast height ≥2.5 cm were measured in 98 0.1-ha plots. We analyzed 18 chemical properties of the soils in each plot. Climatic and topographic variables were obtained from available open access databases. Three measures were calculated for each of the species found at each forest type: (1) regional-scale dominance based on frequency and local abundance, (2) niche breadth along each of the environmental variables, and (3) total niche size.

Results: Oligarchic species showed broader niche breadths than the other species that constituted the community assembly in both Amazonian and Andean rainforests. The niche breadth of any species tended to be positively correlated with its degree of dominance. The Amazonian forest showed a stronger oligarchic pattern than the Andean forest, and the Amazonian common species showed larger niches overall. However, this pattern differed for some particular variables: Amazonian oligarchies had narrower niches along the variables related to the organic matter and most climatic variables, whereas Andean oligarchies had narrower niches along several micronutrient factors and temperature variables.

Main conclusions: The results provide strong empirical support for the NBH in tropical rainforests. However, different patterns of dominance were found in the two habitats: oligarchic species ranged from narrow-niched species to very broad generalist species. Broad-niched oligarchic species have also been reported in other regions, suggesting an important role of niche size linking commonness at different scales. Oligarchic species exhibit relatively narrow niches with respect to soil factors if measured along wide gradients, regardless of the forest type studied. In contrast, the opposite pattern was found for many climatic variables, indicating greater sensitivity to climate in Amazonia compared to the Andes. Despite these differences, Amazonia has much greater total niche sizes for its common species than the Andes overall.

Keywords: Climatic niche, commonness, species dominance, environmental heterogeneity, edaphic niche, *h* index, niche breadth hypothesis, oligarchy hypothesis, rarity, tropical rainforests.

INTRODUCTION

Understanding how common plant species are distributed across the landscape is crucial for the management, conservation and comprehension of any tropical forest ecosystem (Gaston and Fuller 2008, Gaston 2010, Pitman et al. 2013). In particular, a low proportion of the forest's large diversity constitutes the skeleton of tropical forest communities because a limited number of abundant and frequent species account for the majority of the individuals within relatively large areas (Pitman et al., 2001, Macía and Svenning, 2005). This idea is the core of the so-called "oligarchy hypothesis", which has recently been revisited (Pitman et al. 2013). Following the conclusions of this paper, a few empirical studies have examined the causes for this type of pattern, and it is still not clear why some species have such a level of dominance over large expanses. To address these issues, a major focus has been on the habitat specificity or the niche size of species, historically one of the major concerns of ecological research (*e.g.,* Hutchinson, 1957; Levins, 1968; Ashton, 1969; Rosenzweig, 1981). Despite the significant advances reported during recent decades, the role of species niche size in the community assembly of tropical forests is still minimally understood. The major mechanistic hypothesis linking niche size and large-scale commonness is the niche breadth hypothesis (NBH), which, in its most general form, states that common species have broader niches than rare species (Brown 1984). It implies that two general types of species can be recognized: (1) species with broader environmental tolerances that would be able to attain higher local densities in some regions and could colonize new areas, attaining higher regional abundance; and (2) species with specific environmental requirements that are unlikely to find optimal conditions to colonize new areas anywhere and, therefore, would be locally restricted and scarce overall (Brown 1984).

The NBH is often cited in the literature on tropical forest dominance (*e.g.,* Pitman et al., 1999, 2001, 2013; Ruokolainen and Vormisto, 2000; Davidar et al., 2008; Kristiansen et al., 2009, 2012). However, according to Pitman et al. (2013), the NBH has not been properly tested, nor has the extent of species niches been rigorously quantified. To properly test the NBH, there must be some distinction between the resource distribution and the species distribution, as well as the integration of these two distributions in the measurement of species niches. Many niche metrics give the same weight to rare and common resources and, therefore, cannot discriminate the species with strong shifts in resource preferences from those using resources in proportion to their occurrence in the environment (Feinsinger et al. 1981, Smith 1982, Devictor et al. 2010). Hence, these metrics would not reflect the species' requirements because they constitute a mixture of both species characteristics and landscape characteristics.

The oligarchy hypothesis was proposed for *terra firme* Amazonian trees, but the results of many papers that corroborated the hypothesis indicate that it could be a much more general ecological hypothesis (see Pitman et al. (2013) for examples of papers on different vegetation types, geographic areas, life-forms and taxa). However, it is unknown how this hypothesis can be applied to different habitats whose mechanisms and processes differ greatly. The present paper focuses on Amazonian and Andean tropical montane rainforests, which represent two species-rich tropical ecosystems with contrasting biotic and abiotic conditions (Hoorn et al. 2010, Herzog et al. 2012, Cavers and Dick 2013). One marked difference between the two habitats is the more pronounced environmental heterogeneity of the montane forest, which is characterized by a strong elevational gradient and rapid shifts in edaphic and micro-environmental variables at any elevation (*e.g.,* Gentry 1995, Webster 1995, Vitousek 1998, Gerold 2008). It is noteworthy that the oligarchy hypothesis harbors the idea that the oligarchic pattern is weak within highly heterogeneous conditions, particularly edaphic heterogeneity (Pitman et al. 2001, 2013). Three predictions emerge from this pattern: (1) because oligarchic species are generalists, but only to a certain limit, we expect that different sets of oligarchic species would dominate in each of the conditions under high environmental heterogeneity; (2) in the highly heterogeneous montane conditions, we expect weaker oligarchies with relatively narrower niches than in the lowlands, whereas we expect Amazonian oligarchies to be more dominant and relatively broad-niched because the conditions of these forests are relatively more homogeneous; and (3) the relevant niche dimensions for which the environmental heterogeneity is expected to have an effect over the strength of the oligarchic pattern are assumed to be edaphic in Amazonian rainforests at ~10,000 km^2 scale, according to Pitman et al. (2001), but could be different in the contrasting Andean rainforests.

The present study focused on Amazonian and Andean tropical montane rainforests within a 200 × 200 km area in northwestern Bolivia. We tested the NBH and associated predictions in both forest types with two large and fully comparable datasets, comprised of woody plants data and environmental data, particularly edaphic data. We aimed to answer the following five questions: (1) Are the niche breadths of oligarchic species broader than the niche breadths of the other species that constitute a given community assembly? (2) Does the NBH apply to a broad suite of environmental variables or only to a specific set of variables? (3) Which are the most significant environmental factors for the different Amazonian and Andean rainforests? (4) Are Amazonian oligarchies stronger than Andean oligarchies? If so, (5) is this difference associated with relatively broader niches of Amazonian oligarchic species compared to the niche breadths of oligarchic Andean species?

METHODS

Study area and sampling design

Fieldwork was carried out in two regions of northwestern tropical rainforests of Bolivia ~120 km apart, within or close to the Madidi National Park (Fig. 5.1, see also Fig. 1.1). In Amazonian rainforests, we inventoried 44 plots distributed in five sites below 1000 m in elevation, within an area of 30 × 100 km (Macía 2008). In Andean rainforests, we inventoried 54 plots in six sites between 1200 and 3100 m that focused on three elevational ranges: lower montane forest at 1200–1500 m, intermediate montane forest at 2000–2300 m and upper montane forest at 2800–3100 m. Montane plots were established within an area of 40 × 120 km. All studied localities were only accessible by foot, except one in the lowlands that was accessible by motorboat, 1–4 days away from the nearest village.

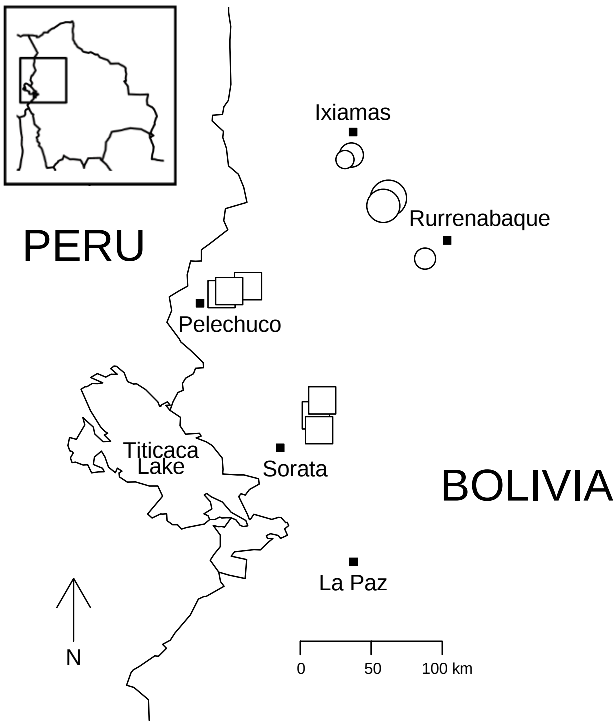

Figure 5.1. Location of the 11 inventoried sites in northwestern Bolivia. Circles represent Amazonian forest sites, and squares represent Andean forest sites. The size of the symbols is proportional to the number of plots.

We studied old-growth mature tropical rainforest that had sporadic pockets of disturbance from landslides in the montane areas but no recent sign of human perturbation in either Amazonian or Andean habitats. Plot locations within a site were selected to document all environmental variation existing in a site, but all plots were internally homogeneous forests. We avoided secondary forests, identified by the high abundance of *Cecropia* trees, bambusoids or vines and lack of large trees. All forests received >2000 mm of annual mean precipitation, and dry periods were 3–4 months per year in Amazonia and 2–3 months in the Andes (Ribera 1992, Navarro et al. 2004, Hijmans et al. 2005). The mean annual temperature varied from 26 °C at the lowest elevations to 10 °C at the highest elevations. Both Amazonian and Andean soils were acidic (mean pH per site <5.5), with some plots of Amazonian rainforests showing higher pH values (Macía et al. 2007). Amazonian soils were relatively sandy (>50%) and had less than 15% organic matter in the top layer, whereas Andean soils were highly organic, with 35–70% organic matter in the top layer at the three elevation ranges (Macía et al. 2007, Schawe et al. 2007).

Floristic data collection

We established 6–12 plots of 0.1-ha (20 × 50 m) in each of the 11 inventoried sites, with a minimum inter-plot distance of 500 m in Amazonian rainforests and 250 m in Andean rainforests, for a total of 98 plots. At each plot, all woody plants with stems rooting within the plot limits and with a diameter at breast height (dbh, measured at 130 cm from the ground) ≥2.5 cm were measured. All measured individuals were identified or assigned a morphospecies name, and each was collected at least once in the sites. The full set of vouchers was deposited at LPB, and almost a full set of duplicates was deposited in MO (acronyms according to Thiers, 2012). Less than 5% of the individuals were excluded in the analysis because they were sterile specimens that could not be assigned to a reliable morphospecies name. All data are available for query at the TROPICOS database (http://www.tropicos.org/PlotSearch.aspx?projectid=20).

Environmental data collection

At each plot, we obtained a compound sample of superficial soil (0–15 cm below the litter layer) from the mixture of five subsamples collected in the center of five subplots disposed in zig-zag fashion. Soil samples were air dried and passed through a 2-mm sieve. Soil pH was determined in deionized water and in 1 M KCl solutions with a soil/solution ratio of 1:2.5. Total C, N and S were determined in a LECO CHNS-932 elemental analyzer. Organic C was determined with the Walkley and Black wet digestion method (Walkley and Black 1974). Extractable Al, Ca, Co, Cu, Fe, K, Mg, Mn, Na, Ni, P and Zn contents were measured with Melhich-3 extractions (Mehlich 1984) followed by determination using inductively coupled plasma-mass spectrometry (ICP-MS) in an Elan 6000 Perkin-Elmer spectrometer.

Climatic data represented in all 19 bioclimatic variables data stored in the WorldClim database were downloaded for the study area (Hijmans et al. 2005). We computed the elevation, slope, eastness and northness aspects from the ASTER Global Digital Elevation Map v. 2, using a digital elevation model with 30 m resolution (http://asterweb.jpl.nasa.gov/gdem.asp). A summary of the environmental conditions of each forest type can be found in Table 5.1.

Table 5.1. Environmental conditions of Amazonian and Andean rainforests in northwestern Bolivia. For the soil data, the aluminum and nutrients content refer to extractable contents with the Mehlich-3 method (Mehlich 1984). The bioclimatic codes and units follow the codes and units of Hijmans et al. (2005) (www.worldclim.org/bioclim).

	Amazonian rainforests				Andean rainforests			
Variables	Mean	Range	SD	CV	Mean	Range	SD	CV
Elevation (m)	650.09	254−1043	249.74	0.38	2169.13	1163−3137	657.37	0.30
Slope (%)	0.28	0.03−0.60	0.16	0.57	0.51	0.04−0.79	0.17	0.33
Northness (degrees)	−0.17	−1.00−1.00	0.79	4.54	0.11	−1.00−1.00	0.78	7.43
Eastness (degrees)	−0.03	−1.00−1.00	0.61	18.13	0.00	−1.00−0.99	0.63	161.43
pH (H_2O)	5.22	3.08−8.01	1.09	0.21	3.34	2.51−4.91	0.52	0.15
pH (KCl)	4.52	2.33−7.4	1.12	0.25	2.58	1.63−4.43	0.65	0.25
Organic C (%)	3.50	0.06−16.53	3.66	1.05	28.92	5.98−47.91	10.90	0.38
Total C (%)	3.07	0.24−15.79	3.29	1.07	32.42	5.18−47.89	12.08	0.37
Total N (%)	0.32	0.04−1.15	0.27	0.83	1.91	0.50−2.94	0.60	0.31
Total S (%)	0.02	0−0.10	0.02	0.76	0.17	0.04−0.28	0.06	0.34
Al (mg/kg)	483.49	11.30−1581.70	366.32	0.76	1281.42	415.7−2026.7	390.72	0.30
Ca (mg/kg)	1463.62	86.80−8137.70	1730.30	1.18	853.33	32.80−6302.00	1360.97	1.59
Co (mg/kg)	0.58	0.01−1.88	0.48	0.82	0.60	0.01−4.80	0.88	1.48
Cu (mg/kg)	2.28	0.74−5.75	1.22	0.54	2.85	0.24−5.52	1.40	0.49
Fe (mg/kg)	138.45	12.10−236.10	52.13	0.38	255.50	85.10−506.00	117.78	0.46
K (mg/kg)	107.18	6.87−313.80	71.69	0.67	395.29	73.20−1002.20	213.11	0.54
Mg (mg/kg)	205.98	17.60−885.00	182.76	0.89	394.76	32.20−1430.20	319.84	0.81
Mn (mg/kg)	111.06	4.50−365.10	88.20	0.79	69.21	2.21−477.00	111.20	1.61
Na (mg/kg)	230.88	131.90−475.20	75.89	0.33	207.91	0.31−906.90	262.55	1.26
Ni (mg/kg)	0.98	0.02−3.44	0.86	0.88	1.57	0.18−3.71	0.85	0.54

Table 5.1 (continued).

	Amazonian rainforests				Andean rainforests			
Variables	Mean	Range	SD	CV	Mean	Range	SD	CV
P (mg/kg)	29.75	5.75−119.80	21.56	0.72	86.07	2.54−383.80	86.38	1.00
Zn (mg/kg)	4.01	0.36−19.20	5.19	1.29	12.81	1.14−44.30	9.49	0.74
BIO1	234.98	220−249	9.51	0.04	172.48	124−210	27.15	0.16
BIO2	105.61	104−110	2.08	0.02	112.41	92−128	11.54	0.10
BIO3	70.48	68−72	1.23	0.02	72.83	71−74	0.82	0.01
BIO4	1298	1188−1542	112.37	0.09	1062.02	914−1260	94.42	0.09
BIO5	305.64	290−324	10.79	0.04	243.13	199−276	22.92	0.09
BIO6	156.84	145−167	7.15	0.05	89.67	25−142	37.94	0.42
BIO7	148.80	144−161	5.62	0.04	153.46	127−177	16.06	0.10
BIO8	244.48	228−261	10.90	0.04	179.94	132−220	28.04	0.16
BIO9	217.73	202−236	11.01	0.05	157.76	106−194	27.04	0.17
BIO10	246.66	232−263	10.03	0.04	182.76	135−221	27.33	0.15
BIO11	215.18	201−226	8.48	0.04	156.02	106−192	26.56	0.17
BIO12	1878.32	1769−1965	63.51	0.03	1264.20	892−1572	224.92	0.18
BIO13	287.00	271−304	10.03	0.03	229.67	199−263	22.02	0.10
BIO14	63.89	57−72	4.46	0.07	16.61	8−36	8.02	0.48
BIO15	51.16	48−53	1.60	0.03	68.50	54−84	9.04	0.13
BIO16	795.95	756−834	24.68	0.03	619.98	491−730	74.55	0.12
BIO17	204.68	175−231	17.63	0.09	73.98	38−138	28.96	0.39
BIO18	599.11	543−805	92.60	0.15	418.69	255−513	88.46	0.21
BIO19	231.09	198−264	21.32	0.09	79.83	50−147	27.15	0.34

Data analysis

Quantification of commonness and delimitation of oligarchic species

We calculated species commonness based on a modified version of the *h* index, a widely known bibliometric tool for measuring academic performance (Hirsch 2005). We assigned to each species a commonness proportional *h* index (h_p), and separeted the common species from the uncommon species with the h_h criterion, which were presented in detail in the previous chapter (Chapter 4).

Niche breadth calculation

For each species i, we calculated the niche breadth along each environmental variable k, separately. To do so, we extended the niche breath measure of Smith (1982) to continuous variables. The niche breath measure of Smith (1982) is based on the differential use of *R* different states of the resource *k* by a given species *i* and is calculated as follows:

$$NB_i = \sum_{j=1}^{R} \sqrt{p_j q_j}$$

where NB_i is the niche breadth of the species i, p_j is the proportion of the resource state j available for use (among the *R* different resource states), and q_j is the proportion of times that the species *i* is observed to use the resource state *j*.

To spread from a discrete suite of *R* states of a given resource to a continuous measure of the resource distribution, we estimated the probability density function of each environmental variable *k* by applying a Gaussian kernel to the observed distribution of values of *k*. This is denoted as $f(k)$. Similarly, and with the same kernel parameters, we estimated the probability density function of the occurrence of the species *i* along the environmental variable *k*. This is denoted as $g(i_k)$. Finally, we calculated the niche breadth of the species *i* for the environmental variable *k* (NB_{ik}) as the overlapping between $f(k)$ and $g(i_k)$:

$$NB_{ik} = \int_{min(k)}^{max(k)} \sqrt{f(k)g(i_k)}$$

The measure takes values between zero and one. The values close to one indicate that the species is insensitive to the environmental conditions. Values close to zero correspond to those species that appear only in very specific and rare conditions.

After computing the niche breadth of all species along each of the environmental variables, we obtained a measure of total niche size (NB_T) for each species. To do that, we repeated all the previously mentioned calculations but used the orthogonal axes from a principal component analysis (PCA) instead of the original environmental variables. This PCA describes an n-dimensional hypervolume in which the dimensions are resources along which the organisms interact with the environment, hence representing the Hutchinsonian realized niche (Hutchinson 1957, Devictor et al. 2010). Finally, the total niche size of each species (total hypervolume) was calculated as the product of all niche breadths along all possible (orthogonal) directions: $NB_T = \prod_{i=1}^{n} NB_i$; n being the number of PCA axes.

Oligarchy and niche breadth

At each forest type, we analyzed the relationship between h_p indexes of species and their total niche size NB_T with Pearson correlations. We repeated the analysis for each environmental variable k by comparing h_p with NB_k. To compare the niche breadth of oligarchic *vs.* non-oligarchic species we performed Kolmogorov-Smirnov tests for NB_T and NB_k along each of the environmental variables. We applied the Bonferroni correction for multiple comparisons to minimize the false-discovery rate.

Amazonian vs. *Andean oligarchies*

To determine if the homogeneous Amazonian rainforests harbor stronger oligarchies than the Andean rainforests, we (1) compared their h_h indexes and (2) compared the h_p indexes of each forests' oligarchic species with Mann-Whitney *U* tests. To determine if the niche breadths of Amazonian oligarchic species are broader than the niche breadths of Andean oligarchic species, we (1) compared the NB_T indexes of each forests' oligarchic species with Mann-Whitney *U* tests and (2) repeated this analysis for NB_k along each environmental variable k individually, applying a Bonferroni correction. Finally, to check the assumption that there are more heterogeneous environmental conditions in Andean rainforests than in Amazonian forest we calculated the coefficient of variation (CV) for each variable k in both forest types.

All calculations and analysis were performed for each forest type separately using R 2.15.1 GUI 1.52 (R Development Core Team and R Core Team 2012). The level of significance for all analyses was 0.05.

RESULTS

Floristic data

A total of 31,519 individuals belonging to 1,518 species of trees and lianas with ≥2.5 cm of dbh were recorded in 98 0.1-ha plots. In the Amazonian region, 808 species were found in 44 plots (12,642 individuals), whereas in the Andean region 877 species were found in 54 plots (18,876 individuals).

Oligarchy and niche breadth

We found a positive and significant correlation between the total niche size and dominance of Amazonian species (Pearson $r = 0.57$; $P < 0.001$) and Andean species ($r = 0.53$; $P < 0.001$) (Fig. 5.2). We found the same trend for most of the environmental variables, except BIO4 and BIO15 (temperature seasonality and precipitation seasonality), although often with weaker correlations in the case of climatic variables and in the Andean rainforests (Table 5.2). For both forest types, the relationship between species dominance and the niche breadth measure along every edaphic variable was always positive and statistically highly significant.

Table 5.2. Results of Pearson correlations (r) between niche breath measure along individual environmental variables and species dominance (h_p index) as recorded in 98 0.1-ha plots of Amazonian and Andean tropical rainforests in northwestern Bolivia. The bioclimatic codes follow Hijmans et al. (2005) (www.worldclim.org/bioclim). The significance was assessed using Bonferroni-corrected P-values: ***: $P < 0.001$; **: $P < 0.01$; * $P < 0.05$.

Variables	r (Amazonian)	r (Andean)
Elevation	0.14*	−0.082
Slope	0.27***	0.331***
Northness	0.31***	0.384***
Eastness	0.31***	0.427***
pH (H_2O)	0.17***	0.260***
pH (KCl)	0.17***	0.218***
Organic C	0.22***	0.163***
Total C	0.20***	0.195***
Total N	0.23***	0.248***
Total S	0.21***	0.263***
Al	0.20***	0.347***
Ca	0.23***	0.259***
Co	0.25***	0.278***
Cu	0.27***	0.383***
Fe	0.21***	0.331***

Table 5.2 (continued).

Variables	*r* (Amazonian)	*r* (Andean)
K	0.21***	0.208***
Mg	0.27***	0.290***
Mn	0.25***	0.300***
Na	0.26***	0.230***
Ni	0.29***	0.297***
P	0.27***	0.232***
Zn	0.28***	0.249***
BIO1	0.14**	−0.056
BIO2	0.15***	0.125*
BIO3	0.14**	0.231***
BIO4	0.10	0.031
BIO5	0.14**	−0.049
BIO6	0.12*	−0.046
BIO7	0.17***	0.177***
BIO8	0.14**	−0.061
BIO9	0.14**	−0.056
BIO10	0.13*	−0.062
BIO11	0.14**	−0.05
BIO12	0.15**	0.131**
BIO13	0.16**	0.287***
BIO14	0.13*	−0.016
BIO15	0.08	−0.006
BIO16	0.15**	0.245***
BIO17	0.16**	−0.013
BIO18	0.13*	0.028
BIO19	0.16***	−0.039

The total niche size of oligarchic species was significantly greater than the total niche size of non-oligarchic species, both in Amazonian rainforests (Kolmogorov-Smirnov $D = 0.68$; $P < 0.001$) and in Andean rainforests ($D = 0.73$; $P < 0.001$). When compared with the niche breadths along each of the environmental variables, we found that the niches of oligarchic species were systematically greater than the niches of the non-oligarchic species (Table 5.3). The only exceptions were in Andean rainforests along elevational gradients and seven climatic variables (BIO1, BIO5, BIO6, BIO8−BIO11: annual mean temperature, maximum temperature of warmest month, minimum temperature of coldest month, and mean temperatures of the wettest, driest, warmest and coldest quarters), for which the differences were not statistically significant. In the case of Amazonian rainforests, all environmental variables were statistically significant.

Table 5.3. Results of Kolmogorov-Smirnov tests (*D*) comparing the niche breadth measure along individual environmental variables of oligarchic *vs.* non-oligarchic species as recorded in 98 0.1-ha plots of Amazonian and Andean tropical rainforests in northwestern Bolivia. In all the significant cases, the niche breadths of oligarchic species were greater than the niche breadth of non-oligarchic species. The bioclimatic codes follow the codes of Hijmans et al. (2005) (www.worldclim.org/bioclim). The significance was assessed using Bonferroni-corrected *P*-values: ***: $P < 0.001$; **: $P < 0.01$; * $P < 0.05$.

Variables	*D* (Amazonian)	*D* (Andean)
Elevation	0.26***	0.130
Slope	0.47***	0.530***
Northness	0.57***	0.464***
Eastness	0.58***	0.642***
pH (H_2O)	0.31***	0.271***
pH (KCl)	0.29***	0.345***
Organic C	0.35***	0.368***
Total C	0.30***	0.407***
Total N	0.40***	0.504***
Total S	0.39***	0.518***
Al	0.35***	0.462***
Ca	0.42***	0.473***
Co	0.48***	0.536***
Cu	0.43***	0.619***
Fe	0.50***	0.542***
K	0.27***	0.428***
Mg	0.42***	0.532***
Mn	0.49***	0.495***
Na	0.53***	0.295***
Ni	0.48***	0.536***
P	0.46***	0.466***
Zn	0.38***	0.511***
BIO1	0.26***	0.123
BIO2	0.37***	0.248***
BIO3	0.44***	0.370***
BIO4	0.21*	0.283***
BIO5	0.26***	0.135
BIO6	0.26***	0.106
BIO7	0.42***	0.237***
BIO8	0.25***	0.123
BIO9	0.25***	0.125
BIO10	0.26***	0.123
BIO11	0.26***	0.123
BIO12	0.25**	0.321***
BIO13	0.25***	0.345***
BIO14	0.31***	0.208***
BIO15	0.25***	0.278***
BIO16	0.22**	0.405***
BIO17	0.29***	0.245***
BIO18	0.31***	0.293***
BIO19	0.16***	−0.039

Amazonian vs. *Andean oligarchies*

In Amazonian rainforests, we identified 115 oligarchic species out of 808 (h_h = 0.14), of which *Rinorea viridifolia* (h_p = 15.91%), *Iriartea deltoidea* and *Rinorea apiculata* (both h_p = 11.36%) showed the highest dominance (Fig. 5.2). In Andean rainforests, we identified 175 oligarchic species out of 877 (h_h = 0.20), of which *Clusia sphaerocarpa* (h_p = 9.26%), *Myrsine coriacea* and *Psychotria carthagenensis* (both h_p = 7.41%) showed the highest dominance. The mean h_p index of commonness for Amazonian oligarchic species was 3.12%, and 2.98% for Andean oligarchic species; these differences were highly significant (Mann-Whitney $U = 13397$; $P < 0.001$).

The average of the total niche size was twofold greater in Amazonian oligarchies (mean NB_T = 0.26) than in Andean oligarchies (mean NB_T = 0.13), and the difference was statistically highly significant (Mann-Whitney $U = 12823$; $P < 0.001$). When particular niche breadths were analyzed along each of the environmental variables, lowland and montane oligarchies did not show significant differences in their niche breadths along half of the environmental variables (Table 5.4). Concerning the climatic variables, Amazonian and Andean oligarchies differed significantly in their niche breadths along 10 out of 19 climatic variables. Amazonian oligarchies showed significantly broader niches than Andean oligarchies for BIO1, BIO2 and BIO7 (annual mean temperature, mean diurnal range and annual temperature range). In turn, Andean oligarchies showed significantly broader niches than Amazonian oligarchies for BIO5, BIO11, BIO12, BIO14, BIO16, BIO17 and BIO19 (maximum temperature of warmest month, mean temperature of coldest quarter, annual precipitation, precipitation of driest month, and precipitation of wettest, driest and coldest quarters).

Concerning the soil variables, Amazonian and Andean oligarchies differed significantly in their niche breadths along 9 out of 18 edaphic variables (Table 5.4). Amazonian oligarchies showed significantly broader niches than Andean oligarchies for some extractable elements (Co, Fe, Mn, Na) but significantly narrower niches along organic C, total C, total N, total S and extractable K contents. Concerning topographic variables, Amazonian oligarchies showed statistically significant broader niches than Andean oligarchies along the northness aspect. The results for elevation, slope and eastness aspect were not statistically significant.

The coefficients of variation showed that Andean rainforests were more heterogeneous overall than Amazonian rainforests and particularly for the climatic and topographic variables, except for isothermality (BIO3) and slope (Table 5.4). Furthermore, montane soils were more heterogeneous for the P, Ca, Fe, Co, and especially Mn and Na extractable contents. However, the Amazonian soils showed greater heterogeneity in pH, organic C, total C, total N, total S, and extractable Al, Cu, K, Mg, Ni and Zn contents.

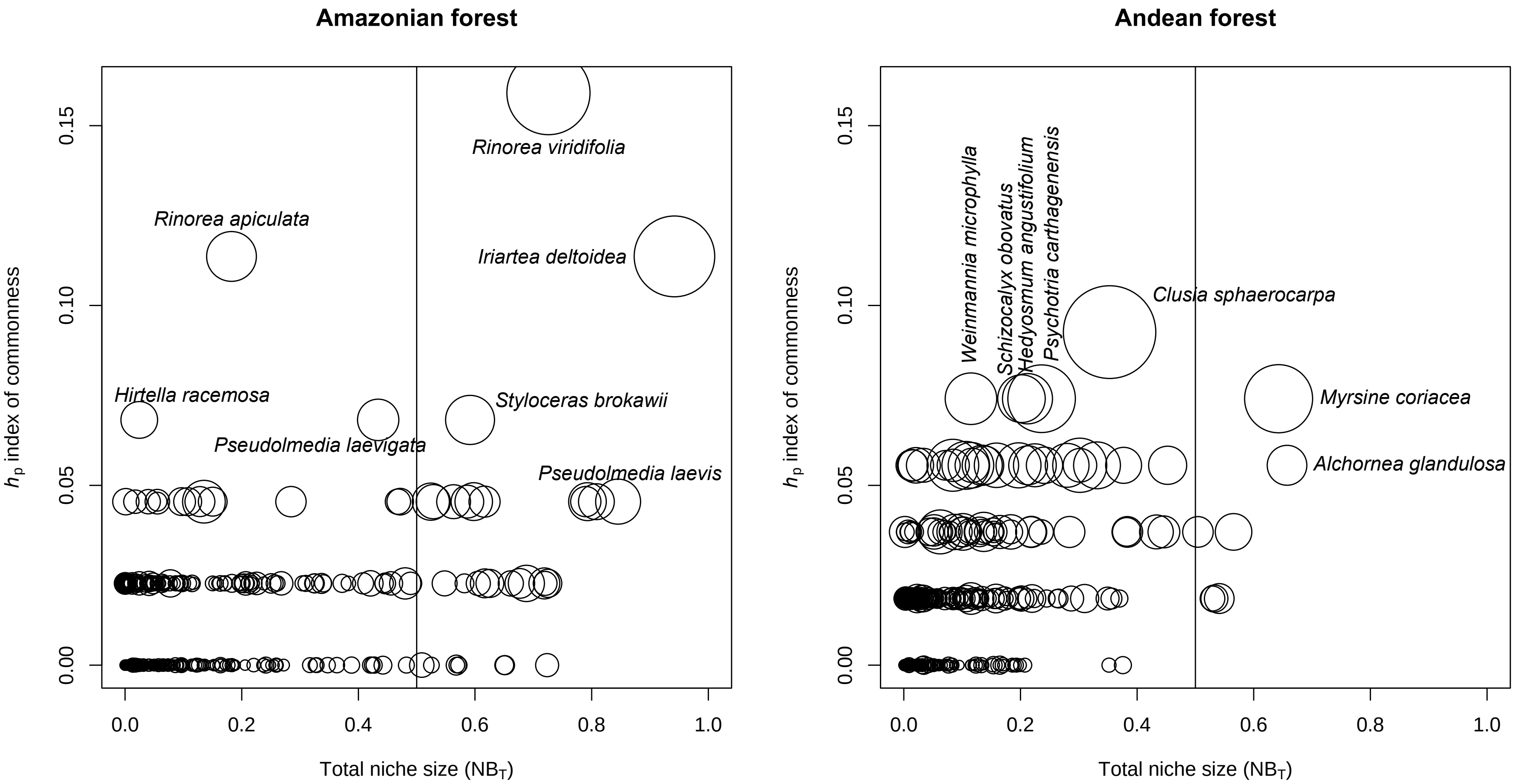

Figure 5.2. Total niche size (NB_T) *vs.* the h_p index of commonness combining local abundance and landscape frequency for all species recorded in 98 0.1-ha plots of Amazonian (n = 808) and Andean tropical montane rainforests (n = 877) in northwestern Bolivia. The vertical line indicates an arbitrary threshold between specialist and generalist species (0.5). The circle size is proportional to the total number of individuals in each type of forest.

Table 5.4. Results of Mann-Whitney *U* tests comparing the niche breadth measure along individual environmental variables of Amazonian and Andean oligarchic species as recorded in 98 0.1-ha plots in northwestern Bolivia. A measure of environmental heterogeneity for each variable and forest type is also presented. The bioclimatic codes follow the codes of Hijmans et al. (2005) (www.worldclim.org/bioclim). The significance was assessed using Bonferroni-corrected *P*-values: ***: $P < 0.001$; **: $P < 0.01$; * $P < 0.05$; n.s.: not significant.

Environmental variables (*k*)	Comparison of niche breadth (NB_k)	*U*	Environmental heterogeneity (CV_k)†		
			Amazonian	*vs.*	Andean
Elevation	n.s.	9130	789 m	<	1974 m
Slope	n.s.	8859	0.57	>	0.33
Northness	Amazonian > Andean	12987**	4.54	<	7.43
Eastness	n.s.	12041	18.13	<	161.43
pH (H_2O)	n.s.	10032	0.21	>	0.15
pH (KCl)	n.s.	9672	0.247	<	0.253
Organic C	Andean > Amazonian	4689***	1.05	>	0.38
Total C	Andean > Amazonian	3800***	1.07	>	0.37
Total N	Andean > Amazonian	2575***	0.83	>	0.31
Total S	Andean > Amazonian	1081***	0.76	>	0.34
Al	n.s.	9732	0.76	>	0.30
Ca	n.s.	11888	1.18	<	1.59
Co	Amazonian > Andean	12651**	0.82	<	1.48
Cu	n.s.	8968	0.54	>	0.49
Fe	Amazonian > Andean	7640*	0.38	<	0.46
K	Andean > Amazonian	5397***	0.67	>	0.54
Mg	n.s.	11787	0.89	>	0.81
Mn	Amazonian > Andean	12607*	0.79	<	1.61
Na	Amazonian > Andean	14384***	0.33	<	1.26

Table 5.4 (continued).

Environmental variables (*k*)	Comparison of niche breadth (NB_k)	*U*	Environmental heterogeneity (CV_k)[†]		
			Amazonian	*vs.*	Andean
Ni	n.s.	10497	0.88	>	0.54
P	n.s.	10461	0.72	<	1.00
Zn	n.s.	8463	1.29	>	0.74
BIO1	Amazonian > Andean	7783*	0.04	<	0.16
BIO2	Amazonian > Andean	15376***	0.02	<	0.10
BIO3	n.s.	11656	0.02	>	0.01
BIO4	n.s.	8728	0.087	<	0.089
BIO5	Andean > Amazonian	7171**	0.04	<	0.09
BIO6	n.s.	8314	0.05	<	0.42
BIO7	Amazonian > Andean	15905***	0.04	<	0.10
BIO8	n.s.	8230	0.04	<	0.16
BIO9	n.s.	8074	0.05	<	0.17
BIO10	n.s.	8230	0.04	<	0.15
BIO11	Andean > Amazonian	7213**	0.04	<	0.17
BIO12	Andean > Amazonian	4465***	0.03	<	0.18
BIO13	n.s.	8550	0.03	<	0.10
BIO14	Andean > Amazonian	5903***	0.07	<	0.48
BIO15	n.s.	8412	0.03	<	0.13
BIO16	Andean > Amazonian	5531***	0.03	<	0.12
BIO17	Andean > Amazonian	6017***	0.09	<	0.39
BIO18	n.s.	8253	0.15	<	0.21
BIO19	Andean > Amazonian	7679*	0.09	<	0.34

† All values are coefficients of variation except those for the elevation, which are ranges.

DISCUSSION

The NBH considering the total niche size

Oligarchic species have broader niche breadths than the other species that constitute the community assembly in Amazonian and Andean rainforests, and the niche breadth of any species tends to be positively correlated with its degree of dominance. The consistency of both results supports the NBH in tropical rainforests. This is in agreement with studies indicating that common species tend to be present at two or more habitat types (Pitman et al. 1999, Macía and Svenning 2005) and that widespread species show broad environmental tolerances (Davidar et al. 2008, Slatyer et al. 2013). However, this is in contrast with other Amazonian studies that were more focused on a family or genus, which found that broad tolerance to topographical or edaphic gradients did not affect the local abundances of palms (Kristiansen et al. 2009) or understory plants, such as Melastomataceae*,* Pteridophyta (Tuomisto et al. 2003) and *Psychotria* species (Kinupp and Magnusson 2005). That these latter works found no support for the NBH may be explained by the fact that these typically understory plants or low-stature trees tend to have a narrower ecological tolerance and stronger turnover compared to larger species, likely because of their more limited dispersal abilities (Ruokolainen and Vormisto 2000, Duque et al. 2002, Chust et al. 2006, Davidar et al. 2008).

The finding that most species, even many oligarchic species, show total niche sizes <0.5 is in agreement with previous studies which found that floristic differences were equally well explained for common and rare species by edaphic differences (Tuomisto et al. 2003, Ruokolainen et al. 2007). Even if common trees dominate the forest in some circumstances, they are not necessarily indifferent to environmental heterogeneity (Phillips et al. 2003, Kristiansen et al. 2012). In fact, different patterns can be recognized among oligarchic species, and most of them represent a mixture of narrow-niched dominant species (*e.g., Hirtella racemosa* and *R. apiculata* in Amazonia or *Weinmannia microphylla* and *Schizocalyx obovatus* in the Andes) and very broad generalists (*e.g., I. deltoidea* and *Pseudolmedia laevis* in Amazonia or *M. coriacea* and *Alchornea glandulosa* in the Andes) occupying different habitats. This is congruent with previous studies, as several authors have reported that both types of species constitute the regional oligarchies (Pitman et al. 2001, 2013, Paoli et al. 2006, Macía 2008, 2011, Honorio Coronado et al. 2009). Remarkably, the broad-niched oligarchic species found here were also reported in the cited studies for northwestern Amazonia, among many other studies (*e.g.,* Duque et al., 2002, 2009; Valencia et al., 2004; Toledo et al., 2012). For example, the most broad-niched species among the 1,518 species studied here is the palm *I. deltoidea*, possibly the oligarchic species most consistently reported in different regions in northwestern Amazonia.

Therefore, broad-niched oligarchic species could constitute the common set of oligarchs between different Amazonian regions at a very large or continental scale (Pitman et al. 2001, 2013, Macía and Svenning 2005), whereas more specialized oligarchic species would be predominantly present at scales on the order of 10,000 km^2. This is in agreement with recent studies reporting that a positive relationship between niche breadth and geographical range is a general ecological pattern (Slatyer et al., 2013). Hence, it is clear that niche size plays a significant role in the consistency of commonness patterns across scales, linking local abundance, landscape frequency and geographical range size, as hypothesized by Brown (1984). Unfortunately, such conclusions cannot be directly applied to the Andean rainforests, given the absence of previous works addressing oligarchy in this ecoregion.

The NBH considering particular environmental variables

The broader edaphic niches of oligarchic species and the significant correlations between dominance and niche breadth along all edaphic variables reinforce the idea that the tolerance to different soil conditions is an important driver of large-scale dominance, as suggested for Amazonian rainforests (Pitman et al. 2001), but can be applied for Andean rainforests as well. However, the results are not as conclusive for the climatic variables (included elevation) in the Andean forest, where the niche breadth of oligarchic species seems to be similar to those of the rest of the species. This could be explained by rare species showing relatively broad climatic niches inherited from the relatively climatic generalist taxa that are assumed to have colonized the Andes during its uplift (Ricklefs and Cox 1972, Frey et al. 2007). Such niche conservatism for the climatic niche dimensions could be more intense than for the edaphic dimensions, along which adaptations usually occur between close-related taxa (Wright 2002, Fine et al. 2005, Kembel and Hubbell 2006, Paoli et al. 2006, Wiens et al. 2010, Hardy et al. 2012). However, the causes underlying this lack of differences between common and rare species with respect to climatic factors in the Andes deserve further research.

Amazonian* vs. *Andean rainforests

Amazonian rainforests showed stronger and much more generalist oligarchic species than Andean rainforests when the total niche size was considered. This could be explained by a greater environmental homogeneity in Amazonia overall, which is congruent with previous works that reported weak or absent oligarchic species under heterogeneous environmental conditions (Tuomisto et al. 2003, Pitman et al. 2008, Réjou-Méchain et al. 2008, Toledo et al. 2011, 2012). As expected, a similar pattern was found for several edaphic variables (Co, Fe, Mn and Na), for which Amazonian rainforests are more homogeneous and Amazonian oligarchic species present broader niches than Andean oligarchs. However, contrary to our expectation, we found that Amazonian soils are more heterogeneous than Andean soils with respect to those variables in relation to the organic matter content (organic C, total C, N, S and extractable K), with narrower niches of Amazonian oligarchic species along these variables. This is most likely caused by the relatively high organic soils of many plots inventoried in the upper limit of the Amazonian rainforests, which also contain a different set of oligarchic species than those oligarchics present on lower plots with 5 to 10 times less organic matter. The inclusion of such a source of edaphic and floristic heterogeneity within the Amazonian dataset is a potential caveat to extrapolate our results to other Amazonian rainforests of more homogeneous conditions (*e.g.,* Pitman et al. 1999, 2001). Nevertheless, it holds that oligarchic species present relatively narrow niches on soil factors if measured along wide gradients regardless of the forest type studied.

Concerning the climatic results, the Andean rainforests show a much more heterogeneous climate than the Amazonian rainforests, as expected for the greater elevational gradient covered. However, and contrary to expectation, Andean oligarchs do not show systematically narrower climatic niches than Amazonian oligarchic species. In fact, this only happens for the annual mean temperature (BIO1) and two thermic variables for which the niche breadth is of rather difficult interpretation: mean diurnal range (BIO2) and temperature annual range (BIO7). For seven other climatic variables (BIO5, BIO11, BIO12, BIO14, BIO16, BIO17 and BIO19), of which five are related to precipitation, the Amazonian oligarchs show narrower niches than the Andean oligarchs, even when measured along a narrower range of conditions. This implies that Andean oligarchic species show a thermic (elevational) zonation along a very wide gradient, which is compatible with a lower sensitivity to climatic conditions than Amazonian oligarchs. As mentioned above, previous authors have proposed that montane floras could be largely composed of climatic-generalists (Stevens 1992, Ghalambor et al. 2006, Frey et al. 2007, Laurance et al. 2011), but the mechanisms involved require further research.

Finally, given that common species constitute the assemblage of forest communities, represent a high number of individuals and are involved in large numbers of biotic interactions (Gaston and Fuller 2008, Gaston 2010), further studies should be focused on understanding the distribution patterns of these species in different forest types and analyzing their responses to different environmental variables; the results could shed light on the management and conservation of tropical rainforests.

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CAPÍTULO 6

Potential determinants of rarity and commonness of woody plants in different types of tropical forests

Este capítulo se ha desarrollado en colaboración con M. I. Loza, L. E. Cayola, A. F. Fuentes, A. Araújo-Murakami, M. Cornejo, W. V. Torrez, J. M. Quisbert, T. B. Miranda, P. M. Jørgensen y M. J. Macía. Forma parte de un manuscrito pendiente de envío a *Ecology*.

ABSTRACT

The present study asks whether local commonness of species is correlated with their landscape commonness, and whether local and landscape patterns of rarity and commonness are related to morphological traits (height, diameter, number of stems, habit). We analysed six different forest types, including dry, Amazonian, lower montane, intermediate montane, upper montane and high Andean forests, along a 3600 m elevation gradient in the Bolivian Andes (Madidi region). We inventoried ~129,000 individuals of ~2500 species, distributed among 407 plots. We found a positive relationship between commonness at local and landscape scales in all forest types. The plant diameter and plant height were generally correlated to the local and landscape commonness, but the number of stems were not. We also found that the apportioning of species into rarity classes depend greatly on the species habit. Two conclusions arise from the study: (1) simple approaches based only on abundance, or occurrence could summarize most of the relevant information to characterize species rarity and commonness; and (2) rarity and commonness patterns are the result of non-neutral trait-based community assembly processes. Both results have important implications in how we understand and manage tropical forests.

Keywords: Landscape dominance, local dominance, oligarchy, Rabinowitz's classification, tropical lianas, tropical trees

INTRODUCTION

Rarity and commonness have attracted the attention of naturalists during decades (*e.g.,* Preston 1948, Rabinowitz 1981, Gaston 1994, 2010, 2012). Some authors even have defined ecology as the study of rarity and commonness among and within species (Kelly et al. 1996). Such important issue has been addressed for many different ecosystems and with very different approaches. Among them, it outstands the consideration of rarity and commonness at different scales or ecological dimensions, which signified a major advance in the study of rarity and commonness patterns of species (Hanski 1982, Brown 1984, Rabinowitz et al. 1986, Pitman et al. 1999, 2001, Kristiansen et al. 2009). Therefore, the abundance of a species in a sample, the frequency with which that species appears across a given region, or the geographical range of the species, would be measures of commonness at different scales (Gaston 1994).

The species can be classified along these and others relevant ecological dimensions, such as the variety of habitats where the species appear, to distinguish different classes of rarity (Rabinowitz 1981, Rabinowitz et al. 1986). Regarding tropical forests, Pitman et al. (1999, 2001) were the first to apply a multi-dimensional approach to rarity and commonness at regional and continental scales. Their most outstanding result was the oligarchy hypothesis, which states that Amazonian forests are dominated by a defined set of locally abundant and widespread species (Pitman et al. 2001). The hypothesis is compatible with the existence of many rare species, and has gathered ample support for different forest types in the Neo and Paleotropics (Pitman et al. 2013).

Beyond the observed patterns, there exists some knowledge about the traits of those species that dominate at different scales or that present different rarity types. First, it is known that the plant size (especially plant height) is assumed to have greater long-dispersal abilities and have been found to be more widely distributed at regional and continental scales in tropical forests (Ruokolainen and Vormisto 2000, Davidar et al. 2008, Kristiansen et al. 2009). Taller species also have the advantage to intercept more light (Wright et al. 2007) and tend to be positively correlated with the maximum diameter, the seed size and reproductive success among species (Westoby et al. 2002, Moles and Westoby 2004, Moles et al. 2004, Wright et al. 2007). Therefore, large species would be also capable to be locally common, because to greater seed release and fecundity (Nathan and Muller-Landau 2000, Aarssen et al. 2006, Kristiansen et al. 2009). Second, the habit may influence the rarity and commonness patterns, or the differences among different environments. By definition, forests are characterized by preponderance of the tree habit. However, liana species are known to attain greater abundance than other species when gap disturbance is present, because liana species sprout easily, show intense vegetative growth and have a suite of other structural and physiological adaptations to disturbance (Schnitzer and Bongers 2002, Pérez-Salicrup et al. 2004, Letcher and Chazdon 2012). Shrubs play an important role in the tropical forest communities mostly at high elevations, where having multiple stems is an advantageous adaptation to low productivity levels and high frequency of disturbances due to steeper slopes (Bellingham and Sparrow 2000, 2009).

The present work explores the relationships between local commonness, landscape commonness, rarity classes and species traits within a 200 × 200 km region that includes dry and wet tropical forests along a *c*. 3600 m elevation gradient, in North-western Bolivia. Specifically, we aim to answer the following questions: (1) Do different forest types show the same apportioning of species into different rarity classes? (2) Is local-scale commonness of species correlated with landscape-scale commonness within each forest type? (3) Are species traits (plant height, plant diameter, number of stems, habit) related to commonness at some scale and/or to certain rarity classes within each forest type?

METHODS

Study region and sampling design

We carried out extensive standardized floristic inventories in the Madidi region, located on the eastern slopes of the Bolivian Andes, between latitude −12.43º and −15.72º and longitude −69.48º and −66.66º. It includes mature forests from the Amazon to the forest limit, *c*. 4000 m. The study region contains different broad forest types, included tropical dry forests (lack of precipitation for 4–5 months per year) and tropical wet forests (>2000 mm of annual precipitation) along the whole elevation gradient (Navarro et al. 2004, Fuentes 2005).

We inventoried 128,970 plant individuals through the establishment of 407 plots of 0.1-ha (20 × 50 m). The plots were distributed among six different forest types: 82 plots were inventoried in semideciduous dry forest (DR; ranging from 650 to 1350 m); 92 in lowland Amazonian forest (AM; from 250 to 1000 m); 102 in lower montane forest (LM, from 1000 to 1700 m); 64 in intermediate montane forest (IM, from 1700 to 2400 m); 38 in upper montane forest (UM, from 2400 to 3100 m); and 29 in high Andean forest (HA; from 3100 o 3800 m) (see Fig. 1.1).

Floristic data

All plots were installed avoiding big gaps and recent human disturbance. At each plot, we inventoried all woody plant individuals rooting within the plot limits with at least one stem with diameter at breast height equal or greater to 2.5 cm at 130 cm from the rooting point ("diameter at breast height", dbh). For each individual, we measured and counted all stems with dbh ≥ 2.5 cm, and estimated the height reached by each individual. All species were collected at least once, and all individuals were identified to a valid species name or assigned to a morphospecies ("species" in the following). Extensive taxonomic work was conducted during 2010 at Herbario Nacional de Bolivia to ensure that all species names were standardized across all plots. Less than 3.5% of individuals were excluded from the analysis because they were sterile specimens that could not be identified to species level, neither assigned to a reliable morphospecies. Voucher specimens are kept in the LPB and MO herbaria (acronyms according to Thiers 2012). All plot characteristics, floristic inventories, and information on voucher specimens are available to query in the TROPICOS database (www.tropicos.org/PlotSearch.aspx?projectid=20).

Plant traits

We calculated four morphological traits for each species:

(1) The *maximum height* of each species was estimated as the 95th percentile of the heights of all the individuals of that species found in the region. To do so, we considered our own dataset of 407 0.1-ha plots and an external inventory of 48 1-ha plots with a cut-off of 10 cm of dbh in the same region (data stored in the same TROPICOS repository).

(2) The *maximum diameter* of each species was estimated as the 95th percentile of the diameters of all the individuals of that species found in the two datasets mentioned above.

(3) The *mean number of stems* by species, considering the individuals in the 0.1-ha plots.

(4) The *habit* in four categories: (a) lianas: species with at least half of the individuals annotated with this life form in the field; (b) canopy trees: self-standing species with maximum diameter ≥10 cm; (c) treelets: self-standing species with maximum diameter <10 cm and whose individuals never presented multiple stems; and (d) shrubs: self-standing species with maximum diameter <10 cm and presented multiple stems. We excluded 14 hemiepiphytes species because were too rare for meaningful analysis. Arecaceae, woody Pterydophyta, woody Cactaceae and woody Poaceae contained relatively few species and therefore were included within tree, treelet, or shrub categories to facilitate analyses interpretation, although they are not properly trees.

Once the traits were calculated for each species, all subsequent analyses were performed separately for each forest type (DR, AM, LM, IM, UM and HA forests).

Rarity and commonness measures

For each forest type and species, we calculated commonness at local and landscape scales as follows: (1) local commonness was measured as the maximum local abundance attained by a species in a given forest type; (2) landscape commonness was measured as the proportion of plots within a given forest type where the species was present.

We calculated four rarity classes by combining commonness at both scales: (1) rare species were those present in less than 5% of the plots of a given forest type, with always <5 individuals in any plot; (2) abundant-but-infrequent species were those whose maximum abundance was ≥5 individuals, but that were present in less than 5% of the plots of a given forest type; (3) frequent-but-scarce species were those species present in at least 5% of the plots in a given forest type but that were present always with <5 individuals in any plot; and (4) common species were those present in at least 5% of the plots in a given forest type and whose maximum abundance was ≥5 individuals.

Statistical analysis

To study the relationship between local commonness and landscape commonness we performed Pearson correlations between maximum local abundance and landscape frequency of species.

To understand how species traits relate with commonness at both local scale and landscape scale, we conducted Pearson correlations between maximum local abundance, landscape frequency and maximum height, maximum diameter and number of stems, respectively. The relationship between habit and the maximum local abundance and landscape frequency was tested with ANOVA tests followed by Bonferroni-corrected Tukey-Kramer post-hoc tests.

We also performed ANOVA and Tukey-Kramer tests to understand how quantitative traits (maximum height, maximum diameter, and number of stems) relate with the four rarity classes. To find how habit relates with different rarity classes, we performed *G*-tests, followed by post-hoc binomial tests to assess for significant deviations within each category of rarity and habit. Post-hoc binomial tests calculate, for each forest type, habit and rarity class, the conditional probability $p(O|E)$, where O is the observed number of species of one habit in one rarity class (for example, rare lianas in Amazonia) and E is the expected number of species of that habit in that rarity class, as computed for the *G*-test. The Bonferroni-corrected $p(O|E)$ was employed as the P value for the post-hoc tests. All calculations and analyses were performed with R (R Development Core Team and R Core Team 2012). The level of significance for all analyses was 0.05.

RESULTS

General results

More than 60% of the species were canopy trees across all forest types with the only exception of the AM forest (Fig. 6.1). The proportion of shrub species increased at higher elevations, whereas the proportion of liana and treelet species decreased with elevation.

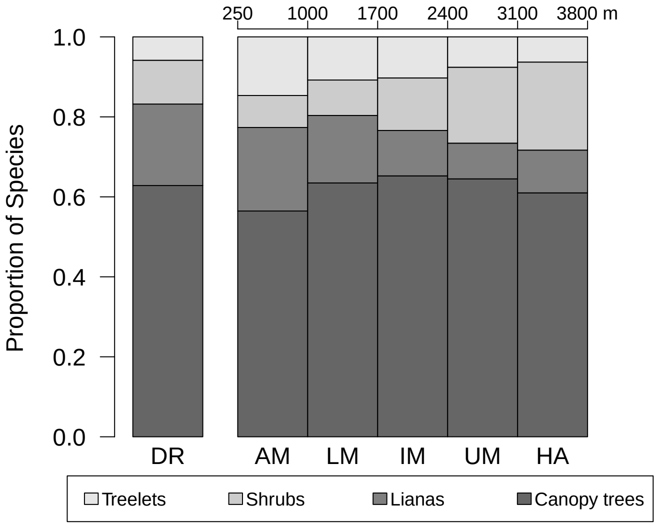

Figure 6.1. Proportion of species belonging to different habits in six tropical forest types in northern Bolivia: dry forest (DR, 394 species), lowland Amazonian forest (AM, 1099 species), lower montane forest (LM, 1201 species), intermediate montane forest (IM, 732 species), upper montane forest (UM, 371 species) and high Andean forest (HA, 160 species).

Rarity classification and relationship between local commonness and landscape commonness

There was a significant and positive relationship between maximum abundance and landscape frequency of species in the six forest types (Fig. 6.2). In all forest types most of the species were included in the rare and common classes. However, below 2400 m there were more rare species than common species, whereas above 2400 m (in the UM and HA forests) there were more common species than rare species. In all forest types the abundant-but-infrequent and the frequent-but-scarce classes only included relatively few species.

Relationship between local commonness, landscape commonness and traits

There was a significant and negative relationship between maximum abundance and maximum height in DR forest, a significant and positive relationship between maximum abundance and maximum height in UM forest and a positive and significant relationship between maximum abundance and maximum diameter in HA forest (Table 6.1).

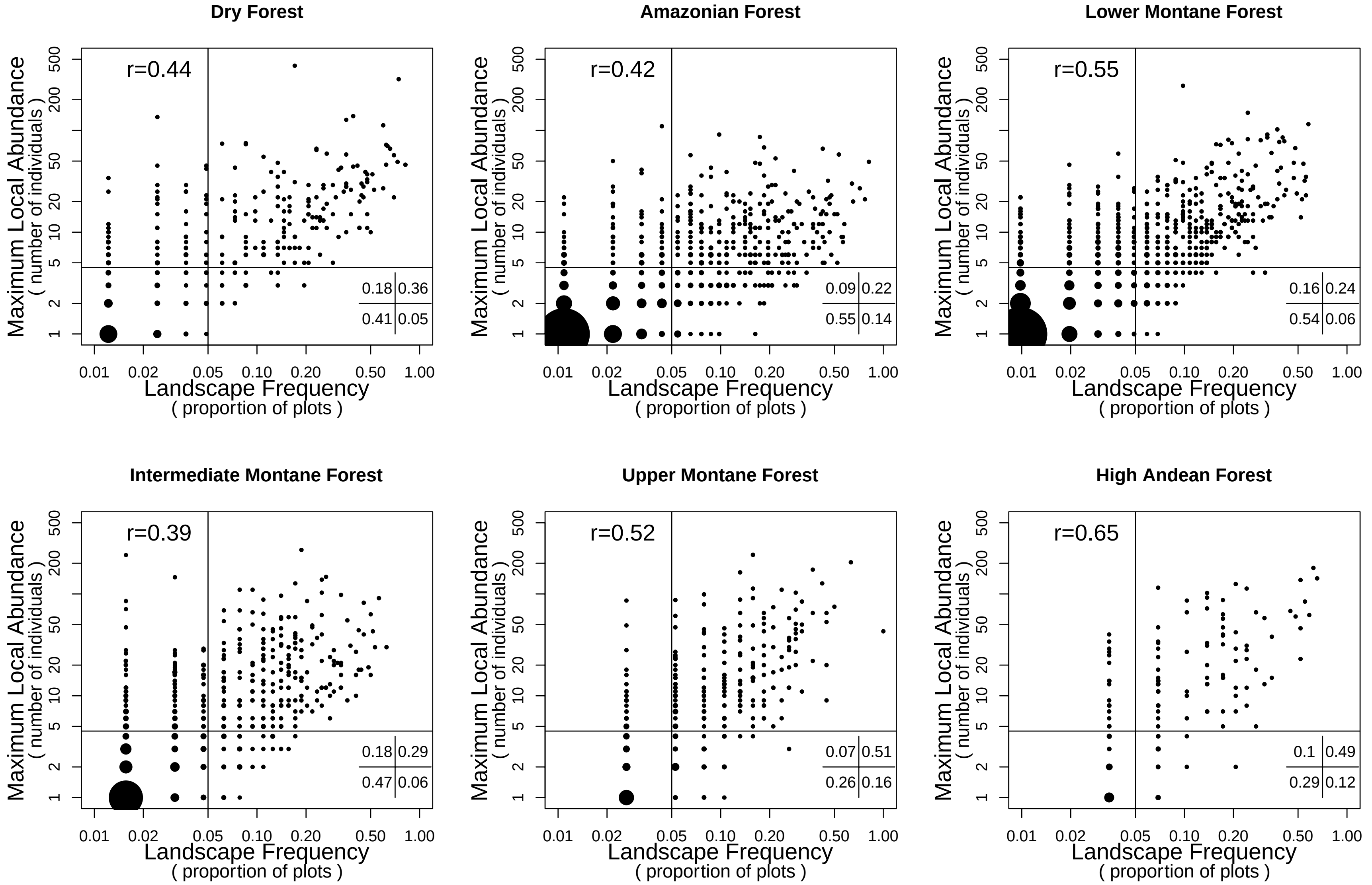
Dry Forest
r=0.44
0.18 0.36
0.41 0.05
Amazonian Forest
r=0.42
0.09 0.22
0.55 0.14
Lower Montane Forest
r=0.55
0.16 0.24
0.54 0.06
Intermediate Montane Forest
r=0.39
0.18 0.29
0.47 0.06
Upper Montane Forest
r=0.52
0.07 0.51
0.26 0.16
High Andean Forest
r=0.65
0.1 0.49
0.29 0.12
Maximum Local Abundance
(number of individuals)
1 2 5 10 20 50 200 500
Landscape Frequency
(proportion of plots)
0.01 0.02 0.05 0.10 0.20 0.50 1.00

Figure 6.2 (previous page). Correlation (Pearson *r*) between maximum local abundance and landscape frequency (proportion of plots where a species appears) in six tropical forest types in northern Bolivia (in all cases Bonferroni-corrected $P < 0.001$). Each point corresponds to one species; several species of exactly the same characteristics are represented by points of increasing size. The horizontal lines separate the species with maximum local abundance ≥5 individuals from the others. The vertical lines separate the species present in 5% or more of the plots from the others. The two criteria are combined to classify the species into four rarity classes: rare species are within the bottom-left quarter; abundant-but-infrequent species are within the top-left quarter; frequent-but-scarce species are within the bottom-right quarter; common species are within the top-right quarter. The bottom-right corner diagram represents the proportion of species in these four rarity classes.

Table 6.1. Results of Pearson correlation (*r*) between maximum local abundance and landscape frequency of species and four morphological traits: potential height (PH), potential diameter (PS), and mean number of stems (NS). The significance is indicated by *** ($P < 0.001$), ** ($P < 0.01$), and * ($P < 0.05$). DR: dry forest; AM: lowland Amazonian forest; LM: lower montane forest; IM: intermediate montane forest; UM: upper montane forest; HA: high Andean forest

Attributes		DR	AM	LM	IM	UM	HA
Maximum local abundance *vs*.	PH	−0.12*	0.04	−0.01	−0.04	0.12*	0.13
	PS	−0.07	0.00	−0.02	−0.01	0.10	0.19*
	NS	0.05	0.02	0.02	0.07	0.08	0.10
Landscape frequency *vs*.	PH	−0.07	0.18***	0.15***	0.16***	0.25***	0.09
	PS	0.05	0.19***	0.13***	0.20***	0.21***	0.17*
	NS	0.11*	−0.05	−0.02	−0.01	0.04	0.00

There was a significant and positive correlation between landscape frequency and maximum height in all forests except DR and HA forests, and a positive significant correlation between landscape frequency and maximum diameter in all forests except the DR forest. The mean number of stems was positively and significantly correlated with landscape frequency in the DR forest.

The results of the ANOVA and the Tukey-Kramer post-hoc tests indicated that there were no significant relationships between the local maximum abundance and the habit, neither between the landscape frequency and habit, in any of the forest types considered (results not shown).

Relationship between the four rarity classes and traits

We found significant differences among the four rarity classes mostly for the maximum height and maximum diameter (Fig. 6.3). In DR, AMA, LM and IM forests the frequent-but-scarce species were the tallest and largest species, differing significantly from rare species (in AM, LM and IM forests, for the maximum height and maximum diameter), abundant-but-infrequent species (in AM and IM forests, for the maximum height and maximum diameter), and common species (in AM forest, for maximum diameter only). The common species were the following tallest and largest species in the mentioned forests, and the tallest and largest species of UM forest, and were significantly taller and larger than rare species in AM, LM, IM and UM forests. In DR and HA forests the rarity classes did not differ significantly in their maximum height or maximum diameter.

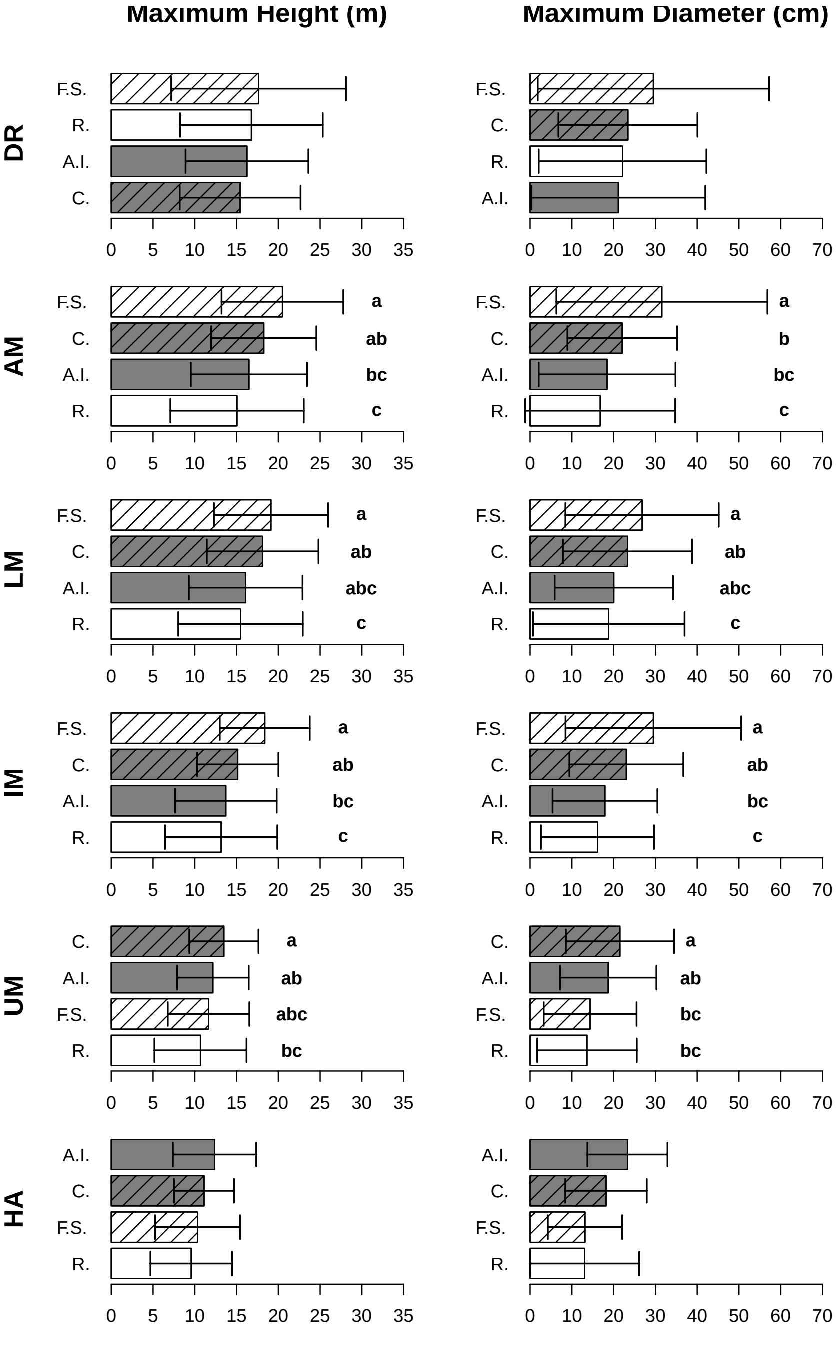

Figure 6.3. Differences in size between species of different rarity classes. C.: common species (grey striped bars); F.S.: frequent-but-scarce species (white striped bars); A.I.: abundant-but-infrequent species (grey non-striped bars); R.: rare species (white non-striped bars). The bar length represent the mean maximum sizes of species within a given rarity class, and the error bars are ±1 standard deviations. Bold lowercase indicate groups according to the post-hoc Tukey-Kramer tests. Rarity classes with the same letter indicate lack of significant differences; rarity classes that do not share any letter have significant differences (alpha level = 0.05, Bonferroni corrected). DR: dry forest; AM: Amazonian forest; LM: lower montane forest; IM: intermediate montane forest; UM: upper montane forest; HA: high Andean forest. In DR and HA forests there were no significant differences among any rarity class.

Regarding the number of stems, the individuals of common species in DR forest presented 0.15 stems more than rare species in average (*P* = 0.03). No significant differences were found in other forest types.

The distribution of species of different habits into rarity classes was not at random, neither in DR (*G* = 38.55; *P* < 0.001), AM (*G* = 138.30; *P* < 0.001), LM (*G* = 122.34; *P* < 0.001), IM (*G* = 134.57; *P* < 0.001), UM (*G* = 56.72; *P* < 0.001) and HA forests (*G* = 50.05; *P* < 0.001). The canopy trees were found to be common more often than expected by chance (significantly in AM, LM, IM and UM forests; Fig. 6.4) and rare less often than expected by chance (significantly in AM, LM and IM forests). The lianas were common less often than expected by chance; this trend increased with elevation (significantly in all forest types except the dry forest). Lianas also were rare more often than expected by chance (significantly in the AM, LM, IM and HA forests). The same pattern was found for treelets, which presented fewer common species than expected (significantly for all forest types) and more rare species than expected (significantly for all forest types except the HA forest). There were fewer rare species of shrubs than expected in all forest types, but never significantly. The only significant result for shrubs was the over-representation in the abundant-but-infrequent class in the IM forest.

DISCUSSION

Community-level patterns

The positive relationship between abundance and spatial distribution found in the six forest types implies that most species are ordered along a single rarity-commonness axis, being infrequent and scarce or frequent and abundant (Fig. 6.2). Our results are not particularly novel in reporting such a positive abundance-frequency relationship since many previous multi-scale studies found the positive relationship between abundance and frequency (*i.e.*, oligarchic patterns, reviewed by Pitman et al. 2013). Previous classifications of species made in tropical forests also found similar apportioning of species (Pitman et al. 1999, Romero-Saltos et al. 2001). Although such relationships have been found to be stronger within a given region or habitat, a positive relationship between abundance and spatial distribution of species is one of the most general patterns in ecology at any scale (Gaston et al. 2000). Therefore strong links from local and landscape commonness to regional and continental commonness are very likely to occur (Kristiansen et al. 2009).

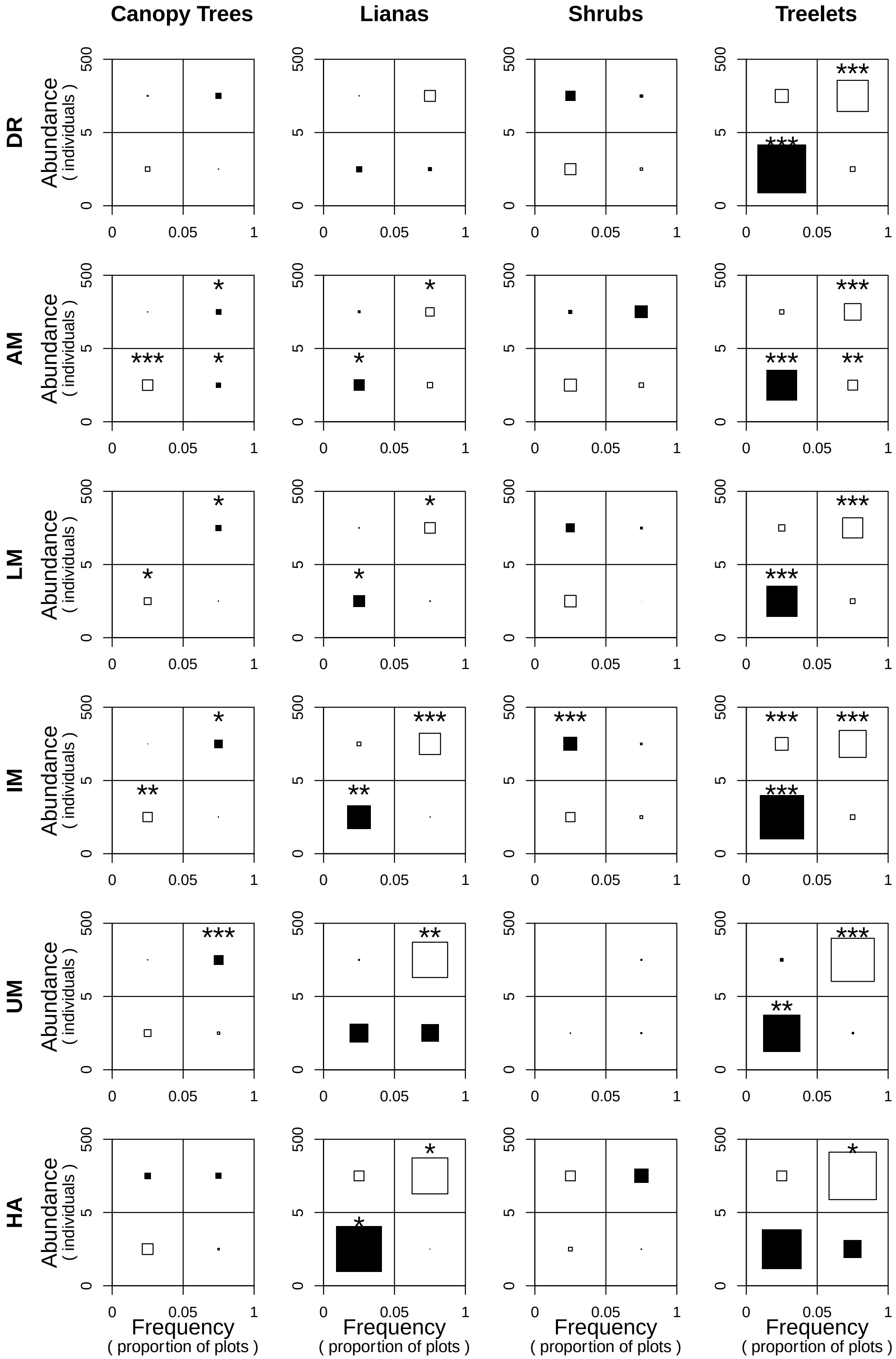
Canopy Trees
Lianas
Shrubs
Treelets
DR
AM
LM
IM
UM
HA
Abundance
(individuals)
500
5
0
0
0.05
1
Frequency
(proportion of plots)
***
***
*
***
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Figure 6.4 (previous page). Classification of species according to habit and rarity classes defined by maximum local abundance and landscape frequency (proportion of plots where a species appear), in six tropical forest types in northern Bolivia. The squares within each of the rarity classes represent deviations from the expected: black squares represent more species than expected, whereas empty squares represent fewer species than expected. The square size is proportional to the magnitude of the deviation, measured as a proportion of species of a given habit by forest type. Deviations large enough to be considered significant by a post-hoc binomial test are indicated with *** ($P < 0.001$), ** ($P < 0.01$), or * ($P < 0.05$); Bonferroni-corrected P values.

Regarding the classification of species, we studied different communities with the same thresholds to define rarity classes. This approach has been seldom adopted before, which has prevented from a general understanding of rarity and commonness patterns among habitats and study regions (Rabinowitz 1981, Rabinowitz et al. 1986, Ricklefs 2000). By doing so, we distinguish habitat-specific from more general ecological patterns, concluding that: (1) the positive relationship between abundance and distribution is a general pattern; but (2) the proportion of rare and common species depends on the habitat considered.

Specifically, we find that the oligarchy hypothesis could be a general pattern, from the Amazonia to the Andes up to ~4000 m in elevation (Pitman et al. 2001, 2013); but also that forests at higher elevations show increasingly stronger oligarchic patterns, as evidenced by the changes in the apportioning of species into rarity classes. Although most papers that support the oligarchic hypothesis has been focused in the lowland forests (*e.g.,* Pitman et al. 2001, Vormisto et al. 2004, Macía and Svenning 2005), it is known that species richness and the degree of dominance of species are negatively correlated (Bazzaz 1975, Huston 1979) and then it seems logical that the species are more common, in average, at higher elevations, where there are fewer species.

Relationship between plant traits and local and landscape-scale commonness

The plant traits, very especially size, determine which species are common and which are rare. As expected, larger plants have broader spatial distributions in all forest types, with the only exception of the DR forest (Table 6.1), a trend widely reported for tropical forests, although not always at the same spatial scale than the examined here (Ruokolainen and Vormisto 2000, Davidar et al. 2008, Kristiansen et al. 2009). Noteworthy, small plant species do not show dominance in any sense, at any of the scales considered, which rises questions on how small and large plants can coexist. Three broad hypotheses have been proposed before to explain why the small species have not disappeared: (1) large plants are adapted only to rather infrequent habitats, when considered across evolutionary time; (2) smaller species compete at finer scales than larger species, and therefore the apparent success of larger species is more a sampling effect than reflecting true competitive interactions; and (3) smaller species generally have higher fecundity allocation, potentially greater number of descendant individuals, and more derived species (Aarssen et al. 2006). The three hypotheses could apply for tropical forests, but further research on the different functional and evolutionary roles of species of different size is clearly needed.

Although there is a general positive relationship between size and commonness, we find that below 2400 m, the largest species considered here are frequent but never attain great population densities. Itoh et al. (1997) reported that some large tree species were characterized by negative autocorrelation at the local scale, and proposed the Janzen-Connell dynamics as the underlying mechanism for such distribution (Janzen 1970, Connell 1971). It is appealing to think about large long-lived individuals as long-term and stable reservoir of host-specific predators/pathogens, with greater influence over their surrounding area than smaller plants. However, it is unclear why such dynamics should be stronger for the emergent species than for the other species, especially the common species that also tend to have larger sizes. This would be expected if the common species have the ability to recruit in close proximity with conspecific adults (Comita et al. 2010, Mangan et al. 2010), which has been proposed to be a major driver of oligarchic dominance in tropical forests, but still requiring more research (Pitman et al. 2001, 2013).

Regarding number of stems, it seems that they provide a slight competitive advantage in the DR forest, but we could not find any evidence of more abundant or frequent species in montane forests. Specifically, although there are more shrub species at higher elevations, these species do not show a clear trend to be more abundant, as we expected. It seems that the shrub habit among montane species is at least as much related to evolutionary heritage of very diversified clades in the Andes (*e.g., Psychotria*, *Miconia*) than to clear competitive advantages of these species at ecological scales.

Species with different habits are apportioned very differently into rarity classes

Species habits are not independent of the apportioning of species into rarity classes. There is an obvious lack of lianas and treelet species in the common category, whereas there are more rare species of these habits than expected, in all forest types. The opposite pattern happens for canopy trees, which clearly tend to be apportioned in the common class more than expected by chance. This result suggests that some caution is needed to infer on rainforest functioning and diversity relying solely on canopy trees inventories, especially those with a cut-off diameter of 10 cm.

Obviously, any inventory method will leave out a given amount of diversity, but it has been reported that different groups of plants usually offer the same results concerning alpha- and beta-diversity gradients, and their relationship with environmental gradients (Macía et al. 2007, Ruokolainen et al. 2007, Réjou-Méchain et al. 2011, Jones et al. 2013, Guèze et al. 2013, Pansonato et al. 2013). Therefore, leaving out the 40% of the species that are lianas, shrubs and treelets that never grow up to 10 cm of dbh should not hamper the comprehension of these phenomena. In the other hand, by excluding these species, the inventories of canopy trees are biased by leaving out scarce and (very specially) rare species, which are also known to play distinctive and vulnerable functions (Mouillot et al. 2013). The implications for conservation planning of relying too much on large individuals inventories are delicate, since these inventories do not focus on how many and which species are rare, but on how many and which species are common.

CONCLUSIONS

Two main conclusions arise from the present study. First, the positive relationship between commonness at local and landscape scales indicate that very simple approaches to rarity and commonness based on abundance only, or occurrence only, could summarize most of the relevant information to characterize species rarity and commonness. Both approaches, in practice, do not supply independent information. Although much further research would be required to understand why this indicates that a wide array of tools could be used to characterize the species, with direct consequences for applied ecology (Hui et al. 2009, 2010).

Finally, the species traits determine which species are to be rare and which to be common, which indicates that rarity and commonness patterns do not result solely from stochastic processes, but are the result of non-neutral trait-based community assembly (McGill et al. 2006a, b, 2007, Violle et al. 2012). The different dispersal abilities, and the different habits among species, are apparently major drivers for the observed pattern at landscape scale, even though complex interactions of unmeasured processes could be also relevant at landscape and local scales.

Acknowledgments

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CAPÍTULO 7

Disentangling species turnover of woody plants in a tropical forest: from local to regional scales

Este capítulo se ha realizado en colaboración con J. S. Tello, P. M. Jørgensen, A. F. Fuentes, L. Cayola, M. Cornejo, M. I. Loza, T. B. Miranda, J. M. Quisbert, V. W. Torrez, V. Cala y M. J. Macía. Forma parte de un manuscrito pendiente de envío a *Global Ecology and Biogeography*.

ABSTRACT

The main purpose of the present study was to find whether the turnover of woody plants in a tropical region could be explained by deterministic processes (*i.e.*, plants changing along environmental gradients) and/or stochastic processes (*i.e.*, plants changing with space). We also aimed to disentangle the relative roles of climate and soil, within the unique influence of the environment. We disentangled the floristic turnover determinants from local to regional scales (16 to 16,000 km^2) in the Madidi region in Bolivia. We found that at greater scales more of the floristic variation remains unexplained, which was coupled with a strong decrease in the proportion of floristic variation jointly explained by environment and space. In contrast, the proportion of variation explained by the environment alone, and the space alone, only suffered only minor changes with scale. There was only a minor proportion of floristic variation explained by climate alone or soil alone. Our main conclusion is that niche-assembly processes occurring along spatially structured environmental gradients are probably of different nature than those occurring along spatially un-structured environmental gradients. This sheds a new perspective on how multiple aspects of the environment and the space should be taken into account for a better understanding of community assembly forces.

Keywords: beta diversity, elevational gradients, null models, tropical Andes, variation partitioning

INTRODUCTION

Understanding patterns of species turnover and its determinants is one of the fundamental issues in ecology and biogeography, and is critical for the elaboration of effective conservation strategies. Most explanations for the structure of natural communities are based on the contribution of either niche-based processes, neutral spatial processes or a combination of the two (Leibold et al. 2004, Chave 2008, Legendre et al. 2009, Vergnon et al. 2009, Tuomisto et al. 2012). Niche assembly theories propose that the presence and abundance of species are linked to the species requirements and impacts regarding its interactions with the abiotic and biotic environment (Hutchinson 1957, Tilman 1990, 1994, Chase and Leibold 2003, Silvertown 2004, Svenning et al. 2004, Götzenberger et al. 2012, Siefert et al. 2013). As a consequence, species are sorted along environmental gradients based on their niches, and environmental heterogeneity places a fundamental role in the structuring of communities. In contrast, neutral theories argue that niche preferences of species are not required to explain species distributions and community-level patterns (MacArthur and Wilson 1967, Bell 2001, Hubbell 2001, Alonso et al. 2006, Rosindell et al. 2011). Variation in species composition through time is proposed to be the result of demographic stochasticity (random drift of species abundances) and dispersal limitation (Hubbell 2001, 2005, 2006, Chisholm and Lichstein 2009). Despite being contrasting mechanisms, research in the last decade has led to the conclusion that most plant communities are distributed along a continuum from purely neutral to entirely deterministic communities, and therefore both approaches are considered complementary rather than conflicting (Gravel et al. 2006, Herault 2007, Adler et al. 2007, Jabot et al. 2008, Halley and Iwasa 2012).

The relative role of environment and space may depend on different factors; here we address the role of spatial scale in the niche-assembly processes of tropical forests, a central problem both for basic comprehension of the ecosystem, and for its management and conservation (Wiens 1989, Levin 1992). Some previous works have been focused on patterns at different scales within the same study region, and their results indicate that spatial processes predominate at finer scales, and loose importance relative to environmental effects at coarser scales (Normand et al. 2006, Laliberté et al. 2009, Hu et al. 2012). Regarding the role of the spatial extent (the size of the study region), it is helpful to compare the spatial extents at which different studies are conducted. A comparison of the available works indicates that there is a slight increase in the contribution of the environment at increasing spatial scales (Chave 2008, Kristiansen et al. 2012), and the same is observed in the very few works that address the issue directly (López-Martínez et al. 2013). Despite of its importance, a robust assessment of the effect of the spatial extent in tropical forests is still lacking.

The literature so far has considered multiple aspects and measures of the environment (topographic position, microtopography, elevation, climate, edaphic variables, soil types, geology…). Two of the most important for plants are the climatic conditions (which determine the vegetation types and biomes at continental scales; Punyasena et al. 2007, Crisp et al. 2009), and soil characteristics (which characterize patchy habitats at local scales; Tuomisto et al. 2003a, John et al. 2007, Pitman et al. 2013). The relative contribution of these two general sources of environmental heterogeneity is not well known. Few studies have shown that the soil alone can summarize all the relevant environmental information from local scales (*e.g.,* John et al. 2007, Jones et al. 2008) to regional scales (*e.g.,* Vormisto et al. 2004, Duivenvoorden et al. 2005, Guèze et al. 2013), whereas climatic variables have been found to be important more often at regional to continental scales (Bjorholm et al. 2008, Slik et al. 2009, Blach-Overgaard et al. 2010). Overall, the contribution of theses processes across scales remains poorly understood, although some authors maintain that there is a generalized transition from a primarily edaphic influence to a primarily climatic influence on plant community composition when increasing spatial scale (Siefert et al. 2012).

In this study, we use data of from an extensive network of plots along a ~3600 m tropical elevational gradient in the Amazonia-Andes transition to answer the following questions: (1) What is the relative importance of environmental and spatial processes on the turnover in plant species composition among local species assemblages? (2) How does climatic and soil heterogeneity contribute to the turnover in species composition? and (3) How do these processes change with spatial scale?,

METHODS

Study region and floristic data

We established a total of 398 0.1-ha plots (20 × 50 m) in mature forests across the eastern slopes of Andes in northwestern Bolivia (between latitude −12.43º and −15.72º, and longitude −69.48º and −66.66º; see Fig. 1.1). The plot network included multiple types of tropical forests distributed along a steep elevational gradient from the Amazon to the tree line, close to 4000 m (Fuentes 2005). Plots were located at least 250 m away from each other, avoiding big gaps or recent human disturbances. At each plot, we inventoried all woody plants rooting within the plot limits with a diameter at breast height (*i.e.*, 130 cm above ground) equal or greater than 2.5 cm. All individuals were identified to species or morphospecies, and voucher specimens were collected at each site. Extensive taxonomic work was conducted during 2010 at Herbario Nacional de Bolivia to ensure that species and morphospecies names were standardized across the entire dataset. Less than 3.5% of individuals were excluded from the analysis because they could not be assigned to a reliable morphospecies. Vouchers specimens are kept in the Herbario Nacional de Bolivia and the Missouri Botanical Garden.

Environmental data

At each plot, we collected environmental data corresponding to climatic and soil characteristics, which were used to explain the turnover in local species composition between plots. The climatic data for each plot were estimated from rasters (30 arc-second resolution) of the 19 bioclimatic variables in the WorldClim database (Hijmans et al. 2005). These variables are often used in ecological niche modeling, and represent potentially biologically meaningful variables derived from the monthly temperature and rainfall values, as annual trends (*e.g.,* mean annual temperature), seasonality (*e.g.,* annual range in temperature) and extreme or limiting environmental factors (*e.g.,* temperature of the coldest month).

At each plot, we took a sample of superficial soil (0−30 cm, below the litter layer). Samples were air-dried and sieved through a 2-mm sieve. Soil pH was measured in a 1:2.5 soil:H_2O suspension, organic C was determined with the Walkley and Black method, total N with the semi-micro Kjeldahl method, and texture with the hydrometer method (Reeuwijk 2002). We also measured exchangeable cations: calcium (Ca), magnesium (Mg) and potassium (K), using two extractive methods for different sets of samples: (a) with 1M ammonium acetate solution and (b) with a Melhich-3 extraction method (Mehlich 1984). Both procedures are highly and linearly correlated in many types of soils (Mallarino 1995, Eckert and Watson 1996, Matula 2009). Therefore, it is possible to combine data obtained through both methods, if the relationship between them is known. To standardize soil measurements across methods, we analyzed a subset of 76 soil samples following both procedures. These samples were chosen to include most of the range in nutrient concentrations observed in the data. Based on these analyses, we found the following relationships between the two methods for each cation: (1) Calcium: $Ca_{\text{Melhich-3}} = 53.032 + 0.3588 \times Ca_{\text{ammonium acetate}}$ ($R^2 = 0.87$; $P < 0.001$). (2) Magnesium: $Mg_{\text{Melhich-3}} = -49.387 + 0.6635 \times Mg_{\text{ammonium acetate}}$ ($R^2 = 0.78$; $P < 0.001$). (3) Potassium: $K_{\text{Melhich-3}} = 28.689 + 0.7326 \times K_{\text{ammonium acetate}}$ ($R^2 = 0.68$; $P < 0.001$).

With these linear models, we transformed all ammonium acetate values into their Mehlich-3 equivalents. Sodium was not included in the analysis because of the weak and not significant correlation between both methods. Finally, the C:N ratio was included as an additional soil variable.

Definition of sub-regions at different spatial scales

To study the effect of the spatial scale on the relative contribution of different factors to floristic turnover, analyses were repeated for sub-regions spanning a broad range of spatial extents. In our analyses, a sub-region was defined as a unique subset of 20 plots. We kept the number of plots constant because we wanted to avoid having larger sample sizes in larger regions as compared to small ones. Spatial scale was defined as the area of the minimum convex polygon that included the 20 plots of a sub-region. Among the many possible subsets of plots, we chose 500 so that all scales were represented in similar proportions and regions never completely overlapped in the plots they included (sub-regions shared <70% of the plots with any other sub-region). The spatial extents of the resulting sub-regions ranged approximately from 16 to 16000 km^2. Elevational showed no bias across scales (Fig. 7.1). Note that the grain sizes among sub-regions remains identical regardless the spatial extent differences. All calculations and statistical analyses were done with R 3.0.1 (R Development Core Team and R Core Team 2012).

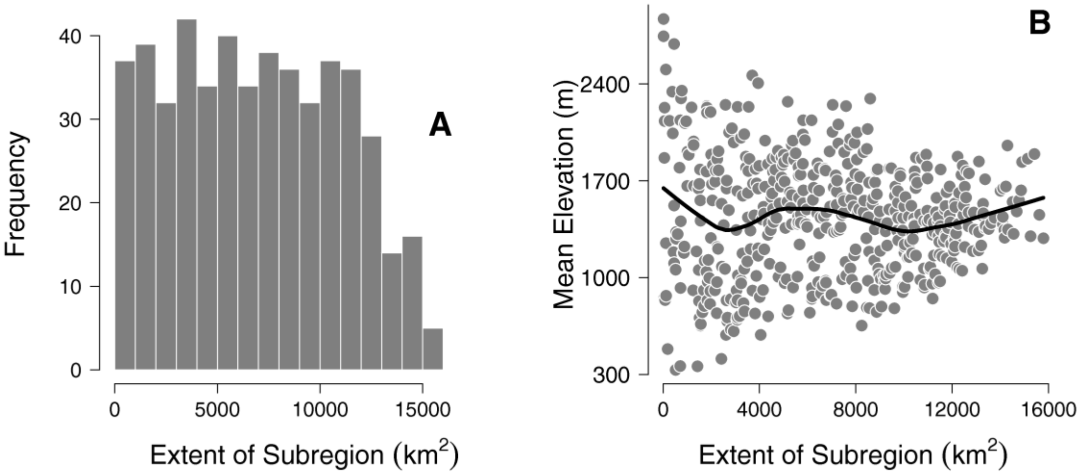

Figure 7.1. Potential biases across scales. (A) Frequency distribution of the extents of sub-regions. These data show that all scales are roughly equally represented in the analyses. (B) Changes across spatial scales in average elevation of plots within a sub-region. The line shows the tendency of the data using a locally weighted fit. There is no systematic change in the average elevation of sub-regions across scales.

Response and explanatory matrices

For each region, we decomposed the variation in floristic composition among multiple spatial and environmental predictor matrices. The dependent matrix of floristic composition was created by performing a principal coordinates analysis (PCoA) on a pair-wise matrix of floristic distances of all plots within a sub-region. We used the Chao dissimilarity index, recommended for datasets with great floristic heterogeneity (Chao et al. 2005). All axes of the PCoA were retained, after applying the correction method proposed by Cailliez (1983) to overcome the non-Euclideanarity problem that can produce negative eigenvalues (Legendre and Legendre 1998). The Chao dissimilarities were calculated with the function *vegdist*, and the PCoA with the function *capscale*, both in R package vegan (Oksanen et al. 2013).

The spatial predictors for each sub-region included latitude, longitude and principal coordinates of a neighborhood matrix (PCNM). PCNMs represent a spectral decomposition of the spatial relationships among the study sites, and can account for complex spatial structures at various scales (Borcard and Legendre 2002, Borcard et al. 2004, Dray et al. 2006). The calculations were done with function *pcnm* in package vegan (Oksanen et al. 2013).

We needed to reduce the number of predictors in each predictor matrix so that a full model (including spatial, soil and climate predictors) could be fit to the data. First, we run three independent principal component analyses (PCA) for climatic, soil and spatial predictors (in this case only PCNMs with positive eigenvalues were considered). Then we used the approach described by Blanchet et al. (2008) to conduct variable selection of each set of predictors independently, using the function *forward.sel* in the R package packfor (Dray et al. 2013). This approach has the benefits of controlling Type I error and not leading to an overestimation of the amount of explained variation (Blanchet et al. 2008). If no variables were retained by the variable-selection procedure, we kept only the variable with the highest univariate relationship with the floristic composition (*i.e.*, highest adjusted R^2). We did this to always have all set of predictors represented in all analyses. A full matrix of environmental predictors was constructed as the combination of selected soil and climate variables. The reduced matrixes were then used in the variation partitioning analysis described below.

Hierarchical variation partitioning

To disentangle the effects of environment and spatial predictors, we performed a hierarchical variation partitioning of the floristic composition among plots at two different levels (Fig. 7.2; Cushman and McGarigal 2002). The variation partitioning analysis quantifies the variation of a response matrix into components accounted for by two or more explanatory matrices and their combined effects.

In the first level of the analysis, we partitioned the total floristic variation among spatial and all environmental predictors leading to four fractions: (a) variation explained only by the environment; (b) variation explained only by the space; (c) variation explained simultaneously by environment and space; and (d) unexplained variation. In the second level, we partitioned the variation explained only by the environment into the contributions of soil and climate predictors. This lead to other three fractions of variation: (a) variation explained only by climate; (b) variation explained only by soil; and (c) variation simultaneously explained by climate and soil.

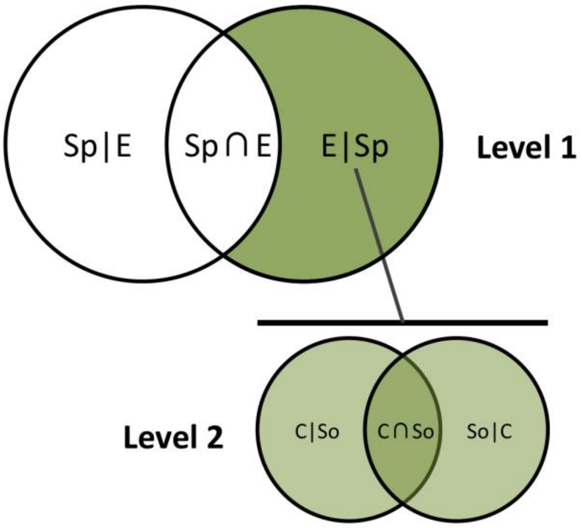

Figure 7.2. Conceptual presentation of the hierarchical variation partitioning approach employed in this study. E: environmental predictors; Sp: spatial predictors; Sp | E: variation explained only by space; Sp∩E: variation explained simultaneously by space and environment; E | Sp: variation explained only by environment; C: climatic predictors (space already partialled out); So: soil predictors (space already partialled out; C | So: variation explained only by climate; C∩So: variation explained simultaneously by climate and soil; So | C: variation explained only by soil.

Variation partitioning analyses were based on distance-based redundancy analysis (dbRDA) using the function *varpart* in vegan (Legendre and Anderson 1999, Oksanen et al. 2013). To know if a given fraction of explained variation in a particular sub-region was significant, we conducted a null model analysis (Tello and Stevens 2010). In this null model, we permuted the rows of the floristic PCoA matrix, and repeated the variation partitioning analyses, saving the proportions of variation that resulted from these analyses. These portions of variation represent the variation that is expected when breaking any relationship between the floristic composition of the plots with the environmental and spatial predictors. The permutation was repeated 999 times, leading to a frequency distribution of null proportions of variation for each fraction. The empirical proportions of variation were compared with the expected null distribution. We concluded that a proportion of variation at a particular scale was statistically significant if it was above the 95 percentile of the distribution of those null values.

Relationship between explained variation and spatial scale

To know if a given fraction of explained variation (at any of the hierarchical levels) changed with the spatial scale, we fitted a lineal regression model to the relationship between the observed fraction of floristic variation and the spatial extent of sub-regions. Then we compared the empirical regression models to regression models produced by fitting linear models to the fractions obtained in the null model described above. Therefore, we obtained 999 regression models relating the null proportions of variation in each fraction with spatial scale. The coefficients of these models were used to create null expectations about the relationship that each fraction of variation should have with scale if species composition has no relationship with the environmental and spatial predictors. We performed univariate significance analyses, were each empirical coefficient was compared against its corresponding distribution of 999 null coefficients. We concluded that the coefficient was statistically significant if it was below the 2.5 percentile or above the 97.5 percentile of the distribution of that coefficient among the 999 null values. We also tested whether the empirical combination of intercept and slope was different than that expected by the null model by creating bi-variate confidence ellipses. These ellipses describe bi-variate null distributions for combinations of two coefficients, by including 95% of bi-variate combinations of two coefficients. If the empirical combination of coefficients falls outside of the confidence ellipse, we concluded that the empirical regression model was different than expected.

RESULTS

We found the tropical forests of the Madidi region to be very species-rich. We found 2,507 species in the inventory of 118,895 individuals in 398 0.1-ha plots. We also found high levels of beta-diversity, with a steep increase in floristic turnover with increasing geographic and environmental distances. Overall, 40.37% pairs of plots shared no species at all, ranging from pairs of plots ~0.5 km apart to pairs of plots ~200 km apart.

The average proportion of total variation explained was 30%, but showed a large amount of variation across sub-regions ranging from 6% to 78%. This fraction of variation was significantly higher than expected by the null model in >98% of the sub-regions analyzed (Fig. 7.3). The total variation explained decreased significantly with the spatial extent from ~35% at local scales to ~25% at regional scales ($P < 0.001$; Table 7.1), but the relationship was only weak ($R^2_{adj} = 0.051$).

The variation explained exclusively by the environment was ~14% on average (Fig. 7.4A), and it was significantly higher than expected by the null model in 79.6% of the sub-regions analyzed. It showed a slight but significant increase with scale ($R^2_{adj} = 0.005$; $P = 0.018$; Table 7.1). The variation explained exclusively by space was ~7% on average, and significantly higher than expected by the null model in 46.8% of the sub-regions analyzed (Fig. 7.4B), and showed no significant changes with scale (Table 7.1). The proportion of floristic variation jointly explained by the environment and the space was ~9% in average (Fig. 7.4C), and it was significantly higher than expected by the null model in 65.8% of the sub-regions analyzed. It showed a very clear and significant decrease with scale, ranging from ~15% at local scales to ~1% at regional scales ($R^2_{adj} = 0.185$; $P < 0.001$; Table 7.1). Overall, in 76% of the sub-regions environment explains more of the floristic variation than space, whereas the opposite happens in 23% of the sub-regions.

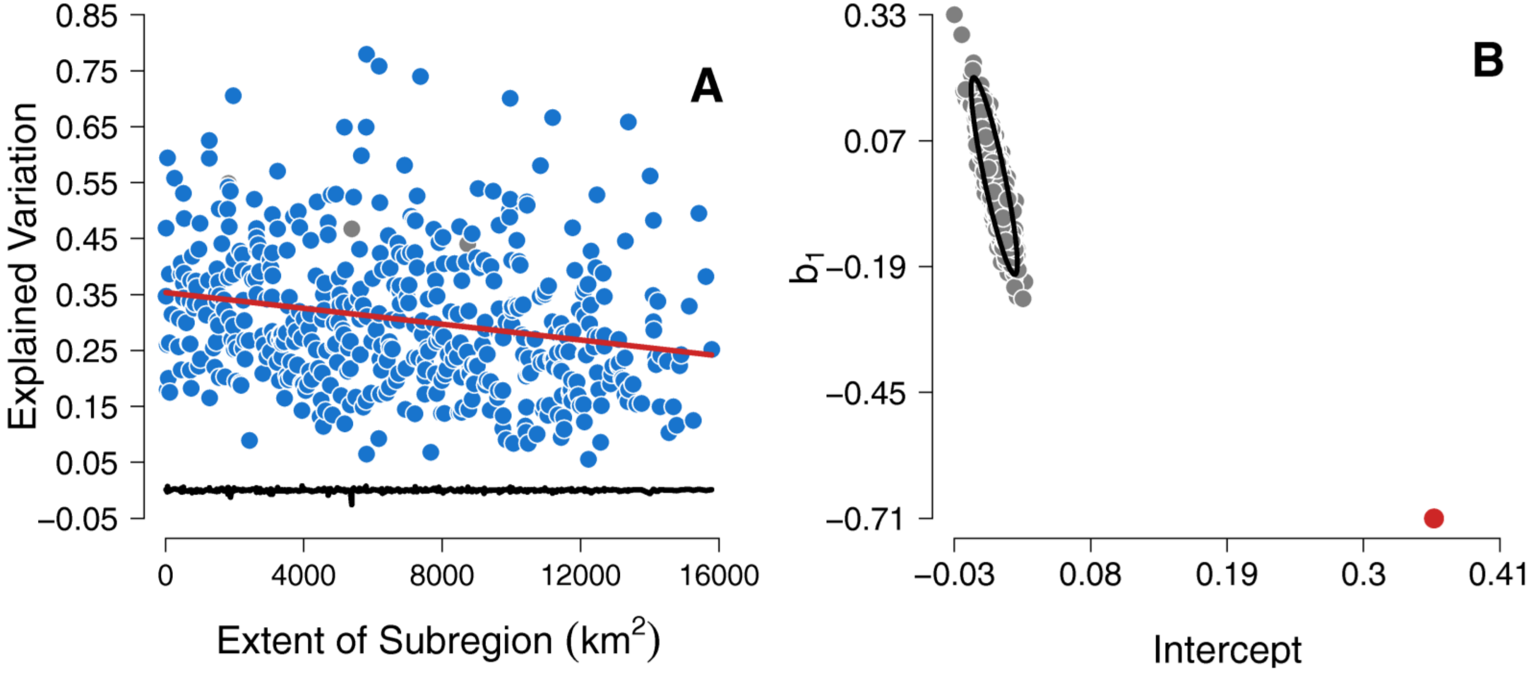

Figure 7.3. Changes across spatial scales in total amount of explained variation. (A) Relationship between total amount of explained variation (a combination of environmental and spatial predictors) and the spatial extent of sub-regions. Blue circles represent sub-regions for which the proportion of variation explained was significantly higher than that expected by the null model. Gray circles represent sub-regions at which the proportion of variation explained did not differ significantly than that expected by the null model (see Methods for details). The red line shows the fit of a linear model to the data. The black line shows the mean amount of explained variation expected given the null model. (B) Bivariate distribution of the intercept and coefficient of scale from a linear fit to the relationship in A. Gray circles represent null bivariate combinations of regression coefficients. This distribution results from fitting linear models to 999 relationships between null total amount of explained variation and the extent of sub-regions. The red point represents the bivariate combination of coefficients for the empirical relationship (red line in A). The ellipse is a 95% data ellipse that defines the confidence region.

Table 7.1. Adjusted coefficients of linear models on the changes with scale of the empirical and 999 null expected fractions of explained floristic variance in northwestern Bolivia. The expected mean is zero in all cases. E: environmental predictors; Sp: spatial predictors; Sp | E: variation explained only by space; Sp∩E: variation explained simultaneously by space and environment; E | Sp: variation explained only by environment; C: climatic predictors (space already partialled out); So: soil predictors (space already partialled out; C | So: variation explained only by climate; C∩So: variation explained simultaneously by climate and soil; So | C: variation explained only by soil. I: Intercept; b_1: coefficient of scale × 100,000.

Fraction		Observed	Expected (95% confidence interval)			Observed > Expected (*P*)	Observed < Expected (*P*)
Total	I	0.354	−0.015	to	0.015	<0.001	0.999
	b_1	−0.707	−0.150	to	0.159	0.999	<0.001
E | Sp	I	0.129	−0.014	to	0.013	<0.001	0.999
	b_1	0.153	−0.153	to	0.144	0.018	0.981
Sp | E	I	0.071	−0.012	to	0.012	<0.001	0.999
	b_1	0.012	−0.136	to	0.134	0.417	0.582
E ∩ Sp	I	0.154	−0.012	to	0.013	<0.001	0.999
	b_1	−0.872	−0.135	to	0.138	0.999	<0.001
C | So	I	0.079	−0.013	to	0.012	0.001	0.999
	b_1	−0.020	−0.128	to	0.133	0.634	0.365
So | C	I	0.031	−0.011	to	0.012	0.001	0.999
	b_1	0.218	−0.121	to	0.125	0.001	0.998
C ∩ So	I	0.020	−0.010	to	0.010	0.001	0.999
	b_1	−0.045	−0.111	to	0.103	0.767	0.232

The proportion of floristic variation explained exclusively by climate was ~7.8% on average, and significantly higher than expected by the null model in 44.8% of the sub-regions (Fig. 7.5A), and showed no significant changes with scale (Table 7.1). The variation explained exclusively by soil was on average ~4.6%, and it was significantly higher than expected by the null model in 31.4% of the sub-regions (Fig. 7.5B), and showed a weak but significant increase with scale ($R^2_{adj} = 0.046$; $P = 0.001$; Table 7.1). The proportion of floristic variation jointly explained by climate and soil was ~1.6% on average, and significantly higher than expected by the null model in 10.4% of the sub-regions analyzed (Fig. 7.5C). It showed no significant changes with scale (Table 7.1). Overall, in 57% of the sub-regions climate alone explains more of the floristic variation than soil alone, whereas the opposite happens in 41% of the sub-regions.

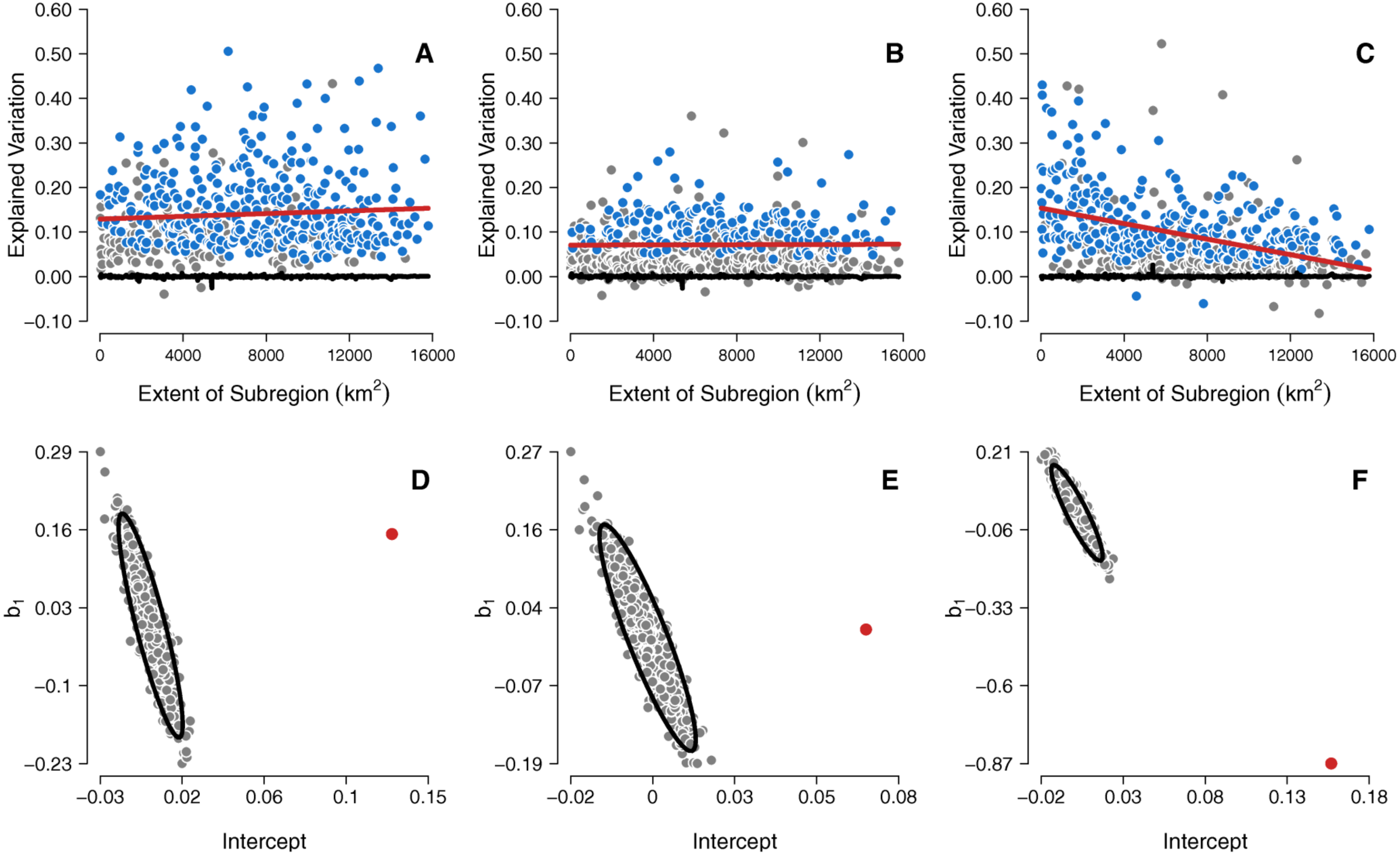
A
B
C
Explained Variation
0.60
0.50
0.40
0.30
0.20
0.10
0.00
−0.10
0
4000
8000
12000
16000
Extent of Subregion (km^2)
D
E
F
b_1
0.29
0.16
0.03
−0.1
−0.23
0.27
0.16
0.04
−0.07
−0.19
0.21
−0.06
−0.33
−0.6
−0.87
Intercept
−0.03
0.02
0.06
0.1
0.15
−0.02
0
0.03
0.05
0.08
−0.02
0.03
0.08
0.13
0.18

Figure 7.4 (previous page). Changes across spatial scales in amount of variation explained by environment or space in first level of hierarchical variation partitioning analysis. (A) Variation explained only by the environment. (B) Variation explained only by the space. (C) Variation explained jointly by the environment and the space. The bottom row shows bivariate combinations of coefficients of fitted linear models across scales for the variation explained only by environment (D), explained only by space (E), and jointly explained by environment and space (F). In A, B and C, blue circles represent sub-regions at which the proportion of variation explained differed significantly to the expected by the null model. Gray circles represent sub-regions at which the proportion of variation explained did not differ significantly than that expected by the null model (see Methods for details). The red line shows the fit of linear models to the data. The black line shows the mean amount of explained variation expected given the null models. In D, E and F, gray circles represent null bivariate combinations of regression coefficients. These distributions results from fitting linear models to 999 relationships between null total amount of explained variation and the extent of sub-regions. The red points represent the bivariate combination of coefficients for the empirical relationships (red lines in A, B and C). The ellipses define the confidence regions at 95% level.

DISCUSSION

Total explained variation decreases with increasing spatial scale

Despite the large floristic turnover in the study region, at any scale one third to one fourth of the total floristic variation in average can be explained by environmental and the spatial processes (up to 78% in some sub-regions). The observed decrease with scale is in agreement with results of other studies at different spatial scales in various tropical forests. For example, while Jones et al. (2008a, 2011) found that between 30−40% of the variation could be explained at very small scales (5 × 5 km), other researchers found that only between 20 and 25% could be explained at larger intermediate scales (in the order of 100 × 100 km; Svenning et al. 2004, Chain-Guadarrama et al. 2012, Myers et al. 2013). Still, the little effect of scale we found spanning three orders of magnitude in spatial extent is surprising, and contradicts the general expectation that steeper environmental gradients at larger scales should lead to stronger relationships between the structure of local assemblages and environmental or spatial predictors (*e.g.,* Kristiansen et al. 2012).

The decreasing of total explained variation at larger scales seems to result from a strong decrease in the floristic variation explained jointly by environment and space. This fraction measures how species are sorted along spatially structured environmental gradients, and often represents a relatively important proportion of floristic variation explained in tropical forests (Ruokolainen et al. 2007, Jones et al. 2011, Chain-Guadarrama et al. 2012). Such kind of gradients are common, since generally the environmental characteristics are spatially structured at some degree (Bell et al. 1993, Borcard et al. 2004, Laliberté et al. 2009).

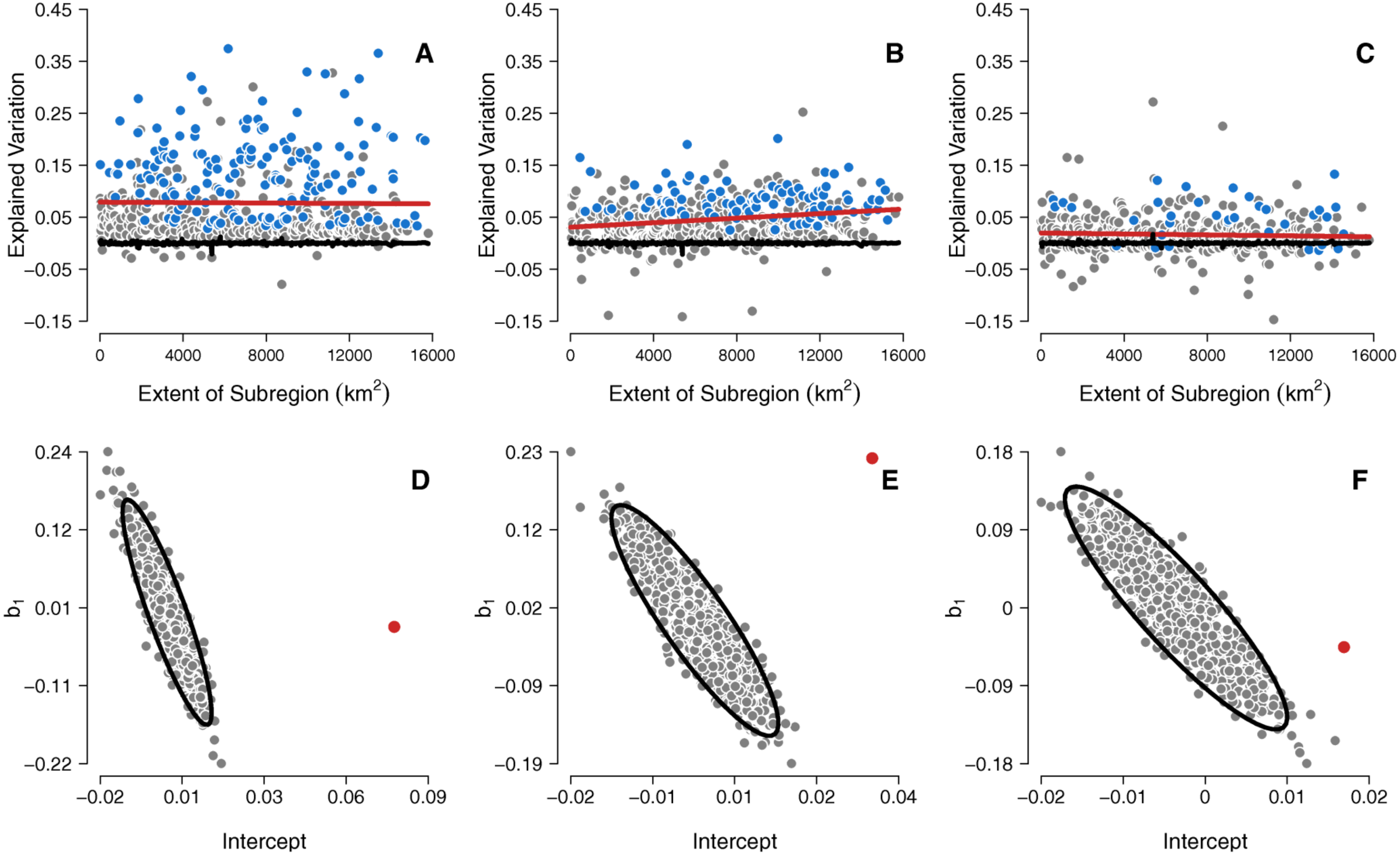
A
B
C
D
E
F
Explained Variation
0.45
0.35
0.25
0.15
0.05
−0.05
−0.15
0
4000
8000
12000
16000
Extent of Subregion (km^2)
b_1
0.24
0.12
0.01
−0.11
−0.22
−0.02
0.01
0.03
0.06
0.09
0.23
0.12
0.02
−0.09
−0.19
−0.02
−0.01
0.01
0.02
0.04
0.18
0.09
0
−0.09
−0.18
−0.02
−0.01
0
0.01
0.02
Intercept

Figure 7.5 (previous page). Changes across spatial scales in amount of variation explained by climate or soil properties in the second level of hierarchical variation partitioning analysis. (A) Variation explained only by climate. (B) Variation explained only by soil. (C) Variation explained jointly by climate and soil. The bottom row shows bivariate combinations of coefficients of fitted linear models across scales for the variation explained only by climate (D), only by soil (E), and jointly explained by climate and soil (F). In A, B and C, blue circles represent sub-regions in which the proportion of variation explained differed significantly from the expected by the null model. Gray circles represent sub-regions at which the proportion of variation explained did not differ significantly (see Methods for details). The red line shows the fit of linear models to the data. The black line shows the mean amount of explained variation expected given the null models. In D, E and F, gray circles represent null bivariate combinations of regression coefficients. These distributions results from fitting linear models to 999 relationships between null amount of explained variation and the extent of sub-regions. The red points represent the bivariate combination of coefficients for the empirical relationships (red lines in A, B and C). The ellipses define the confidence regions at 95% level.

Unfortunately, this fraction of variation does not provide much information that alows us to disentangle underlying processes, an important common limitation to any variation partitioning analysis (Smith and Lundholm 2010). Some findings of strong effects of sampling scale on observed patterns of habitat association in tropical trees (Garzon-Lopez et al. 2013) suggest that the unknown processes reflected by the joint fraction are likely to be deterministic in our study region, although this should be regarded only as a tentative hypothesis. Overall, these results have very limited comparison with previous works, because the relative weigh of this fraction in particular has been found to be highly dependent on the type of data employed (Jones et al. 2008b), the grain size of the sampling design (Hu et al. 2012), and the underlying configuration of the landscape (Smith and Lundholm 2010). Further research with different methodological approaches than the variation partitioning would be needed to understand the underlying processes occurring along spatially structured environmental gradients.

Processes along spatially structured environmental gradients are scale-dependent, whereas processes along un-structured environmental gradients are not

The strong decrease with scale in the variation jointly explained by environment and space differs greatly from the trend with scale of the proportion of floristic variation explained by the environment alone (the spatially un-structured environment), which increases slightly at larger scales as expected (*e.g.,* Chave 2008). These contrasting trends with scale indicate that the processes occurring within the spatially un-structured environment are very likely to be different to those happening within the spatially structured environment, even if the joint fraction was all due to deterministic assembly processes. This implies that: (1) the spatially un-structured environment is not necessary representative of the whole environment; and (2) the deterministic processes occuring along un-structured gradients are not necessary representative of all the niche assembly processes occuring in the community.

It is important to note that both fractions reflect species sorting along environmental gradients, but the inference from the variation explained only by environment is not confounded with potentially important spatial processes like dispersal. For that reason, the unequivocal proportion of floristic variation explained exclusively by the environment has been traditionally employed as the only proxy of the niche partitioning processes occuring within the community. However, these may represent an important bias in the processes considered, if the ecological processes that are scale-dependent are concentrated along environmental gradients that have some kind of spatial structure, as found here.

In principle, the spatially un-structured gradient could be though as a random set of particularities of certain points of the landscape without any measurable spatial structure at any grain size. However, given that our comprehension of niche-assembly in tropical forests relies greatly on the niche partitioning processes that occur in this component of the environment, it seems advisable a careful consideration of the spatial structure of the environment in each analysis (Laliberté et al. 2009, Smith and Lundholm 2010). Overall, very relevant biological and ecological information, with an important bias towards scale-dependent processes, remains hidden in environmental gradients that have some kind of spatial structure.

Effects of environment are more important than those of space across scales

The fraction explained exclusively by the environment is on average double than that explained by the space alone, across scales and for most of the sub-regions, indicating a dominant role of deterministic processes *vs*. stochastic processes overall, as other authors indicate for a broad range of scales (Phillips et al. 2003, Macía et al. 2007, Ruokolainen et al. 2007, Jones et al. 2008b, Myers et al. 2013). Furthermore, the proportion of floristic variation explained by the space alone remains constant with the scale, suggesting that spatial processes are equally important at various scales, which constitutes a very unexpected result (Normand et al. 2006, Laliberté et al. 2009, Hu et al. 2012, López-Martínez et al. 2013). Such result is very unlikely to be biased by how the spatial distribution of plots is measured, because the PCNM describes the spatial patterns at any scale, and therefore is not sensitive to the spatial extent of the study region (Borcard and Legendre 2002).

Climate and soils both contribute to the environmental effect structuring floristic assemblages

Our results show that the environmental effect structuring local species assemblages is driven by both climatic and soil properties. Climate seems to have a scale independent effect that is stronger than the effect of soil, except at largest scales where both effects seem to be of similar magnitude. The relative large importance of climate is in agreement with previous works addressing long climatic gradients (Bjorholm et al. 2008, Slik et al. 2009, Blach-Overgaard et al. 2010), or long elevational gradients (Sesnie et al. 2009). In contrast, the increasing importance of soils with spatial extent is opposite to the pattern that has been proposed to be a general (reviewed by Siefert et al. 2012), whereby soils are expected to more strongly contribute to commnity structure at small scales. In tropical forests soils have been shown to be important at local (John et al. 2007, Jones et al. 2008a), intermediate (Costa et al. 2005, Bohlman et al. 2008, Andersen et al. 2010, 2012, Damasco et al. 2013), and regional scales (Tuomisto et al. 2003b, Vormisto et al. 2004, Macía et al. 2007, Guèze et al. 2013), mirroring our results. Previous studies that have evaluated the importance of soils often report greater importance that what we found; however, typically do not remove the variation that can also be explained by other alternative effects, like climate or spatial processes. By doing so, our results robustly demonstrate that heterogeneity in soils are a mechanism leading to community structure and beta-diversity across a very broad range of spatial scales.

CONCLUSIONS

The differential changes with scale of the different fractions and the high variability in the relative roles of different processes across and within scales indicate that further research is needed on community assembly along very heterogeneous landscapes. Moreover, given the fail (so far) of observational studies to achieve a consensus on the relative roles of different community-assembly processes, experimental approaches seem required to gain understanding on the community-assembly mechanisms in tropical forests. This is most recommended given that niche-assembly processes are very likely to differ along spatially structured *vs*. spatially un-structured environmental gradients, which represents the most important conclusion of the present work.

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CAPÍTULO 8

Conclusiones generales

La región Madidi presenta una serie de patrones ecológicos claramente determinados por el fuerte gradiente altitudinal. Esto mismo aplica directamente al caso particular de los bosques montanos, donde el gradiente altitudinal es el factor más relevante para entender los patrones de diversidad, distribución y dominancia de las plantas leñosas. Por ello, las conclusiones obtenidas a la mayor escala de estudio no difieren mucho de las que se obtienen del estudio particular de los bosques montanos.

Dominancia

Una parte importante del trabajo realizado se ha centrado en el estudio de los patrones de dominancia (y rareza) en la región Madidi a distintas escalas, teniendo la hipótesis de la oligarquía como eje central de análisis. La cuantificación de los patrones oligárquicos ha facilitado el estudio de los vínculos entre oligarquías y otros procesos importantes (reparto de nicho, procesos neutros, procesos biogeográficos) que dan forma a la composición florística y a la diversidad alfa, beta y gamma de los bosques tropicales. Las conclusiones alcanzadas en este bloque de trabajo son las siguientes:

(1) Los bosques montanos y amazónicos presentan siempre ciertas características oligárquicas, con una clara tendencia a que las especies más frecuentes sean más abundantes, y a que las menos frecuentes sean además escasas, independientemente del tipo de bosque, la escala espacial considerada, la heterogeneidad ambiental incluida y el enfoque metodológico adoptado.

(2) El patrón oligárquico es más intenso a mayor altitud y cuando hay menor diversidad gamma, independientemente de la escala espacial a la que se considere esta relación.

(3) Los bosques montanos andinos y los bosques amazónicos tienen el mismo patrón de dominancia a escala regional, ya que el 10−15% de las especies acumulan el 50−75% de los individuos. A pesar de compartir el mismo patrón regional, en los bosques amazónicos tienen mayor relevancia los procesos regionales en la distribución de las especies (*e.g.,* la dispersión de semillas a larga distancia), mientras que en los bosques montanos tienen más relevancia los procesos locales (*e.g.,* determinismo ambiental). La mayor importancia de los procesos locales frente a los procesos regionales aumenta con la altitud y se hace más patente en los bosques altimontanos.

(4) Las especies dominantes tienen nichos ecológicos más amplios que las especies raras. Sin embargo, hay diferencias importantes en la amplitud de nicho entre las diferentes especies dominantes, tanto dentro de un mismo hábitat como entre hábitats diferentes. En general, las especies dominantes en la Amazonía tienen nichos ecológicos más amplios que las especies dominantes del bosque andino. Por tanto, las

especies dominantes en los bosques amazónicos tienden a presentar una amplia distribución espacial y ecológica, mientras que la distribución espacial de las especies dominantes en los bosques montanos tiende a estar limitada a una franja altitudinal concreta.

(5) Para cualquier tipo de bosque tropical (seco, amazónico o montano), la identidad de sus especies dominantes viene dada en parte por las características biológicas propias de las especies, es decir, no es un proceso neutro. La característica más importante es la altura máxima que puede alcanzar una especie, lo que le otorga mayor capacidad de dispersión de sus semillas a larga distancia. El hábito también es una característica muy importante: las especies de árboles de dosel son más comunes que lo esperado por azar, mientras que las especies de árboles de sotobosque y lianas son más raras que lo esperado por azar.

Recambio de especies

Antes de entrar en las conclusiones alcanzadas en este apartado, conviene mencionar que existe un debate metodológico importante respecto a cuál es el modo idóneo de llevar a cabo la partición de la variación florística (el método empleado aquí para estudiar el recambio de especies), y cómo se han de interpretar los resultados de los diferentes análisis. En primer lugar, no existe un acuerdo respecto a qué fenómeno biológico estudia la partición de variación realizada sobre matrices de distancia (ver Legendre et al. 2005, 2008, Tuomisto y Ruokolainen 2006, 2008). Por otra parte y a raíz de lo anterior, se han puesto de relieve múltiples aspectos del diseño y análisis estadístico de la partición de la variación florística que tienen efectos muy importantes en los resultados y su interpretación, entre los que se incluyen: (a) la importancia del uso de coeficientes de determinación ajustados para el tamaño de muestra y el número de variables (*e.g.,* Legendre et al. 2008); (b) la interpretación de los resultados obtenidos tras una selección de variables y cómo ésta ha de llevarse a cabo (*e.g.,* Blanchet et al. 2008); (c) la pérdida de información no métrica y/o no euclidiana al reconstruir matrices de disimilitudes florísticas y el modo de remediarlo (*e.g.,* Legendre y Anderson 1999; McArdle y Anderson 2001); (d) el uso de disimilitudes florísticas extendidas cuando se usan índices de disimilitud saturables (*e.g.,* Tuomisto et al. 2012); (e) el impacto del índice de disimilitud florística empleado (*e.g.,* Legendre y De Cáceres 2013); (f) el impacto de la escala (*grain size*) empleado (*e.g.,* Hu et al. 2012); (g) el impacto de la calidad de la información espacial y ambiental incluida (*e.g.,* Jones et al. 2008).

Dado que el método de partición puede determinar los resultados obtenidos, hemos empleado un modelo nulo para poder controlar cualquier sesgo que pudiera existir en el método de partición de la variación. Aun así, y después de repetir los análisis con diferentes metodologías, los valores absolutos de varianza explicada han de tomarse con cierta cautela. Las conclusiones obtenidas en este bloque de trabajo son las siguientes:

(6) Existe una alta diversidad beta en la zona de estudio a escala regional, como era de esperar por el largo gradiente altitudinal considerado, pero también a escala local, con muchos pares de parcelas distantes menos de 1 km que no comparten ninguna especie.

(7) El peso relativo de los procesos espaciales y de los procesos ambientales sobre una comunidad vegetal, que se cuantifica con el porcentaje de variación florística total explicada, depende mucho de qué conjunto de parcelas se esté examinando, aunque esto se analice dentro de la misma región, con los mismos predictores, las mismas metodologías estadísticas, el mismo tamaño muestral y a la misma escala espacial.

(8) El ambiente y el espacio explican en promedio entre un tercio de la variación florística (a escalas locales, menos de 100 km^2) y un cuarto de la variación florística (a escalas regionales, más de 10.000 km^2) en la región Madidi. Las diferencias ambientales parecen ser más importantes para la composición florística que los procesos espaciales. Dentro de los procesos determinísticos, la influencia del clima predomina frente a la influencia del suelo.

(9) En la región Madidi existe una fuerte disminución en la cantidad de variación florística explicada por el ambiente espacialmente estructurado a grandes escalas, mientras que las cantidades de variación florística explicada por otros factores presentan cambios mucho menores. Esto tiene dos implicaciones importantes: (a) la mayor parte de los procesos dependientes de la escala espacial se concentran en la equívoca fracción conjunta, sin que se pueda inferir si son procesos espaciales o procesos ambientales; y (b) obtener conclusiones a partir de las fracciones “puras” (la variación florística explicada solamente por el ambiente y la variación florística explicada solamente por el espacio) está introduciendo un sesgo importante hacia procesos que no son apenas dependientes de la escala.

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APÉNDICES

Appendixes

Apéndice 1. Abundancia de las especies y morfoespecies encontradas en 54 parcelas de bosque montano, durante el inventario de seis sitios en tres bandas altitudinales en el noroeste de Bolivia (Figura 1.2). En el caso de las morfoespecies se remite a un especímen representativo depositado en el Herbario Nacional de Bolivia. La elección de estos especímenes representativos se llevó a cabo durante la homogeneización del criterio taxonómico e identificación de todas las colecciones botánicas realizadas en la región Madidi, ya que al ser muestras fértiles o de la mejor calidad posible tendrían más probabilidades de ser determinadas por un botánico especialista.

Appendix 1. Abundances of the species and morphospecies found in 54 plots in montane forests, during the inventory of six sites in three elevational bands in northwestern Bolivia (Figure 1.2). In the case of morphospecies it refers to the information of a representative specimen kept in the Herbario Nacional de Bolivia. The choice of these representative specimens was taken during the homogeneization of the taxonomic corterion and determination of all the collected specimens of the Madidi region, and are those with fertile material or the best available quality, and therefore more likely to be identified by a botanic specialist.

Familias y especies	1200−1500 m		2000−2300 m		2800−3100 m	
	Culi	Victopampa	Santa Ana	Lambramani	Piara	Cocapunco
Acanthaceae						
Aphelandra castanifolia Britton ex Rusby				15		
Mendoncia aspera (Ruiz & Pav.) Nees	1					
Mendoncia lindavii Rusby	1					
Actinidiaceae						
Saurauia glabra (Ruiz & Pav.) Soejarto	4	22	30	24	24	
Saurauia peruviana Buscal.					23	
Saurauia aff. *spectabilis* Hook. = L. Cayola - 2601			27			
Saurauia = Gabriel Arellano - 355			3			
Adoxaceae						
Viburnum seemanii (Gand.) Killip & A.C. Sm.		1	7			1
Amaranthaceae						
Chamissoa altissima (Jacq.) Kunth	2					
Hebanthe occidentalis (R.E. Fr.) Borsch & Pedersen	9			4		

Familias y especies	1200−1500 m		2000−2300 m		2800−3100 m	
	Culi	Victopampa	Santa Ana	Lambramani	Piara	Cocapunco
Anacardiaceae						
Mauria heterophylla Kunth	2		1	1		
Tapirira guianensis Aubl.	35	55				
Annonaceae						
Cremastosperma leiophyllum (Diels) R.E.Fr.		14				
Guatteria alutacea Diels		2				
Guatteria boliviana H.J.P.Winkl.	13	56		1		
Guatteria glauca Ruiz & Pav.	65	21	1			
Guatteria oblongifolia Rusby		22		9		
Guatteria tomentosa Rusby	2	5				
Rollinia boliviana (R.E.Fr.) H.Rainer	11			3		
Rollinia pittieri Saff.				2		
Rollinia = Gabriel Arellano - 1707		3		2		
Rollinia = Alfredo F. Fuentes - 17010		6				
Apocynaceae						
Aspidosperma rigidum Rusby	1					
Forsteronia amblybasis S.F.Blake	1					
Forsteronia = Gabriel Arellano - 2267		1				
Mandevilla glandulosa (Ruiz & Pav.) Woodson			1			
Odontadenia laxiflora (Rusby) Woodson	1					
Odontadenia puncticulosa (Rich.) Pulle		11				
Orthosia guilleminiana (Decne.) Liede & Meve			1			
Rauvolfia sprucei Müll.Arg.	2	3				
Apocynaceae = Gabriel Arellano - 582	3					

Familias y especies	1200−1500 m		2000−2300 m		2800−3100 m	
	Culi	Victopampa	Santa Ana	Lambramani	Piara	Cocapunco
Aquifoliaceae						
Ilex amplifolia Rusby		4				
Ilex andicola Loes.						14
Ilex goudotii Loes.			1	1		
Ilex mandonii Loes.						14
Ilex nervosa Triana & Planch.				13	15	9
Ilex aff. *nervosa* Triana & Planch. = L. Cayola - 2925B			1			
Ilex petiolaris Benth.		5				
Ilex = Gabriel Arellano - 911	1					
Ilex = Gabriel Arellano - 1615A	4	1				
Ilex = Gabriel Arellano - 2706						7
Ilex = Gabriel Arellano - 2758						88
Ilex = Gabriel Arellano - 2856						8
Ilex = Gabriel Arellano - 3121				2		
Ilex = Gabriel Arellano - 3278				1		
Ilex = L. Samo - 19						6
Ilex = Alejandro Araujo M. - 3498						24
Araliaceae						
Dendropanax inaequalipedunculatus J. Wen & A. Fuentes	11			31		
Dendropanax membranaceus J. Wen & A. Fuentes	12					
Dendropanax williamsii (Harms) Harms		12				
Dendropanax yungasensis A. Fuentes		7				
Oreopanax membranaceus Rusby	2		1		3	
Oreopanax rusbyi Britton						6
Oreopanax steinbachianus Harms			13		4	

Familias y especies	1200−1500 m		2000−2300 m		2800−3100 m	
	Culi	Victopampa	Santa Ana	Lambramani	Piara	Cocapunco
Oreopanax = Gabriel Arellano - 1676		5				
Oreopanax = Gabriel Arellano - 2857						22
Oreopanax = Gabriel Arellano - 2973				8		
Schefflera herzogii Harms		5	19			66
Schefflera tipuanica Harms			6	1		
Schefflera aff. *trollii* = E. Cachaca - 54					9	
Schefflera = Gabriel Arellano - 1589		33				
Schefflera = Gabriel Arellano - 1618		12				
Schefflera = Alfredo F. Fuentes - 9709				5		
Arecaceae						
Bactris acanthocarpa Mart.	4					
Ceroxylon parvifrons (Engel) H.Wendl.						4
Dictyocaryum lamarckianum (Mart.) H.Wendl.	5	17				
Euterpe precatoria Mart.	29	55				
Geonoma densa Linden & H.Wendl.			16			
Geonoma undata Klotzsch	3	14	4			11
Iriartea deltoidea Ruiz & Pav.	4	1				
Oenocarpus bataua Mart.	1	5				
Socratea exorrhiza (Mart.) H.Wendl.	12					
Asteraceae						
Aspilia aurantiaca Griseb.			3			
Baccharis brachylaenoides DC.					5	4
Baccharis = Gabriel Arellano - 530			2			
Baccharis = Gabriel Arellano - 2564					4	
Baccharis = L.M. Quiñones - 50			1		126	
Baccharis = I. Loza - 644					2	

Familias y especies	1200−1500 m		2000−2300 m		2800−3100 m	
	Culi	Victopampa	Santa Ana	Lambramani	Piara	Cocapunco
Baccharis = L. Cayola - 3483					1	
Baccharis = L. Cayola - 3709					1	
Baccharis = L. Cayola - 3720					11	
Baccharis = Carla Maldonado - 3031					1	
Bidens = Gabriel Arellano - 287			1			
Critoniopsis boliviana (Britton) H.Rob.	2	4	16	17		
Dendrophorbium multinerve (Sch.Bip. ex Klatt) C.Jeffrey					26	
Gynoxys = Gabriel Arellano - 2600					1	
Liabum solidagineum (Kunth) Less.			1		2	
Mikania banisteriae DC.					1	
Mikania aff. *cordifolia* (L.f.) Willd. = Gabriel Arellano - 286			1			
Mikania ferruginea DC.				1		
Mikania guaco Bonpl.		2		3		
Mikania psilostachya DC.				3		
Mikania simpsonii W.C.Holmes & McDaniel		9		1		
Mikania steinbachii B.L.Rob.		1		1		
Mikania urticifolia Hook. & Arn.			6	2		
Mikania = Gabriel Arellano - 915	1					
Mikania = Gabriel Arellano - 1548		1				
Mikania = M. Cornejo - 237				2	1	
Munnozia hastifolia (Poepp.) H.Rob. & Brettell	1		1	1		
Munnozia senecionidis Benth.					1	
Nordenstamia repanda (Wedd.) Lundin					17	1
Ophryosporus axilliflorus (Griseb.) Hieron.					5	
Pentacalia floccosa (Britton) Cuatrec.				1		
Pentacalia jelskii (Hieron.) Cuatrec.			1			

Familias y especies	1200−1500 m		2000−2300 m		2800−3100 m	
	Culi	Victopampa	Santa Ana	Lambramani	Piara	Cocapunco
Pentacalia oronocensis (DC.) Cuatrec.			9	2	9	1
Pentacalia psidiifolia (Rusby) Cuatrec.			2			
Pentacalia = Gabriel Arellano - 959	4	1	1			
Pentacalia = Gabriel Arellano - 2939				2		
Pentacalia = Alfredo F. Fuentes - 17352		3				
Pluchea = Gabriel Arellano - 479			1			
Senecio curvidens Sch.Bip.				33		2
Senecio = Gabriel Arellano - 197			3			
Vernonia patens Kunth					10	
Vernonia = Gabriel Arellano - 2960				5		
Asteraceae = Gabriel Arellano - 614	1					
Asteraceae = Gabriel Arellano - 913	2					
Asteraceae = Gabriel Arellano - 2410					1	
Asteraceae = Gabriel Arellano - 2574					5	
Asteraceae = Gabriel Arellano - 2626					2	
Asteraceae = Gabriel Arellano - 2968				1		
Asteraceae = Gabriel Arellano - 3015				1		
Asteraceae = Gabriel Arellano - 3045				4		
Basellaceae						
Anredera tucumanensis (Lillo & Hauman) Sperling	1					
Begoniaceae						
Begonia parviflora Poepp. & Endl.	1		29	6		
Bignoniaceae						
Arrabidaea egensis (Poepp. ex Bureau & K.Schum.) L.G.Lohmann		2				
Arrabidaea florida (DC.) L.G.Lohmann	1	17				
Arrabidaea patellifera (Schltdl.) L.G.Lohmann	1	13				

Familias y especies	1200−1500 m		2000−2300 m		2800−3100 m	
	Culi	Victopampa	Santa Ana	Lambramani	Piara	Cocapunco
Arrabidaea pearcei (Rusby) L.G.Lohmann	1	1				
Arrabidaea poeppigii (DC.) L.G.Lohmann	1					
Jacaranda glabra (DC.) Bureau & K.Schum.		7				
Bignoniaceae = Gabriel Arellano - 1839		1				
Boraginaceae						
Cordia = Gabriel Arellano - 3169				1		
Cordia = Carla Maldonado - 1815		1				
Brunelliaceae						
Brunellia boliviana Britton ex Rusby			7		1	2
Brunellia rhoides Rusby				3	1	
Brunellia sibundoya Cuatrec.						53
Burseraceae						
Dacryodes aff. *belemensis* Cuatrec. = Gabriel Arellano - 903	1	4				
Protium meridionale Swart	3					
Protium aff. *montanum* Swart = Alfredo F. Fuentes - 15374	55	52				
Buxaceae						
Styloceras columnare Müll.Arg.			8			
Styloceras aff. *laurifolium* (Willd.) Kunth = Gabriel Arellano - 269			7			
Calophyllaceae						
Calophyllum brasiliense Cambess.	3	16		1		
Calophyllum longifolium Willd.	6					
Campanulaceae						
Centropogon = Gabriel Arellano - 2576					1	
Siphocampylus angustiflorus Schltr. & Zahlbr.						1
Siphocampylus dubius Zahlbr.			1			
Siphocampylus membranaceus Britton	3					

Familias y especies	1200−1500 m		2000−2300 m		2800−3100 m	
	Culi	Victopampa	Santa Ana	Lambramani	Piara	Cocapunco
Siphocampylus orbignianus A.DC.					5	
Siphocampylus aff. *flagelliformis* Zahlbr. = E. Cachaca - 20					1	
Cannabaceae						
Celtis iguanaea (Jacq.) Sarg.	3					
Lozanella permollis Killip & C.V.Morton			5			
Trema micrantha (L.) Blume	1					
Capparaceae						
Capparis detonsa Triana & Planch.		4				
Caprifoliaceae						
Valeriana clematitis Kunth					4	
Cardiopteridaceae						
Citronella incarum (J.F.Macbr.) R.A.Howard			1	1		
Caricaceae						
Vasconcellea microcarpa (Jacq.) A.DC.				1		
Caryocaraceae						
Caryocar dentatum Gleason	4					
Celastraceae						
Celastrus liebmannii Standl.		7		2		
Cheiloclinium cognatum (Miers) A.C.Sm.	7					
Cheiloclinium = Gabriel Arellano - 2107		2				
Maytenus conferta (Ruiz & Pav.) Reissek ex Loes.					1	1
Maytenus jelskii Zahlbr.			2		17	
Maytenus verticillata (Ruiz & Pav.) DC.			5			
Peritassa = Alfredo F. Fuentes - 17100	2					
Salacia impressifolia (Miers) A.C.Sm.		1				

Familias y especies	1200−1500 m		2000−2300 m		2800−3100 m	
	Culi	Victopampa	Santa Ana	Lambramani	Piara	Cocapunco
Chloranthaceae						
Hedyosmum angustifolium (Ruiz & Pav.) Solms			44		235	
Hedyosmum cuatrecazanum Occhioni			62	23		
Hedyosmum dombeyanum Solms				61	70	81
Hedyosmum racemosum (Ruiz & Pav.) G.Don	51	60	131			
Hedyosmum = L. Cayola - 3757						2
Hedyosmum = Alejandro Araujo M. - 2852			22		230	
Chrysobalanaceae						
Hirtella = R. Villegas - 613	2					
Licania boliviensis Prance	10	2				
Licania = Gabriel Arellano - 2079		1				
Parinari klugii Prance	2					
Parinari occidentalis Prance	1					
Clethraceae						
Clethra cuneata Rusby			51		78	
Clethra elongata Rusby		1		3		5
Clethra obovata (Ruiz & Pav.) G.Don					6	
Clethra pedicellaris Turcz.			34			
Clethra revoluta (Ruiz & Pav.) Spreng.			26	7	29	4
Clethra scabra Pers.	1			5	2	159
Clethra aff. *fimbriata* Kunth = L. Cayola - 3724					33	
Clethra = L. Samo - 14					1	53
Clethra = Alfredo F. Fuentes - 16188						11

Familias y especies	1200−1500 m		2000−2300 m		2800−3100 m	
	Culi	Victopampa	Santa Ana	Lambramani	Piara	Cocapunco
Clusiaceae						
Chrysochlamys weberbaueri Engl.	1	1				
Clusia ducu Benth.				12		
Clusia elongata Rusby				6		
Clusia lechleri Rusby			9	3		
Clusia martiana Engl.	4					
Clusia sphaerocarpa Planch. & Triana					122	827
Clusia ternstroemioides Rusby					42	
Clusia trochiformis Vesqne	10	5	57	32		
Clusia = Alfredo F. Fuentes - 14913			106			
Clusia = I. Loza - 1862				1		
Clusia = Alfredo F. Fuentes - 6150	2					
Garcinia macrophylla Mart.	6					
Symphonia globulifera L.f.	26	19				
Tovomita brasiliensis (Mart.) Walp.		6				
Tovomita weddelliana Planch. & Triana		9				
Tovomita = Gabriel Arellano - 1568		54		2		
Columelliaceae						
Desfontainia spinosa Ruiz & Pav.						111
Combretaceae						
Terminalia amazonia (J.F.Gmel.) Exell		1				
Convolvulaceae						
Dicranostyles ampla Ducke		3				
Dicranostyles mildbraediana Pilg.		4				

Familias y especies	1200−1500 m		2000−2300 m		2800−3100 m	
	Culi	Victopampa	Santa Ana	Lambramani	Piara	Cocapunco
Cunoniaceae						
Weinmannia balbisiana Kunth						24
Weinmannia bangii Rusby						3
Weinmannia crassifolia Ruiz & Pav.					166	3
Weinmannia cundinamarcensis Cuatrec.				6		
Weinmannia davidsonii A.Fuentes & Z.S.Rogers					8	216
Weinmannia fagaroides Kunth						1
Weinmannia lechleriana Engl.		1		9		
Weinmannia lentiscifolia C.Presl						1
Weinmannia microphylla Kunth						294
Weinmannia multijuga Killip & A.C.Sm.					3	
Weinmannia ovata Cav.				19		
Weinmannia pinnata L.			3		134	
Weinmannia sorbifolia Kunth				1		
Weinmannia yungasensis A. Fuentes & Z.S. Rogers						297
Weinmannia aff. *bangii* Rusby = Gabriel Arellano - 2815						2
Weinmannia aff. *davidsonii* A. Fuentes & Z.S. Rogers = Gabriel Arellano - 2549					2	
Weinmannia aff. *yungasensis* A. Fuentes & Z.S. Rogers = Gabriel Arellano - 2814						1
Weinmannia = Gabriel Arellano - 2788						213
Cyatheaceae						
Alsophila cuspidata (Kunze) D.S. Conant	5	9				
Alsophila erinacea (H. Karst.) D.S. Conant				139		
Cyathea austropallescens Lehnert					1	44
Cyathea bipinnatifida (Baker) Domin	35	15				

Familias y especies	1200−1500 m		2000−2300 m		2800−3100 m	
	Culi	Victopampa	Santa Ana	Lambramani	Piara	Cocapunco
Cyathea brevistipes Sodiro						3
Cyathea caracasana (Klotzsch) Domin	1	16	19	64		12
Cyathea conjugata (Spruce ex Hook.) Domin			1	2		
Cyathea delgadii Sternb.	12	18		1		
Cyathea herzogii H. Karst.				116		30
Cyathea lechleri Mett.	1	11		1		
Cyathea ruiziana Klotzsch			1			
Cyathea xenoxyla Lehnert				5		
Cyathea = L.M. Quiñones - 129				1		
Dicksoniaceae						
Dicksonia sellowiana Hook.				21		
Dilleniaceae						
Davilla kunthii A.St.-Hil.		2				
Davilla = Gabriel Arellano - 2264		1				
Doliocarpus dentatus (Aubl.) Standl.	3	8				
Elaeocarpaceae						
Sloanea eichleri K.Schum.		3				
Sloanea fragrans Rusby	1					
Sloanea grandiflora Sm.		1				
Sloanea multiflora H.Karst.	1	2				
Sloanea = A.L. Moya Huanca - 230	1					
Vallea stipularis L.f.					23	
Ericaceae						
Bejaria aestuans Mutis ex L.			14			
Cavendishia bracteata (Ruiz & Pav. ex J.St.Hil.) Hoerold				11	166	1
Cavendishia martii (Meisn.) A.C.Sm.			1			

Familias y especies	1200−1500 m		2000−2300 m		2800−3100 m	
	Culi	Victopampa	Santa Ana	Lambramani	Piara	Cocapunco
Cavendishia pubescens (Kunth) Hemsl.			6			
Gaultheria bracteata (Cav.) G.Don						2
Gaultheria buxifolia Willd.					4	3
Gaultheria erecta Vent.						3
Gaultheria eriophylla (Pers.) Mart. ex Sleumer			10			
Gaultheria reticulata Kunth			7		27	
Polyclita turbinata (Kuntze) A.C. Sm.						33
Psammisia coarctata (Ruiz & Pav.) A.C. Sm.	10	17				
Psammisia urichiana (Britton) A.C.Sm.	11					
Thibaudia crenulata J. Rémy					15	
Thibaudia floribunda Kunth						5
Thibaudia macrocalyx J. Rémy						1
Vaccinium dependens (G. Don) Sleumer					7	
Erythroxylaceae						
Erythroxylum citrifolium A.St.-Hil.	1	2				
Erythroxylum macrophyllum Cav.	2					
Erythroxylum aff. *citrifolium* A.St.-Hil. = Gabriel Arellano - 1804		2				
Erythroxylum = Gabriel Arellano - 2083		3				
Escalloniaceae						
Escallonia myrtilloides L.f.					5	
Escallonia paniculata (Ruiz & Pav.) Schult.			4			
Euphorbiaceae						
Acalypha macrostachya Jacq.	2					
Alchornea anamariae Secco				3		
Alchornea brittonii Secco			3		9	
Alchornea glandulosa Poepp.	39	26	73	37		

Familias y especies	1200−1500 m		2000−2300 m		2800−3100 m	
	Culi	Victopampa	Santa Ana	Lambramani	Piara	Cocapunco
Alchornea grandiflora Müll.Arg.			37	19		
Alchornea triplinervia (Spreng.) Müll.Arg.	3	5				
Aparisthmium cordatum (A.Juss.) Baill.	90	73				
Chaetocarpus myrsinites Baill.	15	18				
Croton piluliferus Rusby			8			
Croton = Gabriel Arellano - 3235				1		
Croton = Gabriel Arellano - 3012				5		
Sapium = A. Escalante - 369				1		
Tetrorchidium ochroleucum Cuatrec.			2			
Fabaceae						
Abarema jupunba (Willd.) Britton & Killip	1	9				
Amicia lobbiana Benth.					6	
Chaetocalyx = Gabriel Arellano - 711	1					
Collaea speciosa (Loisel.) DC.					1	
Dalbergia frutescens (Vell.) Britton		2				
Dalbergia spruceana (Benth.) Benth.		7				
Diplotropis peruviana J.F.Macbr.		2				
Inga acreana Harms	4	9				
Inga alba (Sw.) Willd.	4	11				
Inga bourgonii (Aubl.) DC.		1				
Inga fendleriana Benth.	1	2	1	6		
Inga heterophylla Willd.	3	2				
Inga laurina (Sw.) Willd.		1				
Inga lopadadenia Harms	2					
Inga marginata Kunth		3				
Inga nobilis Willd.	1					

Familias y especies	1200−1500 m		2000−2300 m		2800−3100 m	
	Culi	Victopampa	Santa Ana	Lambramani	Piara	Cocapunco
Inga striata Benth.		3				
Inga thibaudiana DC.		8				
Inga ynga Mart.	7					
Inga aff. *striolata* T.D.Penn. = Gabriel Arellano - 1258	1	2				
Inga = M. Cornejo - 169	1	23				
Inga = M. Cornejo - 1384		1				
Inga = K. Naoki - 171	6	7				
Inga = Alejandro Araujo M. - 3592A			2			
Machaerium amplum Benth.		1				
Machaerium aff. *complanatum* Ducke = Gabriel Arellano - 1801	1	10				
Machaerium floribundum Benth.	4					
Machaerium multifoliolatum Ducke		1				
Ormosia coarctata Jacks.	1					
Ormosia = Gabriel Arellano - 2043		52				
Stryphnodendron guianense (Aubl.) Benth.		10				
Swartzia simplex (Sw.) Spreng.		1				
Tachigali = Gabriel Arellano - 1956		5				
Gentianaceae						
Macrocarpaea bangiana Gilg				1		
Macrocarpaea cinchonifolia (Gilg) Weaver	2	1	1	3		
Macrocarpaea cochabambensis Gilg-Ben.						21
Tachia parviflora Maguire & Weaver		2				
Gesneriaceae						
Besleria longipedunculata Britton		2				
Columnea = Gabriel Arellano - 785	1					
Columnea = Gabriel Arellano - 943	1					

Familias y especies	1200−1500 m		2000−2300 m		2800−3100 m	
	Culi	Victopampa	Santa Ana	Lambramani	Piara	Cocapunco
Gesneriaceae = Gabriel Arellano - 1204	1					
Hydrangeaceae						
Hydrangea = Gabriel Arellano - 1405	2					
Hypericaceae						
Vismia glabra Ruiz & Pav.	3					
Vismia subcuneata Huber	1					
Lacistemataceae						
Lacistema aggregatum (P.J.Bergius) Rusby	7	6				
Lamiaceae						
Aegiphila herzogii Moldenke			1			
Hyptis tafallae Benth.			11			
Lauraceae						
Aiouea = Alfredo F. Fuentes - 9030	2					
Aniba guianensis Aubl.	1					
Aniba muca (Ruiz & Pav.) Mez	17			13		
Aniba perutilis Hemsl.	1					
Beilschmiedia tovarensis (Klotzsch & H.Karst. ex Meisn.) Sachiko Nishida	18	36	3	11		
Cinnamomum triplinerve (Ruiz & Pav.) Kosterm.		1				
Cinnamomum = F. Zenteno - 1488	5	2				
Cinnamomum = Alejandro Araujo M. - 3551				2		
Cryptocarya = Renate Seidel - 7155	1					
Endlicheria aurea Chanderb.		2				
Endlicheria canescens Chanderbali	8	6				
Endlicheria szyszylowiczii Mez	8	5				
Licaria pucheri (Ruiz & Pav.) Kosterm.	2					
Nectandra acutifolia (Ruiz & Pav.) Mez		8	1			

Familias y especies	1200−1500 m		2000−2300 m		2800−3100 m	
	Culi	Victopampa	Santa Ana	Lambramani	Piara	Cocapunco
Nectandra cissiflora Nees	1		5			
Nectandra cuspidata Nees & Mart.		1		2		
Nectandra laurel Klotzsch ex Nees			53	2		
Nectandra membranacea Nees & Mart.		2				
Nectandra sordida Rohwer	9		3	5		
Nectandra = I. Loza - 334B	4	1		1		
Nectandra = I. Loza - 1006		21	2			
Nectandra = Carla Maldonado - 2353		4				
Nectandra = James C. Solomon - 9565	52					
Ocotea aciphylla (Nees & Mart.) Mez	91	29				
Ocotea albida Mez & Rusby			66	2		
Ocotea cernua (Nees) Mez	1	11				
Ocotea cuprea (Meisn.) Mez	39	11				
Ocotea floribunda (Sw.) Mez			2			
Ocotea jelskii Mez		2				
Ocotea longifolia Kunth				4		
Ocotea mandonii Mez					8	5
Ocotea olivacea A.C.Sm.		1				
Ocotea aff. *camphoromoea* Rohwer = L. Cayola - 4144A	6					
Ocotea aff. *guianensis* Aubl. = Gabriel Arellano - 964	1					
Ocotea aff. *longifolia* Kunth = N. Chapi - 247	1	1				
Ocotea aff. *mandonii* Mez = Alfredo F. Fuentes - 12244				2		
Ocotea = Gabriel Arellano - 1035	7	15				
Ocotea = Gabriel Arellano - 1562	1	1				
Ocotea = Gabriel Arellano - 2421					17	
Ocotea = Gabriel Arellano - 2780						38

Familias y especies	1200−1500 m		2000−2300 m		2800−3100 m	
	Culi	Victopampa	Santa Ana	Lambramani	Piara	Cocapunco
Ocotea = Gabriel Arellano - 3200				2		
Ocotea = Alfredo F. Fuentes - 15396				3		
Ocotea = A.L. Moya Huanca - 253		1				
Ocotea = M. Reguerin - 14				2		
Ocotea = R. Sonco - 25			4			
Ocotea = A. Escalante - 147		1				
Ocotea = A. Escalante - 335	1					
Ocotea = I. Loza - 1334			1			
Ocotea = M. Cornejo - 1281				97		
Ocotea = L. Cayola - 4365A	1	1				
Ocotea = A. Antezana - 113		5				
Ocotea = N. Chapi - 209		1	2	2		
Ocotea = Alejandro Araujo M. - 3387	2	26				
Ocotea = Alejandro Araujo M. - 3644				7		
Ocotea = J. Gutierrez - 38			4			
Persea areolatocostae (C.K.Allen) van der Werff	10	5		7		
Persea peruviana Nees	8	3				
Persea pseudofasciculata L.E.Kopp	7	3				
Persea sphaerocarpa (H.J.P.Winkl.) Kosterm.	1					
Persea subcordata (Ruiz & Pav.) Nees	2	1		2	2	
Persea aff. *ferruginea* J.F.Macbr. = L. Samo - 27						24
Persea aff. *pseudofasciculata* L.E.Kopp = Gabriel Arellano - 1675		3				
Persea aff. *subcordata* (Ruiz & Pav.) Nees = Alejandro Araujo M. - 3320	2			8		
Persea = Gabriel Arellano - 2838						2
Persea = Alfredo F. Fuentes - 12172				4		
Persea = Alfredo F. Fuentes - 12248			13			

Familias y especies	1200−1500 m		2000−2300 m		2800−3100 m	
	Culi	Victopampa	Santa Ana	Lambramani	Piara	Cocapunco
Persea = Alfredo F. Fuentes - 15025A	1				14	5
Persea = Alfredo F. Fuentes - 15646					11	89
Persea = L. Cayola - 3703					8	
Pleurothyrium trianae (Mez) Rohwer	11					
Pleurothyrium = N. Chapi - 118	3	52				
Rhodostemonodaphne kunthiana (Nees) Rohwer	4	9				
Rhodostemonodaphne = Gabriel Arellano - 755	4					
Lauraceae = A. Escalante - 387		1				
Linaceae						
Roucheria laxiflora H.J.P.Winkl.		37				
Loranthaceae						
Gaiadendron punctatum (Ruiz & Pav.) G.Don		4			6	48
Magnoliaceae						
Magnolia = Carla Maldonado - 2546	2					
Malpighiaceae						
Banisteriopsis padifolia (Poepp. ex Nied.) B.Gates	2					
Bunchosia armeniaca (Cav.) DC.		2	6	2		
Byrsonima arthropoda A.Juss.		1				
Tetrapterys styloptera A.Juss.	3					
Malpighiaceae = Gabriel Arellano - 997	1					
Malvaceae						
Malvaceae = Gabriel Arellano - 3223				2		
Marcgraviaceae						
Marcgravia flagellaris (Poepp. ex Wittm.) Poepp. ex Gilg & Werderm.				1		
Marcgravia oblongifolia Ruiz ex Wittm.	2					
Ruyschia andina de Roon		1				

Familias y especies	1200−1500 m		2000−2300 m		2800−3100 m	
	Culi	Victopampa	Santa Ana	Lambramani	Piara	Cocapunco
Sarcopera oxystylis (Baill.) Bedell ex Giraldo-Cañas				1		
Souroubea fragilis de Roon	2		2			
Melastomataceae						
Axinaea glandulosa Ruiz & Pav. ex D. Don					27	
Axinaea lanceolata Ruiz & Pav.				3		
Axinaea = Gabriel Arellano - 2376					3	
Axinaea = J. Gutierrez - 31					12	
Blakea repens (Ruiz & Pav.) D. Don	1	4				
Blakea rosea (Ruiz & Pav.) D. Don	5					
Brachyotum microdon (Naudin) Triana					4	
Clidemia capitellata (Bonpl.) D. Don			1	3		
Clidemia = Gabriel Arellano - 1586	15	1				
Graffenrieda boliviensis Triana		7				
Graffenrieda conostegioides Triana	2					
Graffenrieda cucullata (Triana) L.O. Williams	1					
Graffenrieda emarginata (Ruiz & Pav.) Triana	15	11		12		
Graffenrieda = F. Bascopé - 64	4			22		
Loreya gracilis S.S. Renner	7	4				
Meriania axinioides Gleason	12			19		
Meriania brittoniana Wurdack		2	1	2		
Meriania aff. *axinioides* Gleason = Alfredo F. Fuentes - 17180	1					
Meriania = Gabriel Arellano - 3016				2		
Meriania = Gabriel Arellano - 3281				1		
Miconia amnicola Wurdack	2	1				
Miconia aureoides Cogn.	5					
Miconia axinaeoides Gleason	6					

Familias y especies	1200−1500 m		2000−2300 m		2800−3100 m	
	Culi	Victopampa	Santa Ana	Lambramani	Piara	Cocapunco
Miconia bangii Cogn.	1			1		
Miconia barbeyana Cogn.	7	14	4	11		
Miconia biacuta Cogn.						32
Miconia brittonii (Cogn.) Kuntze	1		85	39		
Miconia calvescens DC.	35	3	6			
Miconia centrodesma Naudin	15	25		1		
Miconia chrysophylla (Rich.) Urb.		1				
Miconia cordata (Triana) Kuntze			2	37		
Miconia cyanocarpa Naudin	5	12	134	9		
Miconia dispar Benth.		15				
Miconia dodecandra Cogn.	18	3				
Miconia dolichorrhyncha Naudin	1					
Miconia elongata Cogn.	2					
Miconia flavescens (Cogn.) Kuntze						131
Miconia herzogii Cogn.		1				
Miconia hygrophila Naudin			52			
Miconia lasiocalyx Cogn.			4	7		
Miconia matthaei Naudin	3					
Miconia micrantha Pittier		1				
Miconia micropetala Cogn.				6	10	308
Miconia minutiflora (Bonpl.) DC.	25	25				
Miconia multispicata Naudin		7				
Miconia obovalis (Sw.) Griseb.	11	25				
Miconia pilgeriana Naudin	18	5	5			
Miconia plumifera Triana					5	2
Miconia poeppigii Triana		1				

Familias y especies	1200−1500 m		2000−2300 m		2800−3100 m	
	Culi	Victopampa	Santa Ana	Lambramani	Piara	Cocapunco
Miconia polygama (Cogn.) Kuntze				1		
Miconia prasina (Sw.) DC.				2		
Miconia punctata (Desr.) D. Don ex DC.	73	57				
Miconia quadrialata S.S. Renner & S. Beck						13
Miconia ruizii Naudin	15					
Miconia rupticalyx Wurdack	3					
Miconia spennerostachya Naudin		7				
Miconia symplectocaulos (Rich.) D. Don ex DC.	1					
Miconia theiformis Triana					75	2
Miconia theizans (Bonpl.) Cogn.		3	5	19	21	
Miconia undata Triana	2	1		12		
Miconia aff. *dolichorrhyncha* Naudin = L. Cayola - 4350A	7	2				
Miconia aff. *theizans* (Bonpl.) Cogn. = Gabriel Arellano - 2775						1
Miconia = Gabriel Arellano - 234			1			
Miconia = Gabriel Arellano - 596	12					
Miconia = Gabriel Arellano - 860	40	2	4			
Miconia = Gabriel Arellano - 876	3			23		
Miconia = Gabriel Arellano - 1158	1					
Miconia = Gabriel Arellano - 1254	16					
Miconia = Gabriel Arellano - 1560		8		1		
Miconia = Gabriel Arellano - 1582		1				
Miconia = Gabriel Arellano - 2322					2	
Miconia = Gabriel Arellano - 2395					5	
Miconia = Gabriel Arellano - 2743						3
Miconia = Gabriel Arellano - 2916				1		
Miconia = Gabriel Arellano - 2926				3		

Familias y especies	1200−1500 m		2000−2300 m		2800−3100 m	
	Culi	Victopampa	Santa Ana	Lambramani	Piara	Cocapunco
Miconia = Gabriel Arellano - 2928				19		
Miconia = Gabriel Arellano - 2941				1		
Miconia = Gabriel Arellano - 3209				43		
Miconia = Gabriel Arellano - 3261				1		
Miconia = R. Sonco - 89				7		
Miconia = A. Escalante - 165						1
Miconia = A. Escalante - 285	9	11		12		
Miconia = L. Cayola - 3463					7	
Miconia = L. Cayola - 3529					5	
Miconia = E. Cachaca - 22					3	28
Miconia = M. Cornejo - 1237			4			
Miconia = Alejandro Araujo M. - 290	7					
Miconia = Alfredo F. Fuentes - 8768						32
Miconia = Alfredo F. Fuentes - 10678						80
Miconia = Alfredo F. Fuentes - 17127	106					
Mouriri = L. Cayola - 4151A	1					
Tibouchina bicolor (Naudin) Cogn.					25	
Tococa erioneura (Cogn.) Wurdack		1		1		
Topobea multiflora (D. Don) Triana	3	2	5	12		
Meliaceae						
Cabralea canjerana (Vell.) Mart.	1			2		
Cedrela fissilis Vell.				2		
Cedrela odorata L.		1				
Guarea kunthiana A.Juss.	1			34		
Ruagea glabra Triana & Planch.				6	9	
Ruagea ovalis (Rusby) Harms			2	18		

Familias y especies	1200–1500 m		2000–2300 m		2800–3100 m	
	Culi	Victopampa	Santa Ana	Lambramani	Piara	Cocapunco
Ruagea aff. *tomentosa* Cuatrec. = Alejandro Araujo M. - 3480		2		1		
Trichilia septentrionalis C.DC.		1				
Meliaceae = Gabriel Arellano - 1946		1				
Menispermaceae						
Abuta aff. *imene* (Mart.) Eichler = Gabriel Arellano - 2118		1				
Abuta = Gabriel Arellano - 1984		1				
Hyperbaena = Gabriel Arellano - 1774		5				
Orthomene schomburgkii (Miers) Barneby & Krukoff	10	13				
Menispermaceae = Gabriel Arellano - 1140B	1					
Menispermaceae = Gabriel Arellano - 1653		5				
Menispermaceae = Gabriel Arellano - 1737		1				
Monimiaceae						
Mollinedia lanceolata Ruiz & Pav.	35		1	1		
Mollinedia ovata Ruiz & Pav.	98			4		
Mollinedia repanda Ruiz & Pav.	45	21	17	15		
Moraceae						
Brosimum guianense (Aubl.) Huber ex Ducke		1				
Brosimum lactescens (S.Moore) C.C.Berg		2				
Ficus americana Aubl.	3	1		5		
Ficus cuatrecasana Dugand	1		7	6		
Ficus insipida Willd.				4		
Ficus maroma A.Cast.	2	1				
Ficus mathewsii (Miq.) Miq.	2	5	1			
Ficus maxima Mill.	6		2			
Ficus obtusifolia Kunth	1					
Ficus subandina Dugand			1			

Familias y especies	1200−1500 m		2000−2300 m		2800−3100 m	
	Culi	Victopampa	Santa Ana	Lambramani	Piara	Cocapunco
Ficus trigona L.f.			1			
Ficus = Gabriel Arellano - 974	1					
Ficus = Gabriel Arellano - 2265		1				
Helicostylis tomentosa (Poepp. & Endl.) J.F.Macbr.	24	39		5		
Helicostylis tovarensis (Klotzsch & H.Karst.) C.C.Berg	11	10		4		
Morus insignis Bureau			12	6	3	
Perebea guianensis Aubl.	65	138				
Perebea = Gabriel Arellano - 1865		2				
Pseudolmedia laevigata Trécul		94		2	1	
Pseudolmedia laevis (Ruiz & Pav.) J.F.Macbr.	2	7				
Pseudolmedia rigida (Klotzsch & H.Karst.) Cuatrec.	84					
Sorocea guilleminiana Gaudich.	1					
Trophis caucana (Pittier) C.C. Berg	4					
Myricaceae						
Morella pubescens (Humb. & Bonpl. ex Willd.) Wilbur					10	50
Myristicaceae						
Otoba parvifolia (Markgr.) A.H.Gentry		1				
Virola elongata (Benth.) Warb.	43	5				
Virola peruviana (A. DC.) Warb.		19				
Virola sebifera Aubl.		41				
Virola aff. *elongata* (Benth.) Warb. = Gabriel Arellano - 1055	1					
Virola aff. *sebifera* Aubl. = Gabriel Arellano - 1916		1				
Virola aff. *surinamensis* (Rol. ex Rottb.) Warb. = R. Villegas - 659	3					

Familias y especies	1200−1500 m		2000−2300 m		2800−3100 m	
	Culi	Victopampa	Santa Ana	Lambramani	Piara	Cocapunco
Myrtaceae						
Calyptranthes = Gabriel Arellano - 1859		1				
Calyptranthes = A. Escalante - 151		3				
Calyptranthes = A. Antezana - 51	6					
Calyptranthes = Alejandro Araujo M. - 3415	1					
Eugenia excelsa O.Berg	2		1			
Eugenia florida DC.		7				
Eugenia limbosa O.Berg		2				
Eugenia muricata Poir.	1					
Eugenia aff. *ligustrina* (Sw.) Willd. = M. Cornejo - 1420	1					
Eugenia aff. *tapacumensis* DC. = Gabriel Arellano - 1027	1					
Eugenia = Gabriel Arellano - 1120	2					
Myrcia aliena McVaugh		7				
Myrcia fallax (Sw.) DC.	3	8		1		
Myrcia fenzliana O.Berg	6		2	4		
Myrcia guianensis (Aubl.) DC.	2	1				
Myrcia magnifolia (O.Berg) Kiaersk.	9					
Myrcia magnoliifolia (Sw.) DC.	3	11				
Myrcia multiflora (Lam.) DC.			1			
Myrcia paivae O.Berg			8			
Myrcia splendens (Sw.) DC.		1				
Myrcia subglabra McVaugh	1	2		3		
Myrcia sylvatica (G.Mey.) DC.		14		5		
Myrcia aff. *aliena* McVaugh = Alfredo F. Fuentes - 17189	11	3				
Myrcia aff. *fallax* (Sw.) DC. = I. Loza - 1332			9	2		

Familias y especies	1200−1500 m		2000−2300 m		2800−3100 m	
	Culi	Victopampa	Santa Ana	Lambramani	Piara	Cocapunco
Myrcia aff. *magnoliifolia* (Sw.) DC. = A. Escalante - 325		25				
Myrcia aff. *paivae* O.Berg = Gabriel Arellano - 2035		4				
Myrcia aff. *splendens* (Sw.) DC. = Gabriel Arellano - 205			13	1		
Myrcia aff. *subglabra* McVaugh = Gabriel Arellano - 1114		1				
Myrcia = Gabriel Arellano - 1514	1	48		15		
Myrcia = Gabriel Arellano - 2047		24				
Myrcia = M. Cornejo - 1359		2				
Myrcia = Alfredo F. Fuentes - 17258	1					
Myrcia = Renate Seidel - 9142	2					
Myrcianthes pseudomato (D.Legrand) McVaugh			1			
Myrcianthes rhopaloides (Kunth) McVaugh					11	
Myrteola = Gabriel Arellano - 2615					6	
Siphoneugena = M. Cornejo - 1076				4		
Nyctaginaceae						
Neea ovalifolia Spruce ex J.A.Schmidt	37	2				
Neea = Gabriel Arellano - 1194	6					
Neea = E. Ticona - 298		2				
Neea = L. Cayola - 2607	6	6				
Ochnaceae						
Cespedesia spathulata (Ruiz & Pav.) Planch.		2				
Ouratea angulata Tiegh.		4				
Quiina cruegeriana Griseb.		1				
Quiina florida Tul.		1				
Olacaceae						
Heisteria scandens Ducke		4				
Olacaceae = Gabriel Arellano - 1764		1				

Familias y especies	1200−1500 m		2000−2300 m		2800−3100 m	
	Culi	Victopampa	Santa Ana	Lambramani	Piara	Cocapunco
Passifloraceae						
Passiflora dalechampioides Killip				1		
Pentaphylacaceae						
Freziera caesariata Weitzman						8
Freziera dudleyi A.H.Gentry	3			2		
Freziera lanata (Ruiz & Pav.) Tul.			10		58	9
Freziera uncinata A.L. Weitzman			1			36
Freziera aff. *lanata* (Ruiz & Pav.) Tul. = Gabriel Arellano - 2793						3
Freziera = Alfredo F. Fuentes - 13962						3
Ternstroemia subserrata (Rusby) Melch.				1		
Ternstroemia aff. *polyandra* Kobuski = Gabriel Arellano - 3270				18		
Ternstroemia aff. *subserrata* (Rusby) Melch. = Gabriel Arellano - 2371					111	
Ternstroemia = Gabriel Arellano - 2772						28
Phyllanthaceae						
Hieronyma asperifolia Pax & K.Hoffm.	14	7		3		
Hieronyma moritziana Briq.		45		18		
Hieronyma oblonga (Tul.) Müll.Arg.	16	44		1		
Hieronyma = Gabriel Arellano - 658	4	4		25		
Hieronyma = Gabriel Arellano - 137	2		52			
Phyllanthus = Gabriel Arellano - 1869		1				
Phyllanthus = Gabriel Arellano - 2297		1				
Richeria grandis Vahl		20				
Phyllonomaceae						
Phyllonoma ruscifolia Willd. ex Roem. & Schult.		1				

Familias y especies	1200−1500 m		2000−2300 m		2800−3100 m	
	Culi	Victopampa	Santa Ana	Lambramani	Piara	Cocapunco
Picramniaceae						
Picramnia gracilis Tul.		3				
Picramnia sellowii Planch.			3	3		
Piperaceae						
Piper aequale Vahl		1				
Piper bangii C.DC.			1	1		
Piper bolivianum Vell.	65		5	73		
Piper crassinervium Kunth	5			11	6	
Piper dasyoura (Miq.) C. DC.					6	
Piper dumosum Rudge			6			
Piper glabratum (Kunth) Steud.			20			
Piper heterophyllum Ruiz & Pav.	1					
Piper hispidum Sw.	3		2	8		
Piper obliquum Ruiz & Pav.		39				
Piper pellitum C. DC.			1			
Piper peltilimbum Yunck.		18				
Piper percostatum Yunck.	74	144				
Piper pilirameum Kunth		11			20	
Piper propinquum NA			2			
Piper rusbyi C. DC.				33		
Piper trichorhachis C. DC.			1			
Piper aff. *psilophyllum* C. DC. = I. Loza - 1003		4				
Piper aff. *reticulatum* L. = Gabriel Arellano - 3105				2		
Piper = Gabriel Arellano - 303			1			
Piper = Alfredo F. Fuentes - 17199		2				

Familias y especies	1200−1500 m		2000−2300 m		2800−3100 m	
	Culi	Victopampa	Santa Ana	Lambramani	Piara	Cocapunco
Podocarpaceae						
Podocarpus ingensis D.Don				6	4	
Podocarpus oleifolius D.Don					60	
Podocarpus rusbyi J.Buchholz & N.E.Gray						55
Polygalaceae						
Monnina bridgesii Chodat					35	
Monnina pseudostipulata Chodat						1
Monnina = Gabriel Arellano - 2463					4	
Monnina = Gabriel Arellano - 2491					1	
Securidaca warmingiana Chodat	8					
Polygonaceae						
Coccoloba mollis Casar.	1	6				
Coccoloba = Alfredo F. Fuentes - 11255		4				
Muehlenbeckia tamnifolia (Kunth) Meisn.					1	
Triplaris americana L.	2					
Primulaceae						
Cybianthus comperuvianus Pipoly	10					
Cybianthus guyanensis (A.DC.) Miq.		1				
Cybianthus lepidotus (Gleason) G.Agostini		2				
Geissanthus bangii Rusby	2					
Myrsine coriacea (Sw.) R.Br. ex Roem. & Schult.			83	62	189	179
Myrsine dependens (Ruiz & Pav.) Spreng.					2	36
Myrsine latifolia (Ruiz & Pav.) Spreng.	4	28		11		
Myrsine pellucida (Ruiz & Pav.) Spreng.	3			1	1	101
Myrsine resinosa (A.C.Sm.) Pipoly				7		
Myrsine youngii Pipoly						5

Familias y especies	1200−1500 m		2000−2300 m		2800−3100 m	
	Culi	Victopampa	Santa Ana	Lambramani	Piara	Cocapunco
Myrsine = M. Cornejo - 1265	1					
Stylogyne ambigua Mart.	10	33	30	8		
Proteaceae						
Euplassa = Alfredo F. Fuentes - 9600	2			5		
Roupala monosperma (Ruiz & Pav.) I.M.Johnst.			1			
Roupala montana Aubl.	1					
Rhamnaceae						
Rhamnus sphaerosperma (Sw.) Kartesz & Gandhi					12	1
Rhamnus aff. *sphaerosperma* (Sw.) Kartesz & Gandhi = Gabriel Arellano - 2108		1				
Rosaceae						
Hesperomeles ferruginea (Pers.) Benth.			1		41	
Hesperomeles obtusifolia (Pers.) Lindl.						3
Prunus amplifolia Pilg.	11					
Prunus brittoniana Rusby					24	
Prunus integrifolia (Sudw.) Sarg.			3		24	
Prunus pearcei Rusby	1			6		
Prunus stipulata J.F. Macbr.			1			20
Prunus williamsii Koehne		2				
Prunus aff. *antioquensis* Pérez-Zabala = Alejandro Araujo M. - 3848						4
Prunus aff. *sana* Koehne = E. Ticona - 160		1				
Prunus = Gabriel Arellano - 2091		13				
Prunus = I. Loza - 482	2					

Familias y especies	1200−1500 m		2000−2300 m		2800−3100 m	
	Culi	Victopampa	Santa Ana	Lambramani	Piara	Cocapunco
Rubiaceae						
Alibertia = Gabriel Arellano - 2099		1				
Amaioua guianensis Aubl.	66	82				
Cinchona asperifolia Wedd.	2					
Cinchona calisaya Wedd.				10		
Cinchona pubescens Vahl	6		21			
Cinchona = Gabriel Arellano - 3090				2		
Coffea arabica L.	8	8				
Condaminea corymbosa (Ruiz & Pav.) DC.	2					
Coussarea paniculata (Vahl) Standl.	10					
Coussarea = M. Cornejo - 1454		1				
Elaeagia mariae Wedd.	24	83	5	15		
Elaeagia microcarpa Steyerm.		6				
Elaeagia = Gabriel Arellano - 2042		3				
Emmeorhiza umbellata (Spreng.) K.Schum.			1			
Faramea bangii Rusby				16		
Faramea candelabrum Standl.	35	93	3	17		
Ferdinandusa chlorantha (Wedd.) Standl.	20	1				
Guettarda crispiflora Vahl				1		
Hillia parasitica Jacq.	1		3	1		
Ladenbergia carua (Wedd.) Standl.	4	1				
Ladenbergia oblongifolia (Humb. ex Mutis) L.Andersson	3	25				
Ladenbergia = Gabriel Arellano - 1160	12					
Margaritopsis boliviana (Standl.) C.M.Taylor	3	2				
Notopleura epiphytica (K.Krause) C.M.Taylor	5					

Familias y especies	1200−1500 m		2000−2300 m		2800−3100 m	
	Culi	Victopampa	Santa Ana	Lambramani	Piara	Cocapunco
Paederia brasiliensis (Hook.f.) Puff			2			
Palicourea attenuata Rusby			1			
Palicourea flavifolia (Rusby) Standl.	2	2				
Palicourea microcarpa (Ruiz & Pav.) Zappi			6			
Palicourea stipularis Benth.			9			
Palicourea = Gabriel Arellano - 1790		2				
Posoqueria latifolia (Rudge) Schult.	1					
Psychotria carthagenensis Jacq.	9	3	489	3		1
Psychotria conephoroides (Rusby) C.M.Taylor	10	59				
Psychotria falcata Rusby						12
Psychotria tinctoria ined.		1				
Psychotria trichotoma M.Martens & Galeotti	6	2				
Psychotria tristis H.J.P.Winkl.	3					
Psychotria trivialis Rusby	9					
Psychotria viridis Ruiz & Pav.	12					
Randia micrantha (K.Schum.) Bullock ex F.White					3	
Psychotria = Gabriel Arellano - 1170	3	5				
Psychotria = Gabriel Arellano - 1333	1					
Psychotria = Gabriel Arellano - 2318					115	
Psychotria = Gabriel Arellano - 2721						19
Psychotria = Gabriel Arellano - 2869			85			4
Psychotria = Gabriel Arellano - 2935				1		
Psychotria = Gabriel Arellano - 2945				61		
Psychotria = Gabriel Arellano - 3194				4		
Psychotria = I. Loza - 1296			79	17		
Rudgea ciliata (Ruiz & Pav.) Spreng.					13	

Familias y especies	1200−1500 m		2000−2300 m		2800−3100 m	
	Culi	Victopampa	Santa Ana	Lambramani	Piara	Cocapunco
Rudgea poeppigii K.Schum. ex Standl.	3					
Rudgea tomentosa Rusby	9	3		3		
Rudgea = Gabriel Arellano - 1706		6				
Rudgea = Gabriel Arellano - 3147				4		
Schizocalyx obovatus (K. Schum. ex Standl.) Kainul. & B. Bremer	122	129				
Schradera subandina K.Krause	19	5				
Rubiaceae = Gabriel Arellano - 1545		2				
Rubiaceae = Gabriel Arellano - 1566		4				
Rubiaceae = Gabriel Arellano - 1811		1				
Rubiaceae = Gabriel Arellano - 1888		1				
Rubiaceae = Gabriel Arellano - 1933		16				
Rubiaceae = Gabriel Arellano - 1953		1				
Rubiaceae = Gabriel Arellano - 1991		2				
Rubiaceae = Gabriel Arellano - 2008		1				
Rubiaceae = Gabriel Arellano - 2182		1				
Rubiaceae = Gabriel Arellano - 2953				6		
Rubiaceae = Gabriel Arellano - 2955				50		
Rubiaceae = Gabriel Arellano - 3037				11		
Rubiaceae = Gabriel Arellano - 3085				7		
Rubiaceae = Gabriel Arellano - 3100				1		
Rubiaceae = Gabriel Arellano - 3212				3		
Rutaceae						
Zanthoxylum = Gabriel Arellano - 729	1					
Sabiaceae						
Meliosma boliviensis Cuatrec.				5		
Meliosma glabrata (Liebm.) Urb.	1					

Familias y especies	1200−1500 m		2000−2300 m		2800−3100 m	
	Culi	Victopampa	Santa Ana	Lambramani	Piara	Cocapunco
Meliosma herbertii Rolfe	1					
Meliosma aff. *petalodentata* Arbeláez = Gabriel Arellano - 2778						17
Meliosma solomonii A.H. Gentry		2				
Meliosma = Gabriel Arellano - 1733		1				
Meliosma = M. Cornejo - 1264	1					
Meliosma = Narel Paniagua Zambrana - 4875		1				
Salicaceae						
Banara guianensis Aubl.				1		
Banara aff. *guianensis* Aubl. = Gabriel Arellano - 345			3			
Casearia arborea (Rich.) Urb.		6				
Casearia aff. *nigricolor* Sleumer = M. Cornejo - 1263				4		
Casearia = I. Loza - 1314			7			
Casearia = F. Bascopé - 306				1		
Sapindaceae						
Allophylus floribundus (Poepp.) Radlk.			42			
Allophylus = Gabriel Arellano - 2261		2		2		
Cupania aff. *oblongifolia* Mart. = Gabriel Arellano - 1762		1				
Cupania = Alfredo F. Fuentes - 17289				6		
Matayba macrostylis Radlk.		4				
Paullinia brentberlinii Croat	2					
Paullinia clathrata Radlk.	3					
Paullinia dasygonia Radlk.		3				
Paullinia = Gabriel Arellano - 2306		1				
Serjania atrolineata C.Wright	4					
Serjania hebecarpa Benth.		1				
Serjania lethalis A. St.-Hil.		3				

Familias y especies	1200−1500 m		2000−2300 m		2800−3100 m	
	Culi	Victopampa	Santa Ana	Lambramani	Piara	Cocapunco
Serjania marginata Casar.	1					
Serjania reticulata Cambess.		2				
Serjania tenuifolia Radlk.		8				
Serjania aff. *tenuifolia* Radlk. = A. Antezana - 788		1				
Talisia = A. Escalante - 232		6				
Talisia = F. Bascopé - 68	2					
Sapotaceae						
Chrysophyllum argenteum Jacq.	3					
Pouteria baehniana Monach.	1					
Pouteria bilocularis (H.K.A.Winkl.) Baehni	12	13				
Pouteria guianensis Aubl.	4					
Pouteria hispida Eyma	2					
Pouteria macrophylla (Lam.) Eyma		4				
Pouteria torta (Mart.) Radlk.				1		
Pouteria = Gabriel Arellano - 634	1					
Pouteria = Gabriel Arellano - 1981		1				
Sarcaulus brasiliensis (A.DC.) Eyma	1					
Scrophulariaceae						
Buddleja montana Britton					5	
Simaroubaceae						
Simarouba amara Aubl.	7	5				
Siparunaceae						
Siparuna aspera (Ruiz & Pav.) A.DC.			2	11		
Siparuna grandiflora (Kunth) Perkins				1		
Siparuna guianensis Aubl.		30				
Siparuna poeppigii (Tul.) A. DC.		1				

Familias y especies	1200–1500 m		2000–2300 m		2800–3100 m	
	Culi	Victopampa	Santa Ana	Lambramani	Piara	Cocapunco
Siparuna thecaphora (Poepp. & Endl.) A.DC.		1				
Siparuna aff. *guianensis* Aubl. = Gabriel Arellano - 2213		22				
Siparuna = Gabriel Arellano - 2002		1				
Solanaceae						
Brunfelsia mire Monach.	1					
Cestrum mariquitense Kunth				1		
Cestrum megalophyllum Dunal				2		
Cestrum microcalyx Francey			5	2		
Cestrum racemosum Ruiz & Pav.			2	1	8	
Cestrum schlechtendahlii G.Don	4					
Cestrum strigilatum Ruiz & Pav.			2		4	
Cestrum = I. Loza - 1322	1					
Sessea dependens Ruiz & Pav.					1	
Solanum aphyodendron S. Knapp		1	3	2		
Solanum asperolanatum Ruiz & Pav.					2	
Solanum conglobatum Dunal				2		
Solanum maturecalvans Bitter				5	38	
Solanum nitidum Ruiz & Pav.			1			
Solanum ochrophyllum Bitter					1	
Solanum polytrichostylum Bitter				11		
Solanum roseum Bohs			1			
Solanum ternatum Ruiz & Pav.					1	
Solanum aff. *lindenii* Rusby = I. Loza - 1197			9			
Solanum = Gabriel Arellano - 332			5	5	2	
Solanum = Gabriel Arellano - 433			1			
Solanum = Gabriel Arellano - 2573					1	

Familias y especies	1200−1500 m		2000−2300 m		2800−3100 m	
	Culi	Victopampa	Santa Ana	Lambramani	Piara	Cocapunco
Staphyleaceae						
Turpinia occidentalis (Sw.) G.Don			5	3		
Styracaceae						
Styrax nunezii P.W.Fritsch				4		
Styrax pentlandianus J. Rémy		1	3			
Styrax = Gabriel Arellano - 2722						5
Symplocaceae						
Symplocos arechea L'Hér.		1				
Symplocos debilis B.Ståhl		34				
Symplocos denticulata B.Ståhl					3	25
Symplocos fimbriata B. Ståhl						30
Symplocos fuliginosa B. Ståhl				2		
Symplocos mapiriensis Brand		2	6	4	7	
Symplocos polyphylla B.Ståhl						230
Symplocos quitensis Brand			11		7	
Symplocos robusta B.Ståhl					1	
Symplocos serratifolia B. Ståhl			1			
Symplocos aff. *serratifolia* B. Ståhl = Gabriel Arellano - 3186				1		
Symplocos aff. *subcuneata* (Herzog) Stahl = Gabriel Arellano - 2760				3		1
Symplocos = Gabriel Arellano - 2404A					9	
Theaceae						
Gordonia fruticosa (Schrad.) H.Keng	2	4		14		12
Thymelaeaceae						
Daphnopsis = M. Cornejo - 1231				2		
Thymelaeaceae = Gabriel Arellano - 3256				1		

Familias y especies	1200−1500 m		2000−2300 m		2800−3100 m	
	Culi	Victopampa	Santa Ana	Lambramani	Piara	Cocapunco
Urticaceae						
Boehmeria caudata Sw.					1	
Boehmeria fallax Wedd.			5			
Cecropia = Gabriel Arellano - 3065				16		
Cecropia angustifolia Trécul	12	3		3		
Cecropia tacuna C.C.Berg & P.Franco			42			
Coussapoa crassivenosa Mildbr.		1				
Myriocarpa stipitata Benth.			19	5		
Pourouma bicolor Mart.	7	11				
Pourouma cecropiifolia Mart.		2				
Pourouma guianensis Aubl.	14	39				
Pourouma minor Benoist	48	25				
Pourouma tomentosa Mart. ex Miq.		2				
Urera baccifera (L.) Gaudich.	2	1				
Vitaceae						
Cissus trianae Planch.			6	1	1	3
Vochysiaceae						
Vochysia boliviana Rusby	1	13				
Vochysia aff. *boliviana* Rusby = R. Villegas - 629		5				
Vochysia = A. Escalante - 329	3					
Indet.						
Pteridophyta = Gabriel Arellano - 1574		3				

Apéndice 2. Códigos, localización y características de 54 parcelas de bosque montano. El Plot Name es el empleado por TROPICOS para indexar el inventario (www.tropicos.org/PlotSearch.aspx?projectid=20). *N*: número de individuos; *S*: número de especies.

Appendix 2. Codes, location and features of 54 plots of montane forest. The Plot Name is employed by TROPICOS to index the inventory (www.tropicos.org/PlotSearch.aspx?projectid=20). *N*: number of individuals; *S*: number of species.

Plot Name	Latitude (South)	Longitude (West)	Elevation (m)	*N*	*S*
PT_Culi_353	14º43’33”	68º49’51”	1240	226	68
PT_Culi_354	14º43’44”	68º50’14”	1277	295	82
PT_Culi_355	14º43’43”	68º50’40”	1497	464	104
PT_Culi_356	14º43’53”	68º50’39”	1329	306	76
PT_Culi_357	14º44’43”	68º51’16”	1443	324	87
PT_Culi_358	14º44’35”	68º51’10”	1438	378	98
PT_Culi_359	14º44’18”	68º51’03”	1271	258	76
PT_Culi_360	14º43’57”	68º50’57”	1457	428	94
PT_Culi_361	14º44’06”	68º50’51”	1286	278	74
PT_Victop_372	15º28’06”	68º21’22”	1490	470	85
PT_Victop_373	15º28’04”	68º21’19”	1482	364	86
PT_Victop_374	15º27’42”	68º20’59”	1537	442	103
PT_Victop_375	15º27’25”	68º21’20”	1163	403	76
PT_Victop_376	15º27’36”	68º21’23”	1246	336	83
PT_Victop_377	15º27’45”	68º21’15”	1353	340	111
PT_Victop_378	15º27’37”	68º21’11”	1423	431	93
PT_Victop_379	15º27’59”	68º21’23”	1362	383	91
PT_Victop_380	15º27’53”	68º21’20”	1283	411	107
PT_Santaa_344	14º46’18”	68º58’18”	2216	228	38
PT_Santaa_345	14º46’22”	68º58’29”	2264	385	28
PT_Santaa_346	14º45’30”	68º57’39”	2296	281	41
PT_Santaa_347	14º46’07”	68º58’46”	2180	402	36
PT_Santaa_348	14º46’05”	68º58’15”	2114	395	50
PT_Santaa_349	14º45’33”	68º57’48”	2235	262	42
PT_Santaa_350	14º45’41”	68º57’52”	2329	229	40
PT_Santaa_351	14º45’45”	68º57’58”	2235	282	29
PT_Santaa_352	14º46’18”	68º58’54”	2352	243	50

Apéndice 2 (continuación).
Appendix 2 (continued).

Plot Name	Latitude (South)	Longitude (West)	Elevation (m)	*N*	*S*
PT_Lambra_434	15º39’20”	68º22’45”	2282	181	41
PT_Lambra_435	15º39’25”	68º22’30”	2021	284	75
PT_Lambra_436	15º38’57”	68º22’27”	2213	198	37
PT_Lambra_437	15º38’56”	68º22’13”	2214	279	56
PT_Lambra_438	15º39’05”	68º22’15”	2033	224	58
PT_Lambra_439	15º39’07”	68º22’38”	2284	175	49
PT_Lambra_440	15º39’20”	68º22’23”	2031	197	64
PT_Lambra_441	15º39’35”	68º22’56”	2208	311	69
PT_Lambra_442	15º39’15”	68º22’37”	2196	328	69
PT_Piara_387	14º46’36”	69º00’54”	2804	319	38
PT_Piara_388	14º46’45”	69º00’56”	2746	414	41
PT_Piara_389	14º47’02”	69º00’54”	2813	235	27
PT_Piara_390	14º46’58”	69º01’14”	2799	310	28
PT_Piara_391	14º47’01”	69º01’17”	2803	276	38
PT_Piara_392	14º47’13”	69º01’36”	3069	382	37
PT_Piara_393	14º47’17”	69º01’10”	2961	351	34
PT_Piara_394	14º47’46”	69º01’48”	2975	307	41
PT_Piara_395	14º47’34”	69º01’33”	2946	304	28
PT_Cocapu_396	15º33’11”	68º23’36”	2786	273	38
PT_Cocapu_397	15º33’20”	68º23’35”	2832	493	38
PT_Cocapu_398	15º33’22”	68º23’43”	2882	228	35
PT_Cocapu_399	15º33’30”	68º23’40”	2984	765	50
PT_Cocapu_400	15º33’35”	68º24’00”	3023	610	45
PT_Cocapu_401	15º33’45”	68º24’08”	3137	395	41
PT_Cocapu_402	15º33’39”	68º23’59”	3091	604	33
PT_Cocapu_403	15º33’46”	68º23’43”	3119	591	45
PT_Cocapu_404	15º33’36”	68º23’50”	3083	598	44

Apéndice 3. Características edáficas de 54 parcelas de bosque montano inventariadas. pH_1: pH en una solución 1:2.5 suelo:agua; pH_2: pH en una solución 1:2.5 suelo:KCl 1M; C_{org}: C orgánico; C_{tot}: C total. Los métodos empleados se detallan en el Capítulo 5.

Appendix 3. Edaphic features of 54 inventoried plots in montane forest. pH_1: pH in a 1:2.5 soil:water solution; pH_2: pH in a 1:2.5 soil:KCl 1M solution; C_{org}: organic C; C_{tot}: total C. The methods employed are detailed in Chapter 5.

pH, materia orgánica, y cationes intercambiables

pH, organic matter, and interchangeable cations

Plot Name	pH_1	pH_2	C_{org} %	C_{tot} %	N %	S %	Ca mg/kg	K mg/kg	Mg mg/kg	Na mg/kg
PT_Culi_353	3.96	3.46	6	5	0.50	0.04	285	117	114	225
PT_Culi_354	3.14	2.56	19	22	1.63	0.15	157	192	137	258
PT_Culi_355	3.09	2.35	24	32	2.03	0.18	271	238	103	464
PT_Culi_356	3.08	2.05	25	31	2.07	0.18	194	366	163	207
PT_Culi_357	3.62	3.05	14	14	0.94	0.08	246	122	117	363
PT_Culi_358	3.02	2.21	17	25	1.72	0.18	118	272	83	177
PT_Culi_359	3.73	3.36	14	18	1.36	0.12	364	156	164	370
PT_Culi_360	3.16	2.45	23	30	1.92	0.19	269	198	114	470
PT_Culi_361	3.05	2.15	38	45	2.67	0.26	329	191	410	552
PT_Victop_372	3.05	2.38	33	30	1.83	0.16	58	256	85	<0.1
PT_Victop_373	2.68	2.18	34	37	2.34	0.27	123	291	304	<0.1
PT_Victop_374	3.18	2.95	13	10	0.82	0.07	90	96	43	<0.1
PT_Victop_375	3.40	3.01	12	10	0.66	0.06	66	120	32	<0.1
PT_Victop_376	3.35	3.05	9	7	0.54	0.05	33	100	43	<0.1
PT_Victop_377	3.44	3.20	10	8	0.66	0.06	39	100	39	<0.1
PT_Victop_378	2.86	1.99	32	35	2.08	0.20	90	391	126	<0.1
PT_Victop_379	2.74	2.03	32	33	2.02	0.18	73	366	339	<0.1
PT_Victop_380	3.42	3.11	9	7	0.63	0.06	53	73	51	<0.1
PT_Santaa_344	3.14	2.23	20	24	1.74	0.14	378	253	288	344
PT_Santaa_345	3.41	2.51	26	36	2.11	0.18	294	480	158	278
PT_Santaa_346	3.18	2.10	29	45	2.40	0.22	651	594	526	544
PT_Santaa_347	4.91	4.43	21	30	2.25	0.16	6302	432	790	258
PT_Santaa_348	3.19	2.17	29	42	2.57	0.28	1176	527	451	464
PT_Santaa_349	3.22	2.36	26	31	2.30	0.22	457	435	393	228
PT_Santaa_350	4.02	3.15	18	29	2.04	0.15	810	392	374	275
PT_Santaa_351	4.30	3.54	17	25	1.95	0.16	3073	418	516	226
PT_Santaa_352	3.57	2.69	26	33	2.29	0.18	1556	334	576	208

pH, materia orgánica, y cationes intercambiables (continuación)
pH, organic matter, and interchangeable cations (continued)

Plot Name	pH_1	pH_2	C_{org} %	C_{tot} %	N %	S %	Ca mg/kg	K mg/kg	Mg mg/kg	Na mg/kg
PT_Lambra_434	2.80	1.70	42	46	2.5	0.24	366	336	161	54
PT_Lambra_435	3.82	2.39	36	39	2.38	0.24	866	618	633	62
PT_Lambra_436	3.11	1.99	37	39	2.44	0.2	333	280	312	54
PT_Lambra_437	3.41	2.92	34	39	2.94	0.27	800	618	421	40
PT_Lambra_438	3.82	3.27	16	13	1.08	0.08	1060	254	323	22
PT_Lambra_439	2.95	2.15	36	44	2.38	0.19	525	406	273	60
PT_Lambra_440	3.56	2.56	29	31	2.12	0.17	496	459	766	35
PT_Lambra_441	4.28	3.88	28	33	2.7	0.16	3657	1002	1365	3
PT_Lambra_442	2.74	1.86	40	45	2.44	0.16	346	294	156	43
PT_Piara_387	3.42	1.90	46	47	2.56	0.24	313	436	275	837
PT_Piara_388	3.42	2.76	30	30	1.69	0.14	495	218	314	859
PT_Piara_389	4.56	4.32	36	34	2.53	0.19	6205	528	1430	806
PT_Piara_390	2.51	1.63	48	48	1.94	0.18	175	390	188	907
PT_Piara_391	2.64	1.71	43	43	2.41	0.22	369	254	210	47
PT_Piara_392	4.11	3.25	34	36	2.4	0.18	2742	574	911	46
PT_Piara_393	4.49	3.76	37	39	2.38	0.2	3953	872	1080	40
PT_Piara_394	3.39	2.77	24	25	1.9	0.16	637	202	318	30
PT_Piara_395	2.63	1.81	40	45	2.04	0.18	892	420	398	62
PT_Cocapu_396	2.87	2.19	41	45	1.73	0.17	455	686	649	<0.1
PT_Cocapu_397	3.25	2.53	40	44	1.73	0.16	401	817	707	<0.1
PT_Cocapu_398	2.97	2.18	41	46	1.82	0.18	553	558	784	<0.1
PT_Cocapu_399	3.10	2.22	38	41	1.74	0.18	327	612	393	<0.1
PT_Cocapu_400	3.30	2.38	36	35	1.91	0.19	411	470	363	<0.1
PT_Cocapu_401	3.14	2.15	36	40	1.53	0.15	475	700	800	634
PT_Cocapu_402	3.14	2.26	38	43	1.70	0.16	834	672	496	<0.1
PT_Cocapu_403	3.25	2.08	40	46	2.05	0.22	432	547	638	671
PT_Cocapu_404	2.95	2.08	39	41	1.97	0.18	409	614	418	<0.1

Aluminio, oligonutrientes y micronutrientes
Aluminum, oligonutrients and micronutrients

Plot Name	Al mg/kg	Co mg/kg	Cu mg/kg	Fe mg/kg	Mn mg/kg	Ni mg/kg	P mg/kg	Zn mg/kg
PT_Culi_353	1192	0.37	2.07	183	57.7	0.85	3.4	1.4
PT_Culi_354	1179	0.23	1.20	247	9.5	1.35	2.9	2.2
PT_Culi_355	1185	0.30	2.44	206	4.3	1.41	7.9	3.7
PT_Culi_356	802	0.05	1.91	184	33.2	1.01	34.7	6.3
PT_Culi_357	1584	0.14	2.00	176	7.5	1.17	0.2	1.8
PT_Culi_358	891	0.43	1.30	251	46.1	1.40	7.1	3.4
PT_Culi_359	1490	0.20	2.80	176	138.9	0.78	<0.05	2.4
PT_Culi_360	1212	0.42	2.32	150	5.6	2.10	4.5	7.1
PT_Culi_361	721	0.09	4.00	85	10.2	1.75	21.2	21.9
PT_Victop_372	1886	0.55	1.23	394	6.3	1.81	12.5	8.0
PT_Victop_373	1770	4.80	3.00	393	83.2	3.51	16.8	8.4
PT_Victop_374	1680	0.12	4.52	480	4.3	0.82	4.1	7.0
PT_Victop_375	1925	0.41	5.52	319	4.7	0.72	5.4	1.4
PT_Victop_376	1818	0.10	1.27	506	5.4	0.60	2.4	1.1
PT_Victop_377	1910	1.49	2.74	189	13.1	1.15	3.6	5.7
PT_Victop_378	1434	0.81	3.00	501	9.6	2.92	13.8	13.4
PT_Victop_379	1588	4.31	2.73	479	15.2	3.71	18.1	39.6
PT_Victop_380	1747	0.55	2.95	380	17.5	0.65	5.5	2.0
PT_Piara_387	622	0.22	4.46	169	23.1	2.10	65.4	17.7
PT_Piara_388	2027	0.99	1.10	299	37.8	1.92	10.9	6.9
PT_Piara_389	846	1.30	3.93	138	422.0	1.76	28.2	44.3
PT_Piara_390	1162	0.82	4.78	270	23.9	3.37	59.6	20.5
PT_Piara_391	1215	0.29	1.84	413	13.1	2.95	33.1	20.6
PT_Piara_392	923	1.63	4.00	318	171.7	2.17	81.6	27.2
PT_Piara_393	1212	1.28	4.48	122	389.9	2.21	48.6	41.4
PT_Piara_394	1834	0.53	0.38	454	54.9	1.69	6.3	5.8
PT_Piara_395	1158	0.53	3.63	309	73.6	3.33	57.3	19.9
PT_Santaa_344	921	0.12	0.77	272	37.6	1.52	18.9	5.9
PT_Santaa_345	1349	0.62	1.20	165	20.3	1.26	13.1	7.7
PT_Santaa_346	903	0.67	4.72	160	148.5	2.31	47.0	18.4
PT_Santaa_347	416	0.98	3.52	131	78.4	0.73	16.6	14.3
PT_Santaa_348	661	0.67	5.24	165	28.6	3.10	52.6	13.1
PT_Santaa_349	867	0.14	1.31	244	52.2	1.81	25.7	5.9
PT_Santaa_350	1245	0.38	1.72	201	477.0	1.54	7.5	15.6
PT_Santaa_351	757	0.95	4.11	140	98.7	0.87	10.8	10.1
PT_Santaa_352	938	1.24	1.44	170	63.7	1.53	13.4	10.9

Aluminio, oligonutrientes y micronutrientes (continuación)

Aluminum, oligonutrients and micronutrients (continued)

Plot Name	Al mg/kg	Co mg/kg	Cu mg/kg	Fe mg/kg	Mn mg/kg	Ni mg/kg	P mg/kg	Zn mg/kg
PT_Lambra_434	837	0.07	2.97	175	2.5	1.53	26.3	12.5
PT_Lambra_435	1537	0.21	2.94	221	46.4	2.13	19.1	12.8
PT_Lambra_436	1096	0.01	3.55	250	2.4	1.66	17.6	10.7
PT_Lambra_437	1882	0.07	2.47	96	390.7	1.08	10.3	9.9
PT_Lambra_438	1668	0.17	2.39	182	169.0	0.61	7.7	5.7
PT_Lambra_439	908	0.06	2.99	154	3.8	1.36	13.1	17.4
PT_Lambra_440	1394	0.12	0.24	303	41.8	0.18	15.2	11.7
PT_Lambra_441	1003	0.32	3.12	150	201.7	1.02	13.4	18.7
PT_Lambra_442	1319	0.18	1.96	225	2.2	1.13	12.5	11.5
PT_Cocapu_396	1096	0.31	4.99	413	7.4	2.72	21.2	14.0
PT_Cocapu_397	1310	0.11	3.92	129	14.1	0.52	17.1	20.7
PT_Cocapu_398	1569	0.19	5.46	205	14.9	1.14	26.5	17.9
PT_Cocapu_399	1566	0.11	0.37	232	9.1	0.90	16.9	11.7
PT_Cocapu_400	1625	0.37	1.71	480	9.1	1.07	12.0	10.1
PT_Cocapu_401	1424	0.16	3.16	468	17.2	0.66	11.9	16.9
PT_Cocapu_402	1169	0.12	4.22	214	83.7	0.56	16.2	17.7
PT_Cocapu_403	1340	0.57	4.66	205	22.6	1.60	20.9	15.3
PT_Cocapu_404	1389	0.27	3.36	255	11.6	1.09	17.8	13.7