2011-05-06

Community and Functional Ecology of Lianas in the Yasuní Forest Dynamics Plot, Amazonian Ecuador

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Recommended Citation

Romero-Saltos, Hugo Geovanny, "Community and Functional Ecology of Lianas in the Yasuní Forest Dynamics Plot, Amazonian Ecuador" (2011). *Open Access Dissertations*. 529.
https://scholarlyrepository.miami.edu/oa_dissertations/529

UNIVERSITY OF MIAMI

COMMUNITY AND FUNCTIONAL ECOLOGY OF LIANAS IN THE YASUNÍ FOREST DYNAMICS PLOT, AMAZONIAN ECUADOR

By

Hugo Geovanny Romero-Saltos

A DISSERTATION

Submitted to the Faculty
of the University of Miami
in partial fulfillment of the requirements for
the degree of Doctor of Philosophy

Coral Gables, Florida

May 2011

UNIVERSITY OF MIAMI

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COMMUNITY AND FUNCTIONAL ECOLOGY OF LIANAS IN THE YASUNÍ FOREST DYNAMICS PLOT, AMAZONIAN ECUADOR

Hugo G. Romero-Saltos

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ROMERO-SALTOS, HUGO G. (Ph.D., Biology)
Community and Functional Ecology of Lianas (May 2011)
in the Yasuní Forest Dynamics Plot, Amazonian Ecuador

Abstract of a dissertation at the University of Miami.

Dissertation supervised by Professor Leonel da S.L. Sternberg.
No. of pages in text: (216)

I studied the community of lianas in the Yasuní Forest Dynamics Plot (YFDP), in Amazonian Ecuador. I found that species diversity of lianas in valley habitat was higher than in ridge habitat, but liana abundance was similar. I also found that community structure (species composition and their abundances) of lianas in ridge was distinct from that in valley because of the differential distribution and abundance of certain species along the topographic gradient. In an attempt to explain this phenomenon deterministically, I took two approaches: (1) to explore if trait expression of leaf-based traits, wood specific gravity and stem growth rate was different among species with ridge habitat association, species with valley habitat association, and generalist species; and (2) to explore if frequencies of different whole-plant growth strategies in the forest understory—defined by whether a liana was free-standing or already climbing, by its climbing mechanism, and by its understory appearance—were different between ridge and valley. My underlying rationale was that if certain trait expression or understory growth strategy can be associated to a given species, or group of species, and such species also drive the community structure difference between ridge and valley, then ecological insight on the biological deterministic mechanisms driving the difference can be gained. I end this one-page dissertation abstract right here and purposely leave you, the reader, perplexed—I invite you to seek answers to the liana distribution conundrum in the YFDP by perusing this dissertation.

I dedicate this work
to my loved children and wife

Acknowledgements

After almost eight years, my Ph.D. program at the University of Miami came to a good end only because many people and institutions dedicated many hours and much money on a young Ecuadorian scientist (well, not too young anymore). I remember the faces of most people who helped me and thank them all, but the problem is that I have never been good with names! My friends at UM and abroad already know how close they are to my heart and so does my family, so I will not name them here, except when they were also scientists whose input for this dissertation was valuable. Often during this journey, I felt the emotional support from friends and family was more important than any academic support, although certainly some people generously gave me both.

For the sake of formality, I ought to mention the names of a few key people and institutions:

- I am deeply grateful to Leo Sternberg, my academic advisor at UM, for his trust and friendship. I also thank the members of my Dissertation Committee: Dave Janos, Jack Fisher and Don DeAngelis—for me, they are all excellent scientists and very special teachers. Needless to say, I am also very grateful to the Biology faculty at UM from whom I learned the many nuts-and-bolts of being a scientist.
- This work would not have been possible without the help of my long-time colleague, collaborator and friend: Esteban Gortaire. I also thank my field and lab assistants, in particular (and in alphabetic order): Carolina Altamirano, Nataly Charpentier, Luis Espinoza, Ronald Grefa, Carlos Padilla, Laura Salazar, and the innumerable Waorani indians from Yasuní National Park. Pablo Loaiza, Mariana Mites, Verónica Sáenz and Diego Torres also helped me with various tasks. I am

also grateful to the personnel affiliated to the 50-ha Yasuní Forest Dynamics Plot project: Renato Valencia, Consuelo Hernández, Álvaro Pérez, and the whole team of mappers. A special appreciation goes to Carmen Ulloa who hosted me during my visit to the Missouri Botanical Garden.

- The following people, which include a number of international specialists, helped me with the plant taxonomy (listed in alphabetical order): Pedro Acevedo-Rodríguez, Pablo Alvia, Gerardo Aymard, Robyn Burnham, Peter Jörgensen, Ron Liesner, Lúcia Lohmann, Rosa Ortiz, Álvaro Pérez, Charlotte Taylor, Hyo Won, and Milton Zambrano. In addition, this dissertation obtained academic input from the following people (listed in alphabetical order): Robyn Burnham, Robert Colwell, John Cozza, Patrick and Patricia Ellsworth, Guangyou Hao, Kyle Harms, Nathan Kraft, Eric Manzané, Nathan Muchhala, Amartya Saha, Stefan Schnitzer, Renato Valencia, and Xin Wang.
- Funding for this dissertation and other related studies (not presented in this dissertation) was obtained from the Center for Tropical Forest Science (Smithsonian Tropical Research Institute), the University of Miami, the UNESCO's Man and Biosphere Program, and "The Romero Foundation". The Yasuní Research Station and the Herbarium QCA at the Pontificia Universidad Católica del Ecuador kindly provided logistic support during field seasons.
- Ecuador's Ministry of Environment supported this scientific study by issuing research permits 002-IC-FL-PNY-RSO and 005-IC-FA-PNY-RSO.

Thank you all

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CHAPTER 1: Introduction

The knowledge gap between what we know about the ecology of trees versus what we know about the ecology of lianas (woody vines) is shrinking very fast in the last few decades, and this dissertation is part of such research impetus among the scientific community. Because comprehensive reviews about the biology of lianas are readily available to the reader (Putz and Mooney 1991, Bongers, Schnitzer, and Taore 2002, Schnitzer and Bongers 2002, Pérez-Salicrup, Schnitzer, and Putz 2004, Isnard and Silk 2009, Vaughn and Bowling 2011, Paul and Yavitt 2011) and the data Chapters on their own already have sufficient liana-related background information, the focus of the Introduction is instead on three topics that are the foundation of this dissertation. First, I will introduce the Yasuní forest (in eastern Amazonian Ecuador) in a general way, including its historical aspects and the conservation challenge it currently faces. Second, I will emphasize the importance of the 50-hectare Yasuní Forest Dynamics Plot (YFDP) by giving an account of plant-related research conducted in Yasuní. Although such account is not intended as a formal nor a complete academic review, I hope it will help to situate this dissertation as an important component along the research history of the YFDP. Third, last but not the least, I will present an overview of this dissertation, i.e. what the over-arching question is and what specific questions I am asking.

TRAPPED BETWEEN REALITY AND MYTH: A PROLEGOMENON ABOUT YASUNÍ

For the average citizen, the Yasuní area in eastern Amazonian Ecuador just became accessible a few decades ago when the construction of two oil company roads—the "vía Auca" (built in the 1980´s) and the "vía Maxus" (built in the 1990´s)—started to "drill" into *terra incognita* territory (Finer et al. 2009). At the time, few scientists, if any, anticipated that Yasuní will be known as one of the most biodiverse forests on Earth. Now we have realized that Yasuní and its surrounding areas, including northern Perú, represent a biogeographic area where high species diversity of vascular plants overlaps with high species diversity of vertebrates, resulting in relatively high alpha diversity compared to other tropical rainforest areas (Bass et al. 2010). This huge area—in which approximately 1.68 million hectares are "officially" protected in Ecuador by Yasuní National Park and contiguous Waorani Ethnic Reserve, which together are known as the Yasuní Biosphere Reserve (Finer et al. 2009)—roughly contains at least 150 species of amphibians, 120 species of reptiles, 600 species of birds, 200 species of mammals, 500 species of fish, 3000 species of trees and 500 species of lianas (see review in Bass et al. 2010, and comments on-line). Yet, despite its biodiversity importance, biological research in Yasuní is still young compared to other Neotropical forests. To exemplify, a web search in Google Scholar/Biology for the term "La Selva" (the renowned biological station in Costa Rica) in the title of an academic work gave 852 results, whereas the same search for "Yasuní" or "Yasuni" gave only 46 results. The real number of publications in each area is probably higher than what the these figures show, but the point is clear: science in Yasuní is still a baby.

The history of Yasuní is quite convoluted. Historically, the deep terra firme forests of Yasuní were inhabited by the Waorani, and their cousins the Tagaeri and Taromenane, some of whom still live in "voluntary" (or should we say "forced"?) isolation (Finer et al. 2009). The forests along the main rivers, on the other hand, historically were inhabited by the Zaparos, an ethnia that went almost extinct because of disease in the late 1800´s (Finer et al. 2009) and that now has been practically absorbed by the Kichwas. The

Waorani represent an ethnographic group so unique that their language is unrelated to any other (Finer et al. 2009). Less than fifty years ago, they still used to roam the vast terra firme forest of Yasuní, mixing horticultural, foraging and hunting life habits (Beckerman et al. 2009). In the 1960´s, it was estimated that there were no more than 500 of them, but today there are at least 2000 Waoranis (Finer et al. 2009). They have a character of their own—they can be friendly or deadly, although, as in any human society, there is quite a bit of variation from one person to another (Beckerman et al. 2009; and pers. obs.). Deadly revenges and raids among different clans within the Waorani have diminished in frequency since contact (religion-driven), but they have not by any means disappeared—the last killing incident involving supposedly “pacified” Waoranis killing Taromenane occurred in 2003 (but rumor says they were paid by illegal loggers to whom the very territorial Taromenane were giving big time trouble; Finer et al. 2009). Throughout the years (since 1999), I have worked with many Waorani, young and old, men and women, and in general they have demonstrated to be dependable, smart and quite entertaining field assistants (except for some bad experiences that, retrospectively, were not worse than the awkward moments experienced with westernized research assistants).

The Waoranis are nowadays one of the main players in the complex challenge to conserve, or should we better say preserve, the forest of Yasuní. This challenge has been in the past few years incandesced by three events: (1) the Yasuní-ITT Initiative, in which the government of Ecuador has asked the international community (in particular the developed countries) for money in exchange of leaving the oil from eastern Yasuní untapped, even though therein lies the second largest oil reserve of the country (Finer et al. 2009, Finer, Moncel, and Jenkins 2010, Vogel 2010); (2) the realization that the ~150-km of the "vía Maxus" that runs deep into Yasuní, although still unpaved and of restricted-access, is the main venue by which approximately 10,500 ± 400 kg (± 95% CI) of bushmeat are illegally extracted every year by the ever-increasing indigenous population settled along the road, and who have seen in the bushmeat (black) market the opportunity to make a living (Suárez et al. 2009); and (3) the strong will of a group of scientists for letting the world know about the incredible megadiversity of Yasuní (see e.g., Bass et al. 2010, Marx 2010). Realistically, I personally think the long-term conservation of Yasuní is an utopia—unless we kick out almost everyone, but the scientists of course!

PLANT ECOLOGY IN YASUNÍ

Brief history and status quo

As in many parts of the world, plant research in Yasuní started with collecting expeditions. The first botanical expeditions occurred in the late 1960´s, basically along or nearby rivers, but did not really peak until the mid-1990´s when two, still active, research stations were founded: Yasuní Research Station and Tiputini Biodiversity Station. The appearance of these research centers occurred concomitantly with the end of the construction of the Maxus road. The road opened the path for intense botanical expeditions within the core of Yasuní (see Pitman 2000 for a chronological account) and was seen as the perfect opportunity to study the diversity, distribution, demography and associated ecological processes of the Yasuní plants in a comprehensive way. Before then, only a few forest plots and transects had been established in the buffer zone of Yasuní National Park where logistics permitted it (Balslev et al. 1987, Korning and

Balslev 1994, Cerón and Montalvo 1997). The largest plant research initiative (or at least the most expensive) was the establishment of a permanent 50-hectare (ha) forest plot (1000×500 m) currently known as the “50-ha Yasuní Forest Dynamics Plot” (YFDP; Valencia et al. 2004a). At the time, the YFDP was envisioned as an ideal complement to Barro Colorado Island´s 50-ha plot (established in 1980–1981) which had become, and still is, one of our most valuable assets to understand many ecological patterns and processes in lowland tropical rainforests (Hubbell 2004).

During the past decade, many plant ecology studies have been undertaken in Yasuní. A set of these studies has solely explored the spatial variation in diversity, distribution, floristics, and community structure of tree, liana and palm communities at the landscape scale within and among the main forest types of Yasuní (terra firme, floodplain and swamp forests), sometimes reinforcing them with analyses of rarity (e.g., Montúfar 1999, Pitman 2000, Romero-Saltos, Valencia, and Macía 2001, Burnham 2002, Tuomisto et al. 2003, Burnham 2004). These studies, in conjunction with the classic studies that studied a handful of terra firme and flooded forest plots/transects in the outskirts of Yasuní (Balslev et al. 1987, Korning and Balslev 1994), showed that the terra firme forest of Yasuní has significantly higher species diversity than floodplain and swamp forests, and that terra firme forest is the least variable of the three forest types in terms of taxa composition (i.e., it has relatively low species turnover across the landscape). These studies were complemented by other studies which did not only study the local landscape variation of Yasuní but also that of other Neotropical areas in order to generate a more comprehensive regional picture. Those studies compared among Yasuní, Manú and Panamá (e.g., Pitman 2000, Pitman et al. 2001, Pitman et al. 2002, Condit et al. 2002), between Yasuní and Bolivia (e.g., Macía and Svenning 2005), between Yasuní and northern Perú (e.g., Vormisto et al. 2004, Montúfar and Pintaud 2006, Pitman et al. 2008), and among Yasuní, Perú and Colombia (Duque et al. 2004a, Duque et al. 2004b), to name some examples. These studies showed that, although terra firme forests of western Amazonia are relatively homogeneous with regard to the presence of common dominant taxa, especially at and above genus level, it is possible to discern types of terra firme forests within apparently homogeneous vegetation when dominant/subdominant species abruptly change in their relative abundances concomitantly with a change (or presumed change) in abiotic variables (e.g., topsoil, climate, topography, geomorphology). Such phenomenon has been observed even within Yasuní terra firme forests (Tuomisto et al. 2003), where there are not abrupt changes as, for example, the presence of white-sand forests surrounded by forests on clay soil (like in Perú or Colombia; see e.g., Duivenvoorden 1995).

To complement the macro-approach of the above mentioned studies, another set of plant research projects in Yasuní have taken the miniaturist approach and have studied local plant communities intensively, although obviously in the publications the results are always compared to other areas in the tropics. This approach has involved either lowering the diameter cutoff below which trees or lianas do not enter a sample (e.g., 1 cm instead of 10 cm or 2.5 cm), or focusing on the ecology of certain species (autecology), groups of species (e.g., taxonomic families, palms, etc.), growth stages (e.g., seedlings), non-tree growth forms (e.g., lianas, epiphytes, herbs, etc.), or whatever other intensive approach the local research question demanded. A few examples of this approach include: the studies on lianas in the vicinity of the Yasuní Research Station, which intensively sampled lianas independent of their diameter (Nabe-Nielsen 2001) and also included studies on the population ecology of *Machaerium cuspidatum*, arguably the most common liana species in Yasuní (Nabe-Nielsen 2002, Nabe-Nielsen and Hall 2002, Nabe-Nielsen 2004); the studies about diversity and distribution of epiphytes (Kreft et al. 2004, Sandoya 2007); a study on reproductive and litterfall phenology on more than a dozen tree species (Cárate 2005); a study about how environmental factors may affect the germination of six *Cecropia* species (Barriga 2002); the studies on the potential effect of hunting pressure on diaspore dispersal by vertebrates (e.g., Holbrook and Loiselle 2009); and several in-depth studies about a variety of research topics conducted within the YFDP and nearby areas. Given the relevance of the YFDP studies to this doctoral dissertation, which was also conducted within the YFDP, such studies are presented below in an independent section.

The Yasuní Forest Dynamics Plot: an account of research topics in a permanent observatory

Since the YFDP was established in 1995 (Valencia et al. 2004a), the number of large research projects conducted within the YFDP, many resulting in more than one publication, have reached at least a dozen. While most projects have been devoted to pure plant ecological research, some have used the experience gained in the YFDP to obtain conservation/educational funding (e.g., Garwood 2008) while also allocating some funds for basic taxonomic and ecological research (e.g., Barriga 2002, Santiana 2005, Moscoso 2010). And there have been projects that even used the YFDP, or parts of it, as habitat to track down animals (e.g., *Drosophila* flies; Acurio, Rafael, and Dangles 2010). The core of the research in the YFDP, however, has been devoted to understand the ecological processes that, synergistically considered, may help to explain the miracle of having so many plant species packed in just half-a-square-kilometer of forest (50 hectares). Indeed, the approximately 1100 species of trees (Valencia et al. 2004a, Valencia et al. 2004c, Valencia et al. 2004b, Valencia et al. 2009) and 250 species of lianas **(see Chapter 2)** occurring in the YFDP are but a sample of the typical megadiversity of the equatorial rainforests from western Amazonia (Bass et al. 2010). These studies strengthen the common conservationist claim that Ecuador is one of the top five most biodiverse countries in the world per unit of area (Mast et al. 1997), a claim that is further supported by the approximately 4,000 formally recognized species of vascular plants occurring at an altitude ≤500 m in Amazonian Ecuador, from which herbaceous vines and woody vines (lianas) are represented by roughly 700 species in all (Jørgensen and León-Yánez 1999).

A set of publications from the YFDP have asked if microenvironmental heterogeneity—usually quantified as spatiotemporal variation in topography, light/gaps/canopy openness, and soil characteristics—plays a role in the observed distribution of plants. The environment vs. plant distribution topic is basic but important, and has been explored for palms (Svenning 1999a), a few common understory species of trees and palms (Svenning 2000), trees in general (Valencia et al. 2004c, Valencia et al. 2004b, John et al. 2007), seedlings (Metz 2007), tree species in the Myristicaceae family (Queenborough et al. 2007b), and lianas **(see Chapter 2)**. In general, these studies have found clear associations between microenvironmental conditions and the distribution of many species, although the strength of such associations change depending on growth form, plant size, and, of course, species and sample size. Given that the environment seems to constrain, at least to some extent, where species can grow or thrive in the

YFDP, another set of studies have evaluated the impact of the environment on the life history and demographic rates of particular species, taxonomical groups or growth forms. These have included studies on the effect of the environment on the recruitment of arborescent palms (Svenning 1999b), on the growth strategies of clonal palms (Svenning 2000), on the growth strategies of lianas **(see Chapter 4)**, and on the population growth rate of a common understory palm species (*Geonoma macrostachys*; Svenning 2002).

More complex and recent studies have gone one step further and have considered not only the abiotic factors but also the biotic factors—in particular the "biotic neighbourhood" (i.e., the plants growing near your focus plant) and community-level density-dependent processes operating at the seedling stage (dispersal assembly)—in an attempt to understand the mechanisms behind the coexistence of countless species in the YFDP. These have been part of the doctoral dissertations of Metz (2007), focused on seedlings, and Queenborough (2005), focused on Myristicaceae, and which are starting to create impact through their resulting publications (so far, Queenborough et al. 2007c, Queenborough et al. 2009, and Metz, Sousa, and Valencia 2010). (Based on data collected in the YFDP, Queenborough also published a paper on the evolution of dioecy in Myristicaceae; Queenborough et al. 2007a). The Metz´s studies, which still continue, are being further supported by the long-term seed/fruit rain data from the 200-traps system (1 m^2 each) that was set up by J. Wright (STRI) and N. Garwood (Southern Illinois University) in the year 2000. Since then, every two weeks or so, all flowers, fruits, or any reproductive part thereof, that fall in every trap have been quantified. At present, the database has approximately 165,000 records (every record representing an observation of a species in a trap at a given time). The accumulated secrets behind this enormous dataset still await publication, although some results from the first years, coupled with climatic data, formed part of a doctoral dissertation (Persson 2005) and an undergraduate thesis (Aguilar 2002).

Lately, another line of research in the YFDP has pointed out that it is illusory to think that we will understand the mechanisms that maintain the high diversity in Yasuní if we do not understand how the community was assembled, evolutionarily speaking. The underlying assumption in these studies is that every species is different, i.e. they are not ecologically equivalent entities subjected to stochastic demographic processes with phenotypes randomly distributed throughout the forest, as in Hubbell´s neutral model (Hubbell 2001). (The neutral model, however, has served as the perfect null hypothesis). In the past decade, powerful tests based on the distribution of phenotypes (functional traits) and taxa relatedness were developed to assess the relative importance of community assembly processes such as niche differentiation (driven by competition), habitat filtering, and neutrality (e.g., Webb 2000, Kraft et al. 2007). Sooner than later, this trendy research reached the YFDP with the challenge of testing these models in a natural setting where a little more than a thousand species coexist in just 50 hectares of forest. The trait- and phylogenetic-based analyses designed to identify the main processes driving tree community assembly in the YFDP have found a clear, although weak, signal of habitat (environmental) filtering up to the 100×100 m spatial scale, in part related to the topographically-defined habitats of ridge and valley in the plot (Silver, Lugo, and Keller 1999, Kraft and Ackerly 2010). However, they have also found, somewhat paradoxically, evidence for differentiation of functional strategies among coexisting species (i.e., “niche partitioning” as a result of competition; this is not to be confused with “topographic niche-partitioning” which is more related to habitat/environmental filtering) and enemy-mediated density dependence at relatively small spatial scales, up to the 20×20 m scale (Silver, Lugo, and Keller 1999, Kraft and Ackerly 2010). I cannot wait to use the functional trait data of the lianas in the YFDP **(see Chapter 3)** to address community assembly questions similar to those asked for the trees.

The increasing interest of the international community and decision-makers in the debate about climate change, and whether tropical forests will serve as net carbon sinks or net carbon sources (e.g., Clark 2004), prompted the questions of how much carbon is there actually in the YFDP (the “stocks” or “reserves”), how it varies over time, and how much and how fast it moves among different ecosystem compartments (i.e., the “fluxes” along the soil-plant-atmosphere continuum). One of the first approaches to increase the accuracy of carbon stocks estimates in the YFDP was to measure wood specific gravity of as many common tree species as possible (Altamirano 2009). These local estimates have allowed to estimate the aboveground carbon stocks in the YFDP relatively accurately, although based only on tree data (Valencia et al. 2009). But the carbon picture in Yasuní is far from complete. For example, belowground carbon stocks as well as ecosystem-level fluxes are basically unknown (but pioneering work is now being conducted by H. Muller-Landau, and Ecuador´s YFDP local team). We do not have either any accurate assessment of how representative the carbon processes in the YFDP are of the whole terra firme forest of Yasuní, not to mention the unknown carbon dynamics in the other forest types in Yasuní: floodplains and swamps.

Finally, it is important to stress that one of the key reasons why the YFDP was created was to represent the equatorial lowland north-western Amazonian forests in regional or worldwide comparative studies. Thus, from time to time the data from the YFDP becomes part of regional or global datasets assembled in order to address a variety of questions (e.g., Condit et al. 2002, John et al. 2007, Chave et al. 2008, Metz et al. 2008, DeWalt et al. 2010, Kraft et al. 2010). Such initiatives are usually (but not necessarily) undertaken by scientists associated to the CTFS-SIGEO worldwide network of permanent forest plots hosted by the Smithsonian Tropical Research Institute in Panamá (www.ctfs.si.edu), which is, in practice, a consortium of many independent institutions, country-based universities and scientists from many parts of the world.

THIS DISSERTATION: THE LIANAS IN THE YASUNÍ FOREST DYNAMICS PLOT

This dissertation represents the first formal approach to study the ecology of lianas (woody vines) within the 50-hectare Yasuní Forest Dynamics Plot (YFDP), in Amazonian Ecuador. It is a study that asks simple questions, but which I think have uttermost relevance in the attempt to build a solid foundation for future research initiatives.

In **Chapter 2**, I (1) describe the liana community in the YFDP and find that various community-level attributes of the lianas in ridge habitat (diversity, species composition, and/or species abundances) are significantly different than those of the lianas in valley habitat, because of the distinct distribution (differential abundance) of several species between ridge and valley. This leads to the main **over-arching question** of this dissertation: ***To what extent is the observed spatial distribution of plants in a forest, in this case lianas, explained by the characteristics of the different species***. To be relevant,

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(1) Because the data for this dissertation were collected with the help of a small team of Ecuadorian biologists and innumerable field and lab assistants, I decided to write the data Chapters (Chapters 2, 3 and 4) in the first person plural. The data Chapters were written in a format suitable for publication in a specialized journal, with the potential authors listed as a footnote.

these characteristics must have an effect on the fitness of the plants, i.e. they must be "functional" traits.

In this dissertation, I explore two groups of functional traits: one group includes traits commonly measured in plants (specific leaf area, leaf dry matter content, leaf morphometry [lamina thickness, length:width ratio, leaf size], leaf carbon, nitrogen, and phosphorus concentrations, leaf ^{13}C and ^{15}N isotopic signatures, wood specific gravity and stem diameter growth rate), while the second group includes traits that are particular to lianas and specifically refer to the way a liana, as a whole, grows in the forest (whether it is free-standing or climbing, the mechanism it uses to climb, whether is creeping or not, and whether it has near-ground branches or not). Partly because the traits in the first group are measured quantitatively (continuous variables), while those in the second group are measured qualitatively (categorical variables), I explore the first group in **Chapter 3** and the second group in **Chapter 4**.

In **Chapter 3**, I explore the expression of the quantitative traits in those species that are driving the community-level differences between ridge and valley,**(2)** which are basically those common species with a statistically significant habitat association to either ridge or valley, and compare their trait expression to that of generalist species (species that show no habitat association at all). I test a number of theory-based hypotheses developed with the underlying idea that if trait expression is different among species guilds of habitat association (or non-association), then there is evidence that the inherent traits of liana species can constrain where in the forest certain species can

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(2) A trait analysis using all the liana species in the community would be imprudent with the present status of the data because many species occur at very low local abundance, and thus the number of individuals sampled for traits in such species were very low, not to mention the lack of data of some traits in many of the rare species.

grow—which would explain, at least partly, the observed differential distribution between ridge and valley that some species show. Go ahead and read Chapter 3 to discover the results.

In **Chapter 4**, I explore if the different strategies lianas use to grow, as whole plants, depend on the topographic habitat. If a particular growth strategy is significantly more common in either ridge or valley, and that growth strategy can be more or less consistently associated to a particular liana species, or to a group of species, then it is possible that the growth strategy exhibited by such species plays a role in determining where in the forest such species can grow—which would explain, at least partly, the observed community-level difference in community structure (species composition and their abundances) between ridge and valley. Of course, the problem in this logic is that one does not know whether the growth strategy is innate to the plant or is shaped by the environment. To partly solve this issue, I approach the data creatively. First, I analyze free-standing lianas (treelet-like lianas) and climbing lianas (lianas already attached to a support) separately. Second, I describe growth strategies only among the climbing lianas by using two whole-plant categorical variables: climbing mechanism (twining, tendrils, branch-twining, scrambling [sensu lato], and adhesive roots/tendrils), and understory appearance (creeping liana with large understory branches [usually stolons], creeping liana with no large understory branches, non-creeping liana with large understory branches, and non-creeping liana with no large understory branches). Among these whole-plant traits, certainly climbing mechanism is phylogenetically constrained and thus not subject to environmental influences. Note that the concept of understory appearance is applicable only to climbing lianas. At the end, by using this approach, only the understory appearance among climbing lianas has the chicken vs. egg problem, i.e. not knowing if understory appearance is innate to the plant or is caused by the environment. So, is there any difference among growth strategies of lianas on ridge vs. those in valley? Find out by reading Chapter 4.

To end this dissertation, in the **Conclusion** chapter I come back to the over-arching question: ***To what extent is the observed spatial distribution of lianas in the YFDP forest explained by the characteristics of the different species?*** In an attempt to contribute to the development of theory to answer this question, in the Conclusion I synthesize the results from the three data Chapters. Note that the distribution problem (why some species of lianas are differentially distributed along the ridge-valley topographic gradient in the YFDP, a phenomenon that eventually results in the ridge having a different species composition and/or species abundances than the valley) is essentially different from, although still related to, the diversity problem (why so many species coexist in such a reduced space). Throughout this dissertation, I focus more on the first problem than on the second, which I think requires much more information than what I presently have (e.g., dispersal processes, competition, phylogenetic relations). I believe the Yasuní lianas will eventually give us insight about both problems.

CHAPTER 2: Liana communities in ridge and valley topographic habitats of the Yasuní Forest Dynamics Plot, Amazonian Ecuador (3)

SUMMARY

We describe the species diversity, species composition, abundance, basal area, floristics and community structure of the lianas in the 50-hectare Yasuní Forest Dynamics Plot (YFDP) in Amazonian Ecuador. The general hypothesis we test is that the liana community will change along the topographic gradient from ridge to valley (250–215 m) that is characteristic of the YFDP terra firme forest. A modified (refined) detailed sampling protocol was used that included the wide variety of lianas. We sampled all lianas with diameter ≥1 cm in thirty 20×20 m quadrats established as a grid design in the western 600×500 m area of the YFDP: 17 in ridge habitat and 13 in valley habitat. We inventoried 1919 individual lianas in all, classified into 195 species-level taxa (155 fully identified to species), 93 genera and 38 families. Only 10 percent of the species (19 species) contained 50 percent of the individuals, whereas nearly 50% of all species (97 species) were represented by only 1–3 individuals. The five most abundant species, representing 30% of the individuals, were *Combretum laxum* (141 individuals), *Machaerium cuspidatum* (135), *Petrea maynensis* (127), *Cuervea kappleriana* (96), and *Clitoria pozuzoensis* (82). *P. maynensis* and *C. kappleriana* were much more common on ridge, while *C. laxum* and *M. cuspidatum*, although widely spread in both habitats, tended to be most abundant in valley. For lianas with diameter ≥1 cm, species density, species

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richness and Fisher’s alpha diversity index were all higher in the valley than in the ridge; these diversity differences were statistically significant, except for species richness. On the other hand, abundance and basal area, including their distributions by diameter classes, were not significantly different between the two habitats, although large lianas (diameter ≥5 cm) tended to occur more commonly in valley. A significant difference in liana species composition between ridge and valley, as represented by species abundances, was found even for lianas with diameter ≥2.5 cm and whether or not rare species were included in the analyses (ANOSIM). Ridge quadrats segregated relatively well from valley quadrats along the first axes of NMDS and DCA ordinations. DCA analyses showed also that rare species increased the species turnover among quadrats, particularly in valley, which we suggest is more heterogeneous than contiguous ridge areas. Overall, these results support the hypothesis that topographic changes in the landscape, probably correlated with biogeochemical changes, can influence liana communities, even at relatively small spatial scales.

BACKGROUND AND HYPOTHESIS

While walking in a lowland tropical rainforest, after marveling at the tallest or widest trees, you ought to wonder about the long woody vines, commonly known as “lianas”, clinging on whatever support available and whose tip you rarely see. To a large extent, the importance of lianas resides in their great capacity to exploit empty space in the forest (see Castellanos et al. 1992) with efficient biomass investment (see Niklas 1994); branch systems can certainly extend tens of meters in all directions, interacting with several tree stems and crowns, while root systems probably are as spread as well, perhaps more conspicuously in those liana species that develop roots along stolons. If abundant, lianas can negatively affect their host trees via resource competition and/or via architectural hindrance, potentially causing malformations, decrease of growth and fecundity rates, and of course less chance for survival (e.g., Stevens 1987, Pérez-Salicrup and Barker 2000, Ingwell et al. 2010). Other important ecological roles of lianas—including their important contribution to the diversity and abundance of woody plants in tropical lowland rainforests (approximately 20–25% in a typical forest; Gentry 1982, Gentry 1991), how they may affect the succession pathway in forest gaps (e.g., Schnitzer and Carson 2010), how they contribute to the nutrient and water cycles (e.g., Restom and Nepstad 2001), or how they may be becoming increasingly dominant in tropical forests (e.g., Phillips et al. 2002)—have progressively come to light since the modern fervor to study their ecology started in the 1980's (e.g., Gentry 1982, Peñalosa 1984, Putz 1984, Stevens 1987). Today, publications about lianas have become relatively common and some extensive reviews are available (Putz and Mooney 1991, Bongers, Schnitzer, and Taore 2002, Schnitzer and Bongers 2002, Pérez-Salicrup, Schnitzer, and Putz 2004, Isnard and Silk 2009, Vaughn and Bowling 2011, Paul and Yavitt 2011). The reader is referred to those reviews to further appreciate the ecological importance of lianas, as it is not our intention here to present an updated review.

Technically speaking, what is a liana? Lianas are defined as woody (except for the sturdy non-woody stems of monocots) terrestrial vines that climb using varied mechanisms such as tendrils, hooks/spines/thorns, twining stems or leaves (or other organs), adhesive adventitious roots, or simply by scrambling on top of other plants (Putz and Mooney 1991, Schnitzer and Bongers 2002, Isnard and Silk 2009). Some lianas have the distinctive ability to reproduce vegetatively by stem resprouting, particularly if damaged (e.g., Peñalosa 1984, Caballé 1994), although liana seedlings of some species can be very common on the forest floor as well (e.g., Metz 2007). Some liana species may first grow upright a few meters, and then wait for the ideal conditions that will trigger their ascent. These free-standing lianas should not be confused with treelets, just as climbing lianas should not to be confused with climbing (hemi-)epiphytes whose roots, as opposed to lianas, may facultatively lose connection to the ground (though there are "intermediate" liana/hemiepiphyte growth forms, such as *Marcgravia*), or with the hanging rope-like woody aerial roots (Tarzan-suitable) of some primary hemiepiphytes that are usually stranglers (e.g., *Clusia*, *Ficus*). See Moffett (2000) for an useful overview and discussion of these growth forms.

The present study introduces the diversity, abundance, basal area, floristics and community structure (defined as species composition and their abundances) of the lianas in the 50-hectare Yasuní Forest Dynamics Plot (YFDP) in northwestern Amazonia, based on a subsample of 1.2 ha (thirty non-contiguous 20×20 m quadrats evenly dispersed as a grid). The 50-ha YFDP is a permanent large-scale observatory of tropical plant ecology associated to the CTFS-SIGEO worldwide plot network (Valencia et al. 2004a, CTFS 2010). It is located in Yasuní National Park, Amazonian Ecuador, a protected area of approximately 10,000 km^2 known to harbor very high levels of plant and animal alpha diversity (Bass et al. 2010), and where lianas are certainly not the exception (Nabe-Nielsen 2001, Romero-Saltos, Valencia, and Macía 2001, Burnham 2002, Burnham 2004). Studies on plant diversity and distribution in the YFDP have demonstrated that the topographically-defined upper-ridge and valley habitats are the most dissimilar in terms of tree and palm species composition (Svenning 1999a, Valencia et al. 2004c), while the diversity of tree species between ridge and valley is not significantly different, although there is a tendency towards higher diversity in valley (Valencia et al. 2004c). The valley also has smaller basal area and density of trees per hectare than the ridge, and in fact tree biomass on the ridge is at least 50% more than that on the valley (Valencia et al. 2004c, Valencia et al. 2009). Because trees with a relatively large diameter are proportionally more common on the ridge than in the valley, mean canopy height is probably higher on ridge than in valley (Valencia et al. 2004c; see also Svenning 1999a). We expected that all these differences in tree communities of ridge and valley habitats in the YFDP may influence the liana community as well.

Our study, therefore, has two specific goals. First, we want to provide comprehensive community-level information about the lianas in the YFDP from which future studies can be built. Because this work represents the first (partial) census of lianas in the YFDP, we have taken special care to work out the liana taxonomy, which has utmost relevance given the long-term vegetation monitoring objective of the YFDP. Second, we want to test the simple hypothesis that liana communities are sensitive to topographic changes in the hilly terra firme forest of Yasuní, specifically between ridge (broadly defined) and valley environments—no study in Yasuní has explored this question at such small spatial scale (for studies at the landscape scale, see, Romero-Saltos, Valencia, and Macía 2001, Burnham 2002, Burnham 2004).

METHODS

STUDY AREA

The present study was conducted from 2006 to 2008 in Yasuní National Park, Amazonian Ecuador, in the 50-hectare Yasuní Forest Dynamics Plot (YFDP). Yasuní

National Park comprises near 10,000 km^2 of mostly undisturbed, highly diverse, lowland evergreen tropical rainforest (ECOLAP and MAE 2007, Bass et al. 2010). The 50-ha YFDP (00°41' S, 76°24' W; altitudinal range: 215–250 m) was established in 1995 and is associated to an ever expanding network of large-scale permanent plots (ca. 40 at present) that monitor millions of trees in several tropical and temperate countries (Valencia et al. 2004a, CTFS 2010). In each plot, all trees with diameter at breast height (DBH) ≥1 cm are censused approximately every five years. In the YFDP, three censuses of all trees with DBH ≥1 cm have been completed in the western 25 ha, while in the eastern 25 ha only two censuses have been completed, the first of which included trees with DBH ≥10 cm only (R. Valencia and C. Hernández, pers. comm.).

The YFDP is located on terra firme (upland) forest, with ridge formations up to 250 m altitude towards the northern, southern and eastern areas of the plot; these are separated by a relatively wide valley or bottomland (ca. 215–225 m altitude) that, except for swampy areas, is considered terra firme as well (Figure 2.1; Valencia et al. 2004a). A few permanent streams crisscross the valley; they may seldom overflow and temporarily flood part of the valley during the rainiest months. Intervening valleys are a common physical feature of the hilly terra firme forest of Yasuní, and under low drainage conditions, they may become swamp forests dominated by the palm tree *Mauritia flexuosa*. In the YFDP, there are some small non-contiguous swampy areas (1.72 ha total; not sampled in our study).

More than 90% of Yasuní is terra firme (upland) hilly forest growing on Ultisol soils that are somewhat clayey, acidic and rich in iron and aluminum (Pitman 2000, Valencia et al. 2004a). The surface soil (0–5 cm) of the terra firme is, when compared to other terra firme areas in northwestern Amazonia, relatively rich in exchangeable bases (particularly Ca, Mg, and Na) and has an average texture of approximately 50% silt, 29% sand and 21% clay (Tuomisto et al. 2003) (for more information on nutrient concentrations at deeper levels in the Yasuní terra firme soil, as well as on swamp and floodplain soils, refer to Lips and Duivenvoorden 2001). The biogeochemical characteristics of the topographically distinct ridge and valley habitats of the YFDP have not been well studied, but differences are expected. The main differences, related to the effect of topography on the hydrological regime, should be on drainage (on average probably lower in the valley, at least in the depressions), soil water content (on average probably higher in the valley; see e.g. Jirka et al. 2007) and soil oxygen concentration (on average probably lower in the valley; see e.g. Silver, Lugo, and Keller 1999). If these differences are marked, other soil characteristics such as pH, aluminum concentration, nutrients concentrations and organic matter concentration should also be different between ridge and valley habitats (Tange, Yagi, and Sasaki 1998, Tuomisto et al. 2003, Kubota, Murata, and Kikuzawa 2004). However, in a recent study no clear difference in soil nutrients was observed between these habitats in the YFDP (John et al. 2007), although the reliability of the soil data collected for that study has been questioned (J. Dalling pers. comm., H. Romero-Saltos pers. obs.).

Climatic records (April 1994 to August 2009) from a weather station at the Yasuní Research Station, located at ca. 1 km from the YFDP, provide a good overview of the local patterns of rainfall, temperature and relative humidity, although complete 12-month data is available for only a few years and monthly data are often incomplete (monthly patterns described below are therefore based on months with at least 20 days of weather data only). Average annual rainfall is 3047 mm (*N*=4 years with complete 12-month data; range: 2699–3446 mm) while average monthly rainfall is 250 mm (*N*=132 months, range: 29–640 mm). Because no month had a multi-year average rainfall <100 mm, Yasuní is considered a non-seasonal forest. However, the abundant rainfall does follow a seasonal pattern with two rainfall peaks: the strongest in May (May's rainfall average=394 mm) and the second, less pronounced, in October (October's rainfall average=243 mm). This double-peak rainfall pattern is typical of easternmost Ecuador and is controlled by yearly fluctuations of the Intertropical Convergence Zone with respect to the Equator (Pitman 2000). The average monthly temperature is 24.6 °C (*N*=127 months, range: 22.1–26.7 °C), but daily minimum and maximum temperatures can fluctuate considerably (all-time hourly records of minimum and maximum temperatures are 14 °C and 50 °C, respectively). Monthly average relative humidity is 86.8% (*N*=11 months, range: 80.0–91.2%); the lowest hourly relative humidity ever registered was 34% while the highest was 98.3%.

RESEARCH DESIGN

We sampled the lianas in thirty non-contiguous 20×20 m quadrats aligned as a perfect rectangular grid in the western 600×500 m area of the 50-ha YFDP (1000×500 m). Each 20×20 m quadrat was located in the center of each square hectare (6 columns × 5 rows), and can be uniquely identified by a combination of a column code (*x*-axis) and a row code (*y*-axis), where each column or row is a 20 m wide forest strip (Figure 2.1). This coding system is the same used for the tree censuses. The quadrats were purposely established in a non-random fashion (grid) to equalize the sampling effort across the YFDP and have a good representation of its liana diversity. Columns 02 to 22 were sampled in 2006, while column 27 was sampled in 2008. In each 20×20 m quadrat, we sampled all liana individuals with a diameter (at the largest stem width) ≥1.0 cm at a Point of Diameter Measurement (PDM) located along the main stem following a standard PDM location protocol (Appendix 1). At a PDM, the largest and smallest stem widths (diameters)—irrespective of stem shape (i.e., even if the stem was terete)—were measured with a Vernier caliper and rounded off to the nearest 0.1 mm. Terete liana stems with a largest stem width ≥5.0 cm were only measured with diameter tape (accuracy: ±1 mm). Adult stems surrounded with profuse and soft cork (e.g., *Aristolochia*, *Chomelia*, some *Paullinia*) were measured without the cork (i.e., the cork was removed). The stem area at a PDM was cleaned and marked with fluorescent orange/red spray paint, and a cross was drawn with permanent black marker on the PDM. An aluminum tag, uniquely numbered, was loosely attached to the stem at or near the PDM using red plastic rope proven to last many years under rainforest conditions (Fortex® 4H). Hemiepiphytic climbers (from various families), which sometimes may look like lianas, were not sampled, and neither were any Araceae or Cyclanthaceae climbers. Although non-woody, the sturdy monocot vines from Smilacaceae (*Smilax*), Dioscoreaceae (*Dioscorea*) and Arecaceae (*Desmoncus*) were included in the sampling, as well as any sub-woody or herbaceous vine with a diameter ≥1 cm.

For each liana we also recorded one of the following three “growth stages”: climbing (liana using a support), free-standing (treelet-like non-climbing liana; YFDP’s taxonomists helped us to unequivocally distinguish them from treelets) or neither of them (e.g., fallen branches that had rooted and leafed successfully, but were not yet climbing).

An individual was defined as an "apparent genet", i.e. a stem or a group of stems obviously connected above- or below-ground, but whose genetic relatedness to nearby lianas of the same species, presumably physically separated, is uncertain because those nearby individuals could either be ramets (vegetative clones) or genets (seed origin) (Gerwing et al. 2006, Schnitzer, DeWalt, and Chave 2006, DeWalt et al. 2010). Thus, under this definition, "apparent genets" might as well be called "apparent ramets". An individual was included in the sample only if its presumable original rooting point was inside the limits of the 20×20 m quadrat at ground level. Such original rooting point, along with any other conspicuous rooting points (those with diameter ≥1 cm), were mapped on paper to facilitate relocation of the liana in the future.

Appendix 1 describes the two different protocols we used to locate the Point of Diameter Measurement (PDM) along the main stem of a liana: the "Gerwing/Romero" (G/R) protocol and the "Basal" protocol. Sometimes, if a liana had complex growth (e.g., creeping, looping, multiple rooting points, multiple stems), we may measure more than one PDM for that liana (see Appendix 1). The G/R protocol was designed as a complement to a sampling protocol for lianas published in 2006 (Gerwing et al. 2006), in particular for the special cases not defined in that publication. We did not take into account the most recent liana sampling protocol (Schnitzer, Rutishauser, and Aguilar 2008)—an update of the original protocol (Gerwing et al. 2006)—because it was not available when we developed our system. To provide perspective, a graphical comparison between our two protocols and the "Gerwing/Schnitzer" (G/S) protocol is also shown in Appendix 1. The G/R protocol is based on a classification key that describes a liana's ground-level general appearance—from approximately 0 to 3 m height—with an alphanumeric code. We used this protocol in 2006 (columns 02 to 22), but not in 2008 (column 27) when we instead decided to use the much simpler and practical Basal protocol (see Appendix 1). Nevertheless, the G/R codes describing the general appearance of a liana were used both in 2006 and 2008. Even though in column 27 we sampled all lianas with a Basal diameter ≥1 cm (at the largest stem width), we also always annotated whether or not a liana had a G/R diameter ≥1 cm (yes/no data); in addition, for 217 random lianas, we measured both the G/R and Basal diameters, so that a correction could be developed later if necessary (see Data Analyses section).

Lianas were identified by collecting botanical samples (mostly leaves only) that were later pressed, dried, and identified in the following herbaria with the support of other botanists (see Acknowledgements), although we always reserved the right for the final decision on a specimen's identity: Herbarium of the Pontifical Catholic University of Ecuador (QCA), National Herbarium of Ecuador (QCNE), Missouri Botanical Garden Herbarium (MO), the University of Michigan Herbarium (MICH) (done by R. Burnham), the United States National Herbarium (US) (done by P. Acevedo-Rodríguez) , and the University of São Paulo Herbarium (SPF) (done by L. Lohmann). Vouchers of nearly all the species-level taxa were mounted and are formally deposited at QCA and at the reference herbarium of the YFDP project at the Yasuní Research Station. In addition, a representative subset of specimens was donated to QCNE and MICH, some Sapindaceae were donated to US, and some Bignoniaceae were donated to SPF. As a further aid, several virtual herbaria (Internet websites) with high-quality images of herbarium specimens from western Amazonia (F, MO, NY, US, among others), were consulted to observe species types and to confirm/solve dubious identifications. Not all lianas were collected, either because of canopy inaccessibility (these lianas were codified as non-collected/non-identified “Zzz zzz” lianas in the database) or because they were easily identifiable, without the need of a collection, by their distinctive foliar and/or non-foliar vegetative characters.

DATA ANALYSES

In our study, each 20×20 m quadrat was considered the unit of replication or *sampling unit*, and thus the set of quadrats in a given topographic habitat (ridge or valley) was considered a *sample* of such habitat. This is the appropriate statistical terminology for our study, as opposed to colloquially refer to each quadrat as a “sample” (Sokal and Rohlf 1995, Colwell, Mao, and Chang 2004). Given that quadrats were separated from each other by at least 80 m (Figure 2.1), we assumed that each quadrat was statistically independent. The 180 non-collected/non-identified “Zzz zzz” lianas were excluded from the diversity and multivariate analyses, but were included in the abundance and basal area analyses.

Habitat classification

The thirty quadrats were classified as 17 ridge quadrats and 13 valley quadrats (Figure 2.1), according to the following procedure (partially based on Valencia et al. 2004c). First, using ArcGIS 9, elevation data collected at the corners of all 20×20 m quadrats in the 50-ha YFDP were used to estimate a mean altitude and a mean slope for each of the 30 quadrats. Second, each 20×20 m quadrat in our sample was classified either as ridge or valley based on these means, and how they differed from median threshold values of elevation (227.2) and slope (12.8°). A ridge quadrat was defined as one with mean elevation ≥227.2 and any slope, or one with mean elevation <227.2 but slope ≥12.8° (low ridge). A valley quadrat was defined as one with mean elevation <227.2 m and slope <12.8°. The quadrats classified as ridge in our study include therefore the low ridge, high ridge, high gully and ridge-top topographic habitats defined by also using convexity/concavity measurements (Valencia et al. 2004c) (convexity/concavity is measured with respect to the imaginary plane that crosses a quadrat from one extreme to the other; the slope of such plane being the mean slope of the quadrat). In studies with trees in the YFDP (Valencia et al. 2004c, Valencia et al. 2009), the use of a detailed topographic classification within the ridge area (where convexity/concavity measurements matter) did not increase the explained variation in tree species composition, species abundances, or biomass distribution. We assumed this is also the case for lianas, although we acknowledge the imperfect generalization of our simple two-habitat classification at the 20×20 m scale. This imperfect classification is particularly evident in quadrats that contain ridge-valley transitional areas; these quadrats, indicated with arrows in Figure 2.1, were identified as those containing ridge-valley transition 5×5 m subquadrats, according to a detailed topographic habitat classification at the 5×5 m scale of the whole YFDP (data not shown).

Diameter criteria for inclusion of liana individuals in analyses

For each liana, the geometric mean of the largest and smallest stem widths (diameters) was calculated. Only those lianas with a G/R mean geometric diameter ≥1 cm were analyzed in our study (1919 individuals out of the 2032 sampled in total). The 113 lianas *excluded* from the present study’s dataset include 26 lianas whose mean geometric diameter was <1 cm (although their largest stem width was ≥1 cm) and 87 lianas from column 27 with a “Basal” diameter ≥1 cm, but a G/R diameter <1 cm. We did not apply any G/R diameter correction to the lianas that only had "Basal" diameters measured because the difference in diameter between these two types of diameters, in the random lianas set (see Research Design section), was minimal (y=1.024x−0.087, where y=G/R diameter and x="Basal" diameter; R^2=0.852; N=217 lianas). The difference is minimal probably because many lianas in the study area start branching within 40 cm from the original rooting point, and therefore in those cases the "Basal" PDM is basically the same as the G/R PDM (see Appendix 1).

Community descriptors

Diversity—To facilitate the comparison between our study and other studies, diversity analyses were conducted not only for lianas ≥1 cm in diameter but also for the sub-dataset of lianas ≥2.5 cm in diameter. *Species density* (the number of species in a given area) and *species richness* (the number of species in a given number of individuals) of ridge and valley habitats were measured by analyzing Mao Tau species rarefaction curves and their confidence intervals (see Gotelli and Colwell 2001, Gotelli and Colwell 2010). We assumed that the data on species identities collected in the set of quadrats of a given topographic habitat provided information about the α-diversity of such habitat; thus, a rarefaction curve of a given habitat represents how α-diversity changes with increasing area (species density) or with increasing number of individuals (species richness) in such habitat. In addition, we also estimated Fisher's alpha diversity indexes (Fisher, Corbet, and Williams 1943) for the ridge and the valley liana communities, and compared them using confidence intervals. Further, to statistically estimate the total number of species in the whole liana community assemblage in our study area (i.e., the 50-ha YFDP), we computed the Chao2 incidence-based total species richness estimator and the Michaelis-Menten function asymptote of the Mao Tau curve, based on all 30 ridge and valley quadrats. All these analyses were conducted using the freeware program EstimateS$^{®}$ (Colwell 2009).

The calculation of a Mao Tau quadrat-based species rarefaction curve and its upper and lower confidence intervals does not require randomizations of quadrat order because the computation is analytical (Colwell, Mao, and Chang 2004, Mao, Colwell, and Chang 2005, Gotelli and Colwell 2010). In contrast, calculations of the Chao2 estimator and the Fisher's alpha diversity index estimator, require randomization in the order of quadrats; thus, for these analyses, in EstimateS we set the number of randomizations, without replacement, to 10,000 (with no random shuffling of individuals among quadrats within species, i.e., the spatial structure of the data was kept intact, just as for the quadrat-based species rarefaction curves).

To compare the *species density* between ridge and valley, the points on the two Mao Tau rarefaction curves at which ridge and valley had the same number of quadrats (i.e., at 13 quadrats) were statistically compared. On the other hand, to compare the *species richness* between both habitats, the *x*-axes of the quadrat-based rarefaction curves were first re-scaled to individuals, and then the points on the two curves at which ridge and valley had the same number of individuals were statistically compared (see Gotelli and Colwell 2010). The statistical comparison between the point on the ridge curve and the point on the valley curve was conducted using the traditional overlap criterion of confidence intervals. Following the recommendation of various authors (Gotelli and Colwell 2010, in turn based on Payton, Greenstone, and Schenker 2003), we used 84% confidence intervals (CI)—not 95% CI—for the statistical comparison between these two points. The 84% CI approximately correspond, in this type of analyses, to a type I error probability of 0.05 (Payton, Greenstone, and Schenker 2003). Similarly, to compare the Fisher's alpha estimator of ridge vs. that of valley, we used the Fisher's alpha values and 84% CI estimated for an equal number of ridge and valley quadrats (i.e., at 13 quadrats).

Abundance, basal area and liana size distributions**—**We calculated abundance (# individuals) and basal area (cm^2) for each 20×20 m quadrat, and then compared the ridge and valley mean per quadrat values. After checking for normality, we used a t test to compare the mean basal area per ridge quadrat to that per valley quadrat. To assess whether there was a significant difference between the diameter-class distributions of liana abundance and liana basal area in the ridge vs. the valley, we used a Kolmogorov-Smirnov test; this analysis used relative abundances to correct for the difference in total number of individuals sampled in each habitat. Diameter classes were defined as equal intervals of 0.5 cm. These analyses were conducted using PAST 1.97 (Hammer, Harper, and Ryan 2001).

To compare our liana density results to other studies from Yasuní that used different sampling areas and diameter cutoffs, we developed expected individuals-area curves for lianas ≥1 cm and for lianas ≥2.5 cm in diameter. These curves (straight lines) resulted from 100 randomizations of quadrat order using abundance values of the 30 quadrats.

Multivariate (multispecies) analyses

We used three complementary and classic multivariate approaches to evaluate how species composition and species abundances changed between ridge and valley quadrats (ANOSIM), and along the ridge to valley topographic gradient (NMDS, DCA). ANOSIM (ANalysis Of SIMilarities) is a non-parametric procedure that directly tests for significant differences in species composition and abundances between communities (Clarke 1993). It is roughly analogous to an ANOVA in the sense that it compares (dis-)similarity distances (converted to ranks) between groups (i.e., ridge and valley) with distances within groups (i.e., among quadrats within a habitat); the distances can be based on any similarity coefficient. The other two multivariate analyses, Non-Metric Multidimensional Scaling Analysis (NMDS) and Detrended Correspondence Analysis (DCA), are ordination techniques mainly used to depict the underlying pattern in species composition (and their species abundances) and, in the case of DCA, to measure the extent of species turnover along the topographic gradient (Lepš and Šmilauer 2003). We considered NMDS and DCA as complementary because they permitted to explore the consistency of the patterns, independent of the underlying statistics. The 180 non-collected/non-identified "Zzz zzz" lianas were excluded from all these analyses.

Similar to the diversity analyses, ANOSIM's were conducted with the dataset of lianas with diameter ≥1 cm and with the (sub-)dataset of lianas with diameter ≥2.5 cm. This allowed us to inquire into the effect of sampling protocols (different diameter cutoff criteria) on the observed composition of species and their abundances. NMDS and DCA analyses, however, were only conducted with the dataset of lianas ≥1 cm in diameter because we did not want to exclude too many species from the ordinations and from the estimation of species turnover (via DCA). In addition, we assessed the effect of rare species by conducting analyses with and without rare species. A rare species, within the ≥1 cm dataset and the ≥2.5 cm dataset, was arbitrarily defined as a species either occurring in a single quadrat only (i.e., with frequency=1; frequency defined as # quadrats where a species occurs) *or* having a total abundance ≤4 individuals. Therefore, the datasets used for the multivariate analyses were the following: the full dataset of lianas with diameter ≥1 cm (195 species and 1739 individuals), the dataset of the most common species of lianas (no rare species) with diameter ≥1 cm (80 species and 1493 individuals), the dataset of lianas with diameter ≥2.5 cm (111 species and 464 individuals; for ANOSIM only), and the dataset of the most common species of lianas with diameter ≥2.5 cm (20 species and 297 individuals; for ANOSIM only).

ANOSIM**—**Using the program PAST 1.97 (Hammer, Harper, and Ryan 2001), we conducted one-way ANOSIM's using the Bray-Curtis index as the similarity coefficient because it is a classical ecological index that works well with abundance data (Hammer 2010, Clarke 1993), and was also the coefficient used for the Non-Metric Multidimensional Scaling analyses (see below). The ANOSIM test statistic is *R* (not to be confused with a correlation coefficient), which can have a value of up to 1 when there is complete dissimilarity among groups (i.e., when all replicates within groups are more similar to each other than to any of the replicates from different groups; Clarke 1993). The significance (type I error probability) of *R* is computed by permuting the group membership of quadrats; for this, we set the number of permutations in PAST to 100,000. Because in our study there are only two groups, ridge and valley, ANOSIM basically became a two-sample comparison (Clarke 1993, Hammer 2010).

Non-Metric Multidimensional Scaling Analyses**—**Non-Metric Multidimensional Scaling Analyses (NMDS) were conducted using the program PAST 1.97 (Hammer, Harper, and Ryan 2001, Hammer 2010). Similar to ANOSIM, NMDS does not work directly on the species data, but on a matrix of (dis-)similarities among quadrats, calculated by any similarity index; in this case, we used the Bray-Curtis index because it works well with abundance data (Clarke 1993, Hammer 2010). In a NMDS ordination, the distances among quadrat points (given by the axes coordinates) represent the rank-order of their (dis-)similarities (not the dissimilarity values themselves). How well the distances among quadrat coordinates in a NMDS diagram represent the real rank similarities among quadrats is measured by the "stress" index, where 0 would be a perfect fit (Lepš and Šmilauer 2003). In other words, stress is equal to 0 when there is a perfect linear correlation between the real and the depicted similarity distances (Shephard diagram). The iterative algorithm of a NMDS tries to find a spatial configuration of points that would give the lowest stress, starting with a random configuration of points (quadrats) in a multidimensional space where the number of dimensions have been *a priori* defined (usually two or three; we used two in our study). In contrast to Detrended Correspondence Analyses (see below), the units of the NMDS axes do not have any particular meaning.

Detrended Correspondence Analyses—The Detrended Correspondence Analyses (DCA) were conducted using CANOCO 4.5 (Jongman, ter Braak, and van Tongeren 1995, ter Braak and Šmilauer 2002, Lepš and Šmilauer 2003). The following CANOCO options were used: species abundances were natural-log transformed (y'=ln[y+1], where y'=transformed abundance and y=original abundance), detrending was done by segments (# segments=26), no down-weighting for rare species was used, and Hill's axes scaling was applied (i.e., quadrat ordination scores were optimized to depict species turnover distances among quadrats). As opposed to ANOSIM and NMDS, DCA works directly with the species data, not with (dis-)similarity coefficients among quadrats. A DCA simultaneously summarizes species to species, species to quadrat, and quadrat to quadrat relations, assuming a unimodal (bell-shaped) species response to hypothetical ("latent") environmental variables represented by the ordination axes—the hope is that the axes will correlate with some real environmental gradients. The latent ordination axes also provide a broad measure of the degree of species turnover among sites (here quadrats) in the study area; in fact, the axes units are in "standard deviations of species turnover", which is a name derived from the "standard deviation" (i.e., width) of a species' multidimensional (multi-axes) unimodal response curve. In practice, if two quadrats, or groups of quadrats, in a DCA diagram are separated by around four "standard deviations", they probably differ significantly in species composition or species abundances. The amount of variation in species composition, and their abundances, explained by an axis is described by its eigenvalue (λ), and the sum of all eigenvalues from all extracted axes is known as total inertia (λ_{total}).The relative comparison between an axis' eigenvalue and the total inertia indicates how much of the variation is explained by such axis.

Dominant species set

To define dominance, we used abundance (# individuals) and frequency (# quadrats where a species occurs) data, but not basal area because large lianas were rather sparse. Dominant species in the community were thus defined by either of the two following criteria: (1) species among the 20 most abundant in the whole area sampled (which corresponded to ~50% of all individuals sampled; see Results), or in the ridge only, or in the valley only; OR (2) species among the 10 most frequent in the whole area sampled, or in the ridge only or in the valley only.

RESULTS

DIVERSITY AND FLORISTICS

In the whole area sampled (thirty non-contiguous 20×20 m quadrats: 1.2 ha), we found 195 species-level taxa (155 fully identified species [34 with “cf.”] and 40 morphospecies; hereafter, for practicality, a species-level taxon will be referred to simply as “species”, unless the distinction between species and morphospecies becomes necessary given the context), 93 genera and 38 families of lianas with “Gerwing/Romero” (G/R) geometric mean diameter ≥1 cm (Appendix 2). From the total number of individuals sampled, 84.5% were assigned an official epithet and 90.3% were identified to genus. In the subset of lianas with G/R diameter ≥2.5 cm, there were 111 species, 71 genera and 31 families. Only four morphospecies were identified to family level only (Appendix 2).

For all quadrats, the average number of liana species (≥1 cm in diameter) in a 20×20 m area was 27. The total number of species, genera and families found in the ridge area (17 quadrats) were relatively similar to those in the valley (13 quadrats), for both diameter cutoffs, ≥1 cm and ≥2.5 cm (Table 2.1). The average number of species in a ridge quadrat vs. that in a valley quadrat did not differ significantly, independent of the diameter cutoff (*t* test: P=0.76 and P=0.85 for the ≥1 cm and ≥2.5 cm diameter cutoffs, respectively; Table 2.1). According to the Mao Tau rarefaction curves—another way to test for a difference in alpha diversity between environments by controlling for sampling effort of area and individuals—species density (number of species in a given area) in the valley was significantly higher than in the ridge for lianas ≥1 cm in diameter (Table 2.1, Figure 2.2), but not for lianas ≥2.5 cm diameter (Table 2.1); in contrast, species richness (number of species in a given number of individuals) of ridge and valley were not significantly different, independent of diameter cutoff (Table 2.1, Figure 2.2). Yet another way to test for a difference in alpha diversity between environments is to use diversity indexes—Fisher's alpha in the present study. According to this diversity index, the valley was more diverse than the ridge for lianas ≥1 cm, but not for lianas ≥2.5 cm (Table 2.1), i.e., we found the same pattern as when using the species density rarefaction curves.

According to the Mao Tau rarefaction curves of the 30 quadrats combined (not shown), the estimated number of liana species and individuals (≥1 cm in diameter) in one hectare—the size commonly used as a standard in many tropical forest inventories—was 183 (95% CI: 169–198) and 1449, respectively. The expected total number of liana species in the study area (i.e. the 50-ha YFDP), according to the Chao2 estimator and the Michaelis-Menten function asymptote (of the Mao Tau curve), based on data from the 30 non-contiguous quadrats, was 280 (95% CI: 240–356) and 242, respectively.

With respect to floristics, Table 2.2 presents data for the most species-rich families and genera only, and for the ≥1 cm and ≥2.5 cm diameter cutoff datasets. For lianas with diameter ≥1 cm, the five most speciose families were, in decreasing order, Sapindaceae, Fabaceae, Malpighiaceae, Bignoniaceae, and Hippocrateaceae, while the families with the greatest number of genera were mostly the same as the most speciose families, although the ranking was different (Table 2.2). The pattern is very similar when considering only lianas ≥2.5 cm, the main difference being that Fabaceae becomes the most diverse family, followed by Sapindaceae (Table 2.2). It is interesting to note that even though Sapindaceae was represented by only three genera, it was still a very speciose family (Table 2.2). Together, the six families just mentioned represented nearly half of the species and generic diversity (of lianas ≥1 cm): 49.2% and 46.2%, respectively. Regarding genera, the five most speciose, in the dataset of lianas ≥1 cm (data for lianas ≥2.5 cm not shown), were *Paullinia*, *Bauhinia*, *Strychnos*, *Mikania* and, *Tournefortia*, representing almost a quarter (23%) of the total number of species (Table 2.2). Note that *Paullinia* was, remarkably, almost three times more diverse than the next most speciose genus (*Bauhinia*); this was the highest relative difference in diversity observed between any two families or genera ranked adjacently.

ABUNDANCE (LIANA DENSITY) AND FREQUENCY

We inventoried 1919 individual lianas with mean geometric G/R diameter ≥1 cm in the thirty non-contiguous 20×20 m quadrats: 1029 lianas in 0.68 ha of ridge habitat (279 of these with diameter ≥2.5 cm: 27.1%) and 890 lianas in 0.52 ha of valley habitat (258 of these with diameter ≥2.5 cm: 29.0%). These data include 180 unidentified (non-collected) lianas: 84 on ridge and 96 in valley. These "Zzz zzz" lianas on average constituted 9.5% of the lianas in a quadrat (range: 0–23%).

Out of the 1919 lianas, 1554 lianas were climbing (attached to a support), 286 were free-standing (treelet-like) lianas (half of the free-standing individuals belonged to four species only: *Cuervea kappleriana*, *Petrea maynensis*, *Callichlamys latifolia* and *Bauhinia guianensis*), and 79 lianas were neither climbing nor free-standing (e.g., alive fallen branches that had rooted and leafed successfully, but were not yet climbing). The 180 unidentified "Zzz zzz" lianas mentioned above included 176 climbing lianas (usually very tall lianas with unreachable leaves) and four lianas that were were neither climbing nor free-standing.

On average, the density of lianas was 64 lianas per 20×20 m quadrat; on ridge, there were on average 61 individuals per quadrat, while in valley there were 68, a non-significant difference (*t*=1.14; *P*=0.26; Figure 2.3A Inset). The maximum density was recorded in a valley quadrat (27,02: 100 individuals), while the minimum density, in a ridge quadrat (12,22: 34 individuals). Regarding the relative abundance (%) of lianas in 5-mm class diameters, we found that the ridge and valley lianas had similar inverse J-shaped distributions (Kolmogorov-Smirnov test, *D*= 0.10; *P*=0.99; Figure 2.3A), with the great majority of lianas having small diameters.

To represent 50% of the total individuals sampled (cumulative distribution), the 20 most abundant species are sufficient (Table 2.3). In contrast, nearly 50% of the species (97 out of 195 species) were represented by 1–3 individuals only, and 25% of the species (49 species) were represented by a single individual only (Appendix 2). The five most abundant species in the whole area (Table 2.3), representing 30% of the individuals sampled, were *Combretum laxum*, *Machaerium cuspidatum*, *Petrea maynensis*, *Cuervea kappleriana*, and *Clitoria pozuzoensis* (Table 2.3). Note the relatively small difference in abundance among the three most abundant species, and the relatively large gap in abundance between these top three-species and the rest. These five species were also the most frequent (# quadrats where the species occurred) in the whole area sampled.

Generally, the most abundant and frequent species on ridge were the same as in valley, but usually those species were not equally dominant in the two habitats (Table 2.3). At the generic level, *Paullinia* was the only dominant genus occurring in every single quadrat (Appendix 2). Within the 20 most abundant species, *Petrea maynensis*, *Cuervea kappleriana*, *Salacia multiflora*, *Adenocalymna impressum*, *Tetrapterys nitida* and *Hylenaea comosa* were at least twice as abundant on ridge as in valley, while *Combretum laxum*, *Machaerium cuspidatum*, *Bauhinia rutilans*, *Fridericia schummaniana*, and *Dicella julianii* were approximately twice as abundant in valley as on ridge (Table 2.3). A similar pattern resulted from an analysis of frequencies, except that the apparent preference of *B. rutilans*, *F. schummaniana*, and *D. julianii* for valley decreased notably, and the preference of *M. cuspidatum* for valley disappeared (Table 2.3).

BASAL AREA AND SIZE DISTRIBUTION

On average, a ridge quadrat had less basal area than a valley quadrat (381.4 vs. 504.0 cm^2; Figure 2.3B Inset), but the difference between these means was not statistically significant (t=1.42, P=0.17; Figure 2.3B Inset). This trend toward higher basal area in valley quadrats is more apparent, although still insignificant, if the two high outlier values are excluded (one from ridge and one from valley) (t=1.9, P=0.07). Further, when we compared the mean number of large lianas (diameter ≥5 cm) per quadrat on ridge to that in valley, a trend towards larger lianas in valley than on ridge was apparent (Mann-Whitney U=68.5, P=0.08).

The stems of the 1919 individuals sampled in the thirty 20×20 m quadrats summed to a total basal area of 13,036.3 cm^2, i.e. there was an average basal area of 434.5 cm^2 per quadrat. Combined ridge quadrats (N=17) summed a basal area of 6484.5 cm^2, while combined valley quadrats (N=13) summed 6551.8 cm^2. The basal area distribution by 5-mm diameter classes is no different between ridge and valley (Kolmogorov-Smirnov test, D= 0.158, P=0.956; Figure 2.3B). Yet, in the 50–55 mm class and in the 70–75 mm class, the valley had at least twice as much basal area as the ridge (related to abundance, compare Figures 3.3A and 3B). In the present study, 129 individuals from 40 liana species had diameters ≥5 cm, and half of these species had large individuals occurring only in valley. The two largest individuals were both *Combretum laxum*: one grew in the valley quadrat 12,07 (diameter=31.5 cm) and the other one grew in the ridge quadrat 22,17 (diameter=18.3 cm). The two species that dominated the species with large individuals (diameter ≥5 cm), and thus contributed significantly to basal area in a quadrat, were also the two most abundant species (see Table 2.3): *Combretum laxum* (25 out of 141 individuals had diameters ≥5 cm) and *Machaerium cuspidatum* (19 out of 135 individuals had diameters ≥5 cm). Also, both species had larger individuals (diameter ≥5 cm) growing in valley than on ridge (15 out of 25 for *C. laxum*, and 12 out of 19 for *M. cuspidatum*). The species *Doliocarpus dentatus*, *Dioclea ucayalina* and *Piptadenia anolidurus* also had a few large lianas of diameter ≥5 cm: four individuals each. In the case of *D. dentatus* and *P. anolidurus*, these four individuals were all growing in valley; but in the case of *D. ucayalina*, they were all growing on ridge.

MULTIVARIATE ANALYSES

According to ANOSIM, species composition, or abundances, differed significantly between ridge and valley for all datasets analyzed (for all lianas ≥1 cm in diameter: R=0.34, $P=1\times10^{-5}$; for most common lianas ≥1 cm: R=0.35, $P<1\times10^{-5}$; for all lianas ≥2.5 cm: R=0.18, P=0.0028; for most common lianas ≥2.5 cm: R=0.18, P=0.0029).

Analyses using NMDS and DCA (of lianas ≥1 cm in diameter), showed ridge and valley quadrats separated relatively well along the first axis. This reflected the topographic (altitudinal) gradient (Figures 4 and 5). For all ordinations, Pearson correlations between the quadrats' first axis scores (*x* coordinates) and the quadrats' mean elevations were all strong and highly significant (for NMDS's in Figures 4A and 4B: $r=-0.74$, $P<0.001$; for DCA in Figure 2.5A: $r=-0.62$, $P<0.001$; for DCA in Figure 2.5B: $r=-0.63$, $P<0.001$). Further, those quadrats that contained valley-ridge transitional zones, and thus a mean elevation somewhat higher than a typical valley quadrat, were mostly located in the center of the NMDS ordinations (quadrats with arrows in Figures 1 and 4).

In the DCA diagrams (Figure 2.5), the inclusion of the rare species in the analyses practically doubled the variation (compare values of λ_{total}) and extended the axis lengths. The percentages of total variation explained by the first two axes, based on the axes' eigenvalues (λ) in relation to the total λ (total inertia), were 13.6% for the all-species DCA (Figure 2.5A) and 16.8% for the most common species DCA (Figure 2.5B). Axes lengths were all <4 "standard deviation" units, and even <3 in the most common species DCA (Figures 5A and 5B). The inclusion of the rare species in the analysis increased the species turnover in the valley more so obviously than in the ridge (i.e., valley quadrats in Figure 2.5A tended to disperse more than the valley quadrats in Figure 2.5B, whereas the ridge quadrats more or less maintained a similar dispersion).

To simplify the description of the relations between species and quadrats in the DCA diagrams, only the species scores (*x-y* coordinates) of the most dominant species (Table 2.3) were plotted in Figure 2.5. In the DCA diagrams, a greater number of dominant species seem to gravitate towards ridge quadrats than towards valley quadrats (Figure 2.5). The diagrams also show that *Combretum laxum* and *Machaerium cuspidatum*, the two most common species, although widespread (had high frequency; Table 2.3), apparently prefer valleys to ridges (i.e, are relatively more abundant in valley habitat) (Figure 2.5, Table 2.3). That *Adenocalymna impressum* and *Moutabea aculeata* were restricted to ridge, and that *Piptadenia anolidurus* and *Mansoa verrucifera* were restricted to valley (Table 2.3) is also clearly reflected in the diagrams (Figure 2.5).

DISCUSSION

ACROSS YASUNÍ COMPARISONS

Diversity, abundance and floristics

The 195 species found in the present study (Appendix 2) represented 39% of the regional (gamma) diversity of Yasuní, estimated at 500 species (Burnham 2002). In addition, throughout the course of our study we opportunistically collected a total of 264 liana species in the YFDP area and nearby forest (246 inside the YFDP only). Out of these 264 species, 200 were assigned an official taxonomic epithet and the rest were morphospecies mostly identified to genus. In the YFDP area, we thus have collected approximately half of the estimated regional (gamma) diversity. According to the Chao2 estimator and the Michaelis-Menten function asymptote of the species-area Mao Tau curve (all 30 quadrats pooled, not shown), the total number of species in the study area, statistically estimated, were 280 (95% CI: 240–356) and 242 species, respectively (but see Mao, Colwell, and Chang 2005 to understand the caveats in this type of analysis). Because these estimated values compare relatively well to the actual values, we conclude that, through our study and its accessory collection efforts, a good compilation of the existing liana species in the YFDP area has been achieved.

With regard to the contribution of lianas to the total diversity and abundance of woody plants in the YFDP (trees and lianas ≥1 cm only; other woody growth forms excluded), we estimate on a per-hectare basis an average contribution of ~22% to diversity (183 liana spp. / [183 liana spp. + 655 tree spp.]) and ~20% to abundance (1449 liana ind. / [1449 liana ind. + 5830 tree ind.]), respectively (values obtained from the rarefaction curves estimates of all 30 quadrats pooled [not shown], and the average tree values per hectare reported by Valencia et al. 2009). Our estimates agree relatively well with the commonplace claim that lianas typically constitute ~20–25% of the woody plant density and species density in many tropical forests (Gentry 1982, Gentry 1991, Schnitzer and Bongers 2002).

Although diversity values from the present study and those of the three other studies about lianas in Yasuní (Nabe-Nielsen 2001, Romero-Saltos, Valencia, and Macía 2001, Burnham 2002, Burnham 2004) are not directly comparable because of methodological differences (Appendix 3), we can use Mao Tau rarefaction curves (species-area and species-individuals; including those shown in Figure 2.2) to approximate the comparisons (Table 2.4). The number of species in a given area (species density) and the number of species in a given number of individuals (species richness) obtained in the present study agree relatively well with the values reported in other studies in Yasuní, in particular when lianas ≥2.5 cm are compared (Table 2.4). Across Ecuadorian Amazonia, to find 20 to 30 species of lianas of diameter ≥2.5 cm in 0.1 ha of mature terra firme forest is probably commonplace. For instance, 21 species of lianas ≥2.5 cm in diameter were found in an Amazonian pre-montane rainforest (850 m altitude) some 200 km west of the YFDP (Romero-Saltos 1999). Because of the general agreement between the diversity results from our study and other studies that use liana data from Yasuní (Nabe-Nielsen 2001, Burnham 2004, Duque et al. 2004a, Quisbert and Macía 2005, and Macía and Svenning 2005), the regional comparisons that appear in those publications, although dated, are still valid.

To broadly compare our liana density results to other studies from Yasuní that used different sampling areas, we developed individuals-area curves for ≥1 cm and ≥2.5 cm diameter cutoffs (curves not shown) and compared the density of liana individuals among different studies using these curves (Table 2.4). The YFDP liana density estimates were similar to the values reported in other liana studies from Yasuní terra firme forests, although the YFDP values for 0.1 ha were somewhat higher than the other studies, probably reflecting that our study was the only one that sampled free-standing lianas (Table 2.4). In a regional comparison of liana density between Neotropics and Paleotropics (DeWalt et al. 2010), we reported for Yasuní the datum of 377 lianas/ha (diameter ≥2.5 cm) based on data from a 20×500 m transect within the YFDP (unpublished data). However, according to our individuals-area curve, we now estimate 448 lianas/ha (diameter ≥2.5 cm) in the YFDP, a value that in fact is very close to the average value of 446 lianas/ha (diameter ≥2.5 cm) reported for Yasuní (DeWalt et al. 2010).

Two studies present floristic information comparable to the present study. The first study (Nabe-Nielsen 2001) sampled only 0.4 ha near YFDP, while the second study (Romero-Saltos, Valencia, and Macía 2001) spread their terra firme 0.1 ha samples across an area of near 140 km^2. For the comparisons, we only applied a diameter cutoff correction to our data (no other correction such as the standardization of area sampled or number of individuals sampled was applied). Thus, the floristic comparisons below should be considered preliminary. At the family level, it is striking that the seven most speciose families from the present study (Table 2.2) were also the seven most speciose in both studies (Nabe-Nielsen 2001, Romero-Saltos, Valencia, and Macía 2001). The ranking of families is of course not exactly the same, but consistencies exist. In the mature terra firme forest of Yasuní, Sapindaceae and Fabaceae are certainly always the two most liana species-rich families when lianas ≥1 cm of diameter are sampled (in particular Sapindaceae, given it contains *Paullinia*, the most species-rich liana genus; Table 2.2). For lianas with diameter ≥2.5 cm, Fabaceae is usually the most species-rich family in terra firme forest, followed by Bignoniaceae (as in Nabe-Nielsen 2001 and Romero-Saltos, Valencia, and Macía 2001) or by Sapindaceae and then Bignoniaceae (as in our study; Table 2.2). If a lower diameter cutoff is used, Asteraceae, because of its relatively diverse genus *Mikania*, will usually appear among the ten most species-rich families (Nabe-Nielsen 2001; and Table 2.2). At the genus level, the two most species-rich genera found in the present study, *Paullinia* (21 spp.) and *Bauhinia* (8 spp.), were also the most species-rich in another study (Romero-Saltos, Valencia, and Macía 2001), thus assuring their place as the dominant liana genera in Yasuní.

The general consistency among Yasuní liana studies on diversity, abundance, and floristic data (at least the floristics of the most species-rich families and genera) supports the common hypothesis that the communities of lianas and trees in Yasuní's terra firme forest, and in fact in the whole western Amazonia, are relatively homogenous and predictable (Burnham 2002, Burnham 2004, Pitman et al. 2001, Macía and Svenning 2005). This relative terra firme forest homogeneity of Yasuní is also reflected, to a certain extent, by liana species composition and species abundances, as we discuss below (but see ridge vs. valley discussion).

Species composition and species abundances

Species composition, and their relative abundances, in the 1.2 ha of terra firme forest sampled in the present study was similar to what was observed in two other studies in Yasuní that sampled terra firme forest (Burnham 2002 and Romero-Saltos, Valencia, and Macía 2001), particularly with regard to the most dominant species. The two studies that are the most comparable because of their identical diameter cutoff sampling protocol (≥1 cm) (Burnham 2002 and the present study) had five shared species among the top ten most abundant. The five shared liana species are: *Bauhinia guianensis*, *Clitoria pozuzoensis*, *Combretum laxum*, *Machaerium cuspidatum*, and *Petrea maynensis*. Most of the rest of the species in the two top-ten datasets do still appear variously ranked among the dominant species sets from these studies (31 species in the present study [Table 2.3], and 35 species in Burnham 2002). The exceptions are *Bauhinia rutilans* and *Tontelea fuliginea* (from our study), and *Maripa peruviana* and *Clitoria javitensis* (from Burnham 2002). *T. fuliginea* and *C. javitensis* perhaps are identification issues (*T. fuliginea* was just recently described by Lombardi 2006, i.e. after Burnham's publications, while Burnham's *C. javitensis* might be what we identified as *Dioclea ucayalina*). These exceptions argue in favor of a flexible concept of "oligarchy" at the species level that accommodates local realities, as opposed to the existence of a strict set of "oligarch" species, whose members are expected to be always present among the top ten (Burnham 2002).

All things considered, the most important similarity among Yasuní liana studies is the uttermost dominance of *Machaerium cuspidatum*, usually the most abundant species but which ranked second in the present study, after *Combretum laxum* (Table 2.3). The great importance of *C. laxum* in our study is a result of its great abundance and frequency in the valley (Table 2.3). It is also a liana species that can grow very large in diameter (in fact, the two widest lianas in the present study [diameters=18.3 and 31.5 cm] belonged to this species) and certainly in length (e.g., during a forest clear-cut in Yasuní, we observed an individual with a basal diameter of 7.5 cm and a length of 255 m, branches included). Further, *C. laxum* has always been among the top 10 most abundant species in any of the Yasuní studies, whatever the habitat sampled (terra firme, floodplain, or swamp) or whatever the diameter cutoff used (Burnham 2002, Romero-Saltos, Valencia, and Macía 2001). Future research efforts to explain why *M. cuspidatum* and *C. laxum* have become so dominant in the forest of Yasuní are thus justified, and at least for *M. cuspidatum* these are already underway (Nabe-Nielsen 2002, Nabe-Nielsen 2004, Nabe-Nielsen and Hall 2002). Other candidate species for future population and ecophysiological studies could be those dominant species shared between different studies (e.g., with Burnham 2002; see above).

RIDGE VS. VALLEY: A CONUNDRUM WITHIN YFDP'S TERRA FIRME FOREST

Differences (or similarities) in diversity, abundance and basal area

In the YFDP, we observed that the diversity of liana communities changed along the ridge to valley altitudinal (topographic) gradient. When all sampled lianas (diameter ≥1 cm) were included in the analyses, the change in diversity was reflected in species density (Table 2.1, Figure 2.3A) and in Fisher's alpha estimates (Table 2.1), but not in species richness (Table 2.1, Figure 2.2B) nor in density of individuals (Figure 2.3A Inset). When only relatively large, established, lianas were considered (diameter ≥2.5 cm), the difference in diversity between ridge and valley disappeared (Table 2.1). Thus, the 84 species of thin lianas that did not have individuals with diameter ≥2.5 cm were responsible for the difference in diversity between ridge and valley. These species were not only thin but also were, for the most part, rare species (average abundance=3 individuals; mode=1 individual; median=2 individuals; 69 species [82%] had 1–4 individuals) that occurred more or less evenly in ridge habitat and in valley habitat (22 species were exclusive to ridge, 26 were exclusive to valley, while 36 were shared). Small and rare plants are clearly important contributors for the high species diversity in Yasuní.

Species richness [spp./ind.] and species density [spp./area] are mathematical ratios related through the density of individuals [ind./area] by the following equation: [spp./ind] = [spp./area] / [ind./area] (Gotelli and Colwell 2010). Thus, by deduction, the conclusion of no difference in species richness between ridge and valley, $[\text{spp./ind.}]_{\text{ridge}} = [\text{spp./ind.}]_{\text{valley}}$, is a logical contradiction because species density was not equal between habitats but lower in the ridge than in the valley, $[\text{spp./area}]_{\text{ridge}} < [\text{spp./area}]_{\text{valley}}$, and thus species richness should also have been lower in the ridge, $[\text{spp./ind.}]_{\text{ridge}} < [\text{spp./ind.}]_{\text{valley}}$. This paradox is true whether or not the density of individuals [ind./area] is different between the two habitats. Are we thus facing a Type II statistical error when we conclude that there is no difference in species richness between ridge and valley? (i.e., failure to detect a significant difference, when in reality there is one). We think so, considering that: (1) the CI of the species richness of ridge and valley (Table 2.1, Figure 2.2B) barely overlap and probably would cease to overlap if the number of comparable individuals (=794 ind.) were to increase a little more; (2) already, the number of species in valley at 794 individuals is notably greater than the number of species on ridge (151 spp. vs. 135 spp.; Figure 2.2B), as logically expected from the analysis of ratios above;

and (3) the minimum sample size recommendation for our quadrat-based rarefaction analyses (at least 20 quadrats per habitat; Gotelli and Colwell 2010) was not possible to apply in our study. Considering these observations, we hypothesis that additional sampling (here we only sampled 1.2 ha total) will detect consistent differences in diversity between ridge and valley, independent of the diversity measurement used. The eastern area of the YFDP plot, where lianas have not been yet sampled, offers an opportunity to test this *a priori* hypothesis.

Diversity and abundance patterns of lianas in our study agree and disagree at the same time with those observed for trees (Valencia et al. 2004c) in the YFDP. A direct comparison is not possible because, for trees, 25 continuous hectares (500×500 m) were sampled, Mao Tau curves were not used, and the ridge's topographic subdivisions were not lumped into a single ridge habitat for analyses. In any case, trees in the YFDP had, similar to what was observed in lianas, higher diversity in valley than on ridge according to Fisher's alpha, although this difference was not significant in trees (Valencia et al. 2004c) but was significant in lianas (Table 2.1). On average, there were fewer tree species per quadrat and fewer tree individuals per hectare in valley than on ridge, but whether or not these differences were significant was not reported (Valencia et al. 2004c). For lianas, on the other hand, there was not a significant difference between ridge an valley in both the mean number of liana species per quadrat (Table 2.1) and in the mean number of liana individuals per quadrat (Figure 2.3A). In Yasuní, at the landscape scale (forest type), both tree and liana diversity and abundance are, on average, highest in terra firme forest, intermediate in floodplain forest, and lowest in swamp forest—in other words, there is concordance between tree and liana patterns (Romero-Saltos, Valencia, and Macía 2001). However, at the other extreme of the spatial scale, i.e. when trees and lianas are studied at the topographic scale within the same terra firme forest, the comparison of diversity and abundance patterns of trees vs. those of lianas can be more of a conundrum.

In any case, the diversity and abundance patterns of lianas and trees in ridge and valley habitats in the YFDP may be informative for understanding tree-liana interactions at the community scale. Here we propose a few simple testable hypotheses on this topic:

(1) Given that trees occur less densely in valley than on ridge while liana abundance does not seem to be limited by topography, the average number of lianas per host tree should be higher in valley.

(2) The higher abundance of lianas per host tree in valley should result in higher number of liana species per host tree.

(3) The putative overload of lianas per host tree in the valley might cause decreased fitness of trees there relative to the fitness of conspecific/congeneric trees in the ridge (e.g., reduced growth, reduced fecundity, higher mortality; see e.g., Stevens 1987, Peña-Claros et al. 2008, Ingwell et al. 2010)—this potentially strong negative effect of lianas on host trees in the valley may partly explain why trees there tend to be smaller, and/or have less biomass, than trees in the ridge (Valencia et al. 2004c, Valencia et al. 2009). This conjecture can only be tested experimentally and is probably associated whith other processes such as treefall rates (Ferry et al. 2010). To elaborate more on the evolutionary or ecological processes responsible for the difference in diversity between ridge and valley in the YFDP is beyond the scope of this paper, but useful approaches to this topic,

using data from Yasuní, can be found in some doctoral dissertations (Pitman 2000, Queenborough 2005, Metz 2007and Kraft 2008) and their resulting publications (e.g., Pitman et al. 2001, Queenborough et al. 2007b, Kraft, Valencia, and Ackerly 2008, Kraft and Ackerly 2010).

The abundance and basal area of lianas in different diameter classes did not differ significantly between ridge and valley (Figure 2.3), suggesting that in both habitats, lianas probably face similar mechanisms that shape their size structure. For instance, we can anticipate that community-wide recruitment, growth, and mortality rates are probably very similar in both habitats, producing the typical inverted J-shaped abundance distribution commonly seen in tropical forests. An interesting exception to the broad similarity in the physiognomy (size structure) of ridge and valley liana communities was the slightly higher abundance of large lianas (diameter ≥5 cm) in the valley (Figure 2.3A), and the concomitant trend of higher average per-quadrat basal area there (Figure 2.3B Inset). This trend is similar to what was observed in Borneo where large lianas tended to occur in the alluvial forest (DeWalt et al. 2006). In the present study, most of the large individuals in valley belong to the two most common species, *Combretum laxum* and *Machaerium cuspidatum*, and to the species *Piptadenia anolidurus* and *Doliocarpus dentatus*. These species probably have physiological traits that allow them to better exploit the valley environment, so they can grow faster and/or grow older (larger) there (i.e., under higher soil moisture, low soil O_2 concentration, distinct nutrient availability, lower tree density, among other conditions; e.g., Tange, Yagi, and Sasaki 1998, Silver, Lugo, and Keller 1999, Tuomisto et al. 2003, Kubota, Murata, and Kikuzawa 2004, Valencia et al. 2004c, Jirka et al. 2007).

Differences in composition of species or their specific abundances

Whereas the valley had higher species density, higher species richness, and higher Fisher's alpha estimates than the ridge (although the difference was only significant for species density and Fisher's alpha), species composition, or their abundances, differed significantly between ridge and valley (ANOSIM). This was true independently of the diameter cutoff criteria and whether or not rare species were included (ANOSIM). The distinction between ridge and valley is so clear that it persists even if the analysis is conducted with only the 20 most common species among the lianas ≥2.5 cm in diameter (ANOSIM's R=0.18, P=0.0029; see Results). This difference in liana species composition (or in their abundances) between the two habitats was also observed for trees, in particular between upper-ridge and valley (Valencia et al. 2004c). Thus, despite the different growth mechanisms of its constituent plants, YFDP's tree and liana communities seem to be responding similarly to environmental mosaics. We can further expect that the ecological processes shaping tree and liana communities are probably similar, in particular at the seedling/sapling stage when some believe the fate of many forest plants is decided (see Metz 2007).

In all NMDS and DCA ordinations, ridge and valley quadrats segregated relatively well along the first axes, all of which were highly correlated (r>0.62; P<0.001) with the altitudinal gradient (Figures 4 and 5; see Results). A meaning for the second axes is unclear. Although the NMDS's stress indexes of ~0.26 are relatively high (Figure 2.4; certainly, with stress index >0.35, the placement of the sites would be effectively random; Clarke 1993), and although the DCA's first axis explain no more than ~11% of the total variation in the system (Figure 2.5), it is important to emphasize that the topographic (altitudinal) gradient (or any other variables correlated with it) represented by the first axis in all these ordinations, is indeed the main underlying structure or pattern in the data. In other words, although other factors relatively independent of topography may affect liana species compositions (or their abundances) in the YFDP (e.g., enemy-mediated density dependence), taken individually, no factor has as much influence as topography—even when the effect of topography itself is relatively weak or minor (cf. Valencia et al. 2004c, Kraft and Ackerly 2010). Trait- and phylogenetic-based analyses designed to identify the main processes driving tree community assembly in the YFDP have found a clear, although weak, signal of habitat (environmental) filtering up to the 100×100 m spatial scale, in part related to the topographically-defined habitats of ridge and valley (Kraft, Valencia, and Ackerly 2008, Kraft and Ackerly 2010). However, such analyses also have found, somewhat paradoxically, evidence for differentiation of functional strategies among species (also known as “niche partitioning”, but not to be confused with “topographic niche-partitioning” which is more related to habitat/environmental filtering) and enemy-mediated density dependence up to the 20×20 m (quadrat) scale (Kraft, Valencia, and Ackerly 2008, Kraft and Ackerly 2010). What the underlying community assembly processes are for lianas, and more interestingly how they interplay with the tree processes, remains to be explored.

Undoubtedly, the ridge vs. valley difference in community structure of lianas was mainly caused by differential abundances of the most common species, the majority of which occurred in both habitats (Table 2.3). Rare species also did contribute to differentiate the habitats, but more importantly they contributed to increase the variation (species turnover) in the system, in particular within valley, the moister habitat (valley quadrats in Figure 2.5A are more spread out than those in Figure 2.5B, whereas ridge quadrats are more or less equally spread in both figures; compare also λ_{total} values). Similarly, at the landscape scale, the variation in tree and liana community structure (plants with diameter ≥2.5 cm) was much higher in those forests with relatively high soil moisture—swamps and floodplains—than in the well-drained ridge (terra firme) forest (Romero-Saltos, Valencia, and Macía 2001). Therefore, the general claim that the terra firme forest of Yasuní is relatively homogenous (see "Across Yasuní comparisons" section above) certainly applies best to ridge areas. Valley areas, on the other hand, seem more physically and biologically heterogeneous, apparently having microhabitats in which environmental conditions considered stressful to most plant species (e.g., periodic soil saturation) make only uniquely adapted species successful. To illustrate this point, we analyzed the distribution of singleton species (total abundance=1) in ridge and valley quadrats (49 singleton species total) and found that the three quadrats with highest number of singletons were all valley quadrats (27,22: five species; 17,07 and 17,22: four species). When repeating this same analysis using those species with frequency (# quadrats where a species occurs)=1, the result was similar: the two quadrats with the highest number of species were valley quadrats 27,22 (8 species) and 17,22 (7 species), whereas the rest of quadrats had four or less species only.

Statistical analyses of topographic habitat preference for the most common species in our dataset are part of an accompanying study, but in the meantime we emphasize here the obvious patterns (see Results). Among the 31 most dominant species, there were only five species solely occurring in either ridge or valley, from which only one occurred within the set of 20 most abundant species: *Adenocalymna impressum*, a species that in the present study was restricted to ridge habitat (Table 2.3). Other studies in Yasuní

(Romero-Saltos, Valencia, and Macía 2001, Burnham 2002) also observed that *A. impressum* was among the dominant species in terra firme (although in Burnham 2002, *A. impressum* also occured in floodplain but was not among the most dominant in that habitat). Another obvious pattern was that observed with the two most common species: *Combretum laxum* and *Machaerium cuspidatum*. These species, although widespread, were relatively more abundant in valley, the moister habitat (Table 2.3, Figure 2.5). In another study (Burnham 2002), proportionally more lianas of these two species were also observed in the moister habitat, floodplain, than in terra firme. The next two most common species, *Petrea maynensis* and *Cuervea kappleriana*, in contrast, occurred much more abundantly and frequently in ridge habitat (Table 2.3, Figure 2.5). In Burnham's study, *P. maynensis* also preferred terra firme but *C. kappleriana* did not. We suspect, however, that our *C. kappleriana* is Burnham's *Hylenaea comosa*, as the two species are vegetatively very similar. In Burnham's, *H. comosa* was the tenth most abundant species in terra firme, based on data of climbing lianas alone, whereas in our study *C. kappleriana* was the fourth most abundant species (Table 2.3), but based on data of climbing and free-standing lianas together. *C. kappleriana* in our study was the most common species among the free-standing lianas (18.9% of the 286 free-standing lianas sampled overall), and in fact a little more than half of the individuals of this species were free-standing.

CONCLUSION

Based on a sample of 17 ridge quadrats (20×20 m each) and a sample of 13 valley quadrats, containing in total 1919 lianas with diameter ≥1 cm and 195 species, we have comprehensively described the liana community in the 50-ha Yasuní Forest Dynamics

Plot (YFDP). We also tested the general hypothesis that the diversity, abundance and species composition of lianas respond to the characteristic ridge-valley topographic gradient of the plot, similar to what has been observed with trees (Valencia et al. 2004c). We have found evidence supporting this hypothesis with respect to diversity and species composition, but not with respect to abundance. We conclude that topographic changes in the landscape, probably correlated with changing biogeochemical characteristics, can influence liana communities even at relatively small spatial scales.

TABLES

Table 2.1. Diversity of lianas in ridge (*N*=17 20×20 m quadrats) and valley (*N*=13 quadrats) habitats of the YFDP. Diversity was measured using species density (the number of species in a given area), species richness (the number of species in a given number of individuals) and a Fisher's alpha diversity index estimator. To compare species density and species richness between habitats, we used Mao Tau rarefaction curves and their associated 84% confidence intervals (CI; in parentheses). To compare Fisher's alpha between habitats, we also used their associated 84% CI estimated at the same number of quadrats (i.e., the number of quadrats in valley). As complementary information, the average number of species per 20×20 m quadrat (± 1 standard deviation, SD), and the total number of taxa sampled on ridge and in valley are shown.

	DIAMETER ≥ 1.0 cm			**DIAMETER ≥ 2.5 cm**		
	RIDGE		**VALLEY**	**RIDGE**		**VALLEY**
SPECIES DENSITY (rarefacted)[a]	130 (122–139)	*	151 (141–161)	62 (55–68)	**NS**	70 (61–69)
			84% CI at 13 quadrats (0.52 ha)			
SPECIES RICHNESS (rarefacted)[a]	135 (126-144)	**NS**	151 (141–161)	68 (61–75)	**NS**	70 (61–79)
	84% CI at 794 ind.[b]			84% CI at 223 ind.[b]		
FISHER'S ALPHA ESTIMATOR	46.4 (42.4–50.4)	*	55.3 (50.8–59.8)	32.5 (27.1–37.9)	**NS**	35.1 (29.9–40.3)
			84% CI at 13 quadrats (0.52 ha)			
# SPECIES PER QUADRAT						
mean ± 1 SD:	26.9 ± 6.5	**NS**	27.7 ± 7.7	9.8 ± 3.5	**NS**	10.0 ± 3.0
range:	15–40		12–41	4–19		5–15
***N* (# quadrats):**	*N* = 17		*N* = 13	*N* = 17		*N* = 13
	In 0.68 ha:		**In 0.52 ha:**	**In 0.68 ha:**		**In 0.52 ha:**
TOTAL # SPECIES	145		151	71		70
	(# shared species: 101)			(# shared species: 30)		
TOTAL # GENERA	83		77	54		50
TOTAL # FAMILIES	35		35	26		23

[a] Species density and species richness estimated via Mao Tau rarefaction curves and their 84% CI (rounded to whole numbers). Rarefaction curves for lianas with diameter ≥1 cm are shown in Figure 2.2.

[b] The abundances used as reference for this comparison are those from the valley, after excluding "Zzz zzz" lianas.

* Significant difference between ridge and valley ($P \leq 0.05$).

NS Non-significant difference between ridge and valley.

Table 2.2. Most diverse families (# species ≥3) and genera of lianas in ridge (*N*=17 20×20 m quadrats) and valley (*N*=13 quadrats) habitats of the YFDP. The number of species and genera in each family are shown for two diameter cutoffs: ≥1 cm and [≥2.5 cm]. List is primarily ordered from the most to the least species-rich family, and then from the most to least genus-rich family. The fourteen families represented by one or two species are not shown.

FAMILY	**# SPECIES IN FAMILY**	**# GENERA IN FAMILY**[a]	**GENUS NAMES (# species in parentheses, morphospecies included)**
SAPINDACEAE	23 [12]	3 [3]	*Paullinia* (21), *Serjania* (1), *Thinouia* (1)
FABACEAE	19[b] [16]	7 [7]	*Bauhinia* (8), *Machaerium* (3), *Clitoria* (2), *Piptadenia* (2), *Acacia* (1), *Dalbergia* (1), *Dioclea* (1)
MALPIGHIACEAE	18[b] [10]	10 [8]	*Diplopterys* (4), *Hiraea* (3), *Mascagnia* (2), *Tetrapterys* (2), *Alicia* (1), *Dicella* (1), *Ectopopterys* (1 *Heteropterys* (1), *Jubelina* (1), *Stigmaphyllon* (1)
BIGNONIACEAE	17[b] [11]	9 [7]	*Bignonia* (3), *Fridericia* (3), *Amphilophium* (2), *Stizophyllum* (2), *Tanaecium* (2), *Adenocalymna* (1), *Callichlamys* (1), *Mansoa* (1), *Martinella* (1)
HIPPOCRATEACEAE	10 [8]	7 [7]	*Salacia* (3), *Tontelea* (2), *Anthodon* (1), *Cheiloclinium* (1 *Cuervea* (1), *Hylenaea* (1), *Peritassa* (1)
MENISPERMACEAE	9 [4]	7 [4]	*Abuta* (2), *Telitoxicum* (2), *Anomospermum* (1), *Curarea* (1), *Disciphania* (1), *Odontocarya* (1), *Sciadotenia* (1)
DILLENIACEAE	7 [5]	5 [4]	*Doliocarpus* (2), *Tetracera* (2), *Davilla* (1), *Neodillenia* (1), *Pinzona* (1)
CUCURBITACEAE	7 [1]	4 [1]	*Gurania* (3), *Cayaponia* (2), *Psiguria* (1), *Siolmatra* (1)
ASTERACEAE	7 [1]	3 [1]	*Mikania* (5), *Ichthyothere* (1), *Piptocarpha* (1)
CONVOLVULACEAE	6 [3]	2 [2]	*Dicranostyles* (3), *Maripa* (3)
LOGANIACEAE	6 [4]	1 [1]	*Strychnos* (6)
CONNARACEAE	5 [4]	3 [2]	*Connarus* (2), *Rourea* (2), *Pseudoconnarus* (1)
APOCYNACEAE	5 [4]	2 [2]	*Odontadenia* (3), *Forsteronia* (2)
VERBENACEAE	5 [2]	2 [2]	*Aegiphila* (4), *Petrea* (1)
BORAGINACEAE	5 [2]	1 [1]	*Tournefortia* (5)
ARISTOLOCHIACEAE	4 [2]	1 [1]	*Aristolochia* (4)
DICHAPETALACEAE	4 [2]	1 [1]	*Dichapetalum* (4)
PASSIFLORACEAE	3 [3]	2 [2]	*Passiflora* (2), *Dilkea* (1)
RUBIACEAE	3 [3]	2 [2]	*Chomelia* (2), *Randia* (1)
ACANTHACEAE	3 [1]	1 [1]	*Mendoncia* (3)
LILIACEAE	3 [0]	1 [0]	*Smilax* (3)
MARCGRAVIACEAE	3[b] [0]	1 [0]	*Marcgravia* (2)
POLYGONACEAE	3 [1]	1 [1]	*Coccoloba* (3)
RHAMNACEAE	3 [2]	1 [1]	*Gouania* (3)

[a] Morphospecies with no genus identification excluded.

[b] Includes *a single* morphospecies with no genus identification.

Table 2.3. Relative abundance (# individuals / total # individuals in a habitat), mean absolute abundance per quadrat (mean # individuals ± 1 standard deviation, with range in parentheses), and relative frequency (# quadrats / total # quadrats in a habitat) of the 31 most dominant liana species in ridge (*N*=17 20×20 m quadrats) and valley (*N*=13 quadrats) habitats of the YFDP. Also shown is total absolute abundance, overall mean absolute abundance per quadrat, and total absolute frequency. Dominant species were defined by either of the two following criteria: (1) species among the 20 most abundant in the whole sample (numbered 1 to 20), or only in ridge habitat or only in valley habitat; OR (2) species among the 10 most frequent in the whole sample, or only in ridge habitat or only in valley habitat. Species are ordered by decreasing total abundance, and then by decreasing total frequency. The full species list (195 spp.) is in Appendix 2.

	RIDGE			VALLEY					
SPECIES[a,b]	**REL. ABUND.(%)**	**ABUNDANCE PER QUADRAT**	**REL. FREQ.(%)**	**REL. ABUND.(%)**	**ABUNDANCE PER QUADRAT**	**REL. FREQ. (%)**	**TOTAL ABUND.**	**ABUNDANCE PER QUADRAT**	**TOTAL FREQ.**
*1 **COM**bretum **lax**um*	4.5[C]	2.7±3.5 (0–10)	47.1[F]	10.7[C]	7.3±4.2 (0–13)	92.3[F]	141	4.7±4.4 (0–13)	20
*2 **MAC**haerium **cus**pidatum*	4.9[C]	2.9±2.3 (0–7)	94.1[F]	9.6[C]	6.5±4.8 (0–16)	92.3[F]	135	4.5±4.0 (0–16)	28
*3 **PET**rea **may**nensis*	9.4[C]	5.7±4.3 (0–15)	88.2[F]	3.4[C]	2.3±5.3 (0–18)	30.8	127	4.2±5.0 (0–18)	19
*4 **CUE**rvea **kap**pleriana*	7.3[C]	4.4±2.6 (0–10)	94.1[F]	2.4[C]	1.6±2.5 (0–8)	46.2[F]	96	3.2±2.8 (0–10)	22
*5 **CLI**toria **poz**uzoensis*	5.2[C]	3.1±2.0 (0–7)	88.2[F]	3.3[C]	2.2±1.8 (0–6)	84.6[F]	82	2.7±1.9 (0–7)	26
*6 **CAL**lichlamys **lat**ifolia*	2.3[C]	1.4±2.9 (0–10)	29.4	3.3[C]	2.2±2.6 (0–9)	61.5[F]	53	1.8±2.7 (0–10)	13
*7 **BAU**hinia **rut**ilans*	1.6[C]	0.9±1.5 (0–5)	41.2	4.0[C]	2.8±4.6 (0–17)	69.2[F]	52	1.7±3.3 (0–17)	16
*8 **BAU**hinia **gui**anensis*	2.8[C]	1.7±2.5 (0–8)	58.8[F]	1.5[C]	1.0±1.5 (0–5)	46.2[F]	42	1.4±2.1 (0–8)	16
*9 **PAU**llinia **bra**cteosa*	1.7[C]	1.0±1.3 (0–5)	52.9[F]	1.3[C]	0.9±1.5 (0–5)	46.2[F]	29	1.0±1.4 (0–5)	15
*10 **TON**telea **ful**iginea*	1.7[C]	1.0±1.6 (0–6)	52.9[F]	1.1[C]	0.8±1.6 (0–5)	23.1	27	0.9±1.6 (0–6)	12
*11 **SAL**acia **mul**tiflora*	1.9[C]	1.2±1.4 (0–5)	58.8[F]	0.7	0.5±0.7 (0–2)	38.5	26	0.9±1.2 (0–5)	15
*12 **ADE**nocalymna **imp**ressum*	2.3[C]	1.4±3.5 (0–14)	29.4	0	0	0	24	0.8±2.7 (0–14)	5
*13 **LER**etia **cor**data*	1.1[C]	0.6±0.9 (0–2)	41.2	1.1[C]	0.8±1.0 (0–3)	46.2[F]	21	0.7±0.9 (0–3)	13
*14 **TET**rapterys **nit**ida*	1.7[C]	1.0±1.8 (0–5)	29.4	0.1	0.1±0.3 (0–1)	7.7	18	0.6±1.4 (0–5)	6
*15 **HYL**enaea **com**osa*	1.5[C]	0.9±1.1 (0–4)	58.8[F]	0.2	0.2±0.4 (0–1)	15.4	17	0.6±0.9 (0–4)	12
*16 **PER**itassa **pru**inosa*	1.3[C]	0.8±1.2 (0–4)	41.2	0.4	0.3±0.5 (0–1)	30.8	17	0.6±1.0 (0–4)	11
*17 **PAU**llinia **mic**roneura*	1.3[C]	0.8±1.3 (0–4)	35.3	0.4	0.3±0.6 (0–2)	23.1	17	0.6±1.1 (0–4)	9
*18 **FRI**dericia **sch**ummaniana*	0.6	0.4±0.7 (0–2)	23.5	1.2[C]	0.8±1.2 (0–3)	38.5	17	0.6±1.0 (0–3)	9
*19 **BIG**nonia **aeq**uinoctialis*	1.0	0.6±1.9 (0–8)	17.6	0.8	0.5±1.5 (0–5)	15.4	17	0.6±1.7 (0–8)	5
*20 **DIC**ella **jul**ianii*	0.6	0.4±0.7 (0–2)	23.5	1.1[C]	0.8±1.5 (0–5)	30.8	16	0.5±1.1 (0–5)	8
***CHE**iloclinium **cog**natum*	1.0	0.6±0.8 (0–3)	47.1[F]	0.6	0.4±1.0 (0–3)	15.4	15	0.5±0.9 (0–3)	10
***DIC**hapetalum **spr**uceanum*	0.7	0.4±1.1 (0–4)	17.6	0.9[C]	0.6±1.0 (0–3)	38.5	15	0.5±1.0 (0–4)	8
***DIO**clea **uca**yalina*	1.2[C]	0.7±0.9 (0–3)	47.1[F]	0.2	0.2±0.4 (0–1)	15.4	14	0.5±0.8 (0–3)	10
***FOR**steronia **aff**inis*	1.3[C]	0.8±1.2 (0–4)	41.2	0.1	0.1±0.3 (0–1)	7.7	14	0.5±1.0 (0–4)	8
***PAU**llinia **ing**ifolia*	0.4	0.2±0.4 (0–1)	23.5	1.0[C]	0.7±1.2 (0–4)	38.5	13	0.4±0.9 (0–4)	9
***DOL**iocarpus **den**tatus*	0.2	0.1±0.3 (0–1)	11.8	1.1[C]	0.8±0.9 (0–3)	53.8[F]	12	0.4±0.7 (0–3)	9
***PAU**llinia **das**ystachya*	0.3	0.2±0.4 (0–1)	17.6	1.0[C]	0.7±1.2 (0–4)	38.5	12	0.4±0.9 (0–4)	8
***MOU**tabea **acu**leata*	1.1[C]	0.6±1.1 (0–3)	35.3	0	0	0	11	0.4±0.9 (0–3)	6
***MAN**soa **ver**rucifera*	0	0	0	1.2[C]	0.8±1.7 (0–6)	38.5	11	0.4±1.2 (0–6)	5
***PIP**tadenia **ano**lidurus*	0	0	0	1.2[C]	0.8±1.9 (0–6)	23.1	11	0.4±1.3 (0–6)	3
***CHO**melia **est**rellana*	0	0	0	1.1[C]	0.8±2.8 (0–10)	7.7	10	0.3±1.8 (0–10)	1

[a] Six-letter acronyms of species in **bold**.

[b] Species listed after the 20th. most abundant species (***DICjul***) are not necessarily the subsequent species in terms of total abundance.

[C] Species is among the top 20 most common in that habitat.

[F] Species is among the top 10 most frequent in that habitat (note that several species may have the same frequency).

Table 2.4. Liana diversity (number of species, #spp.) and abundance (number of individuals, # ind.) data from other studies in Yasuní terra firme forest selected for comparison to this study's data (from Appendix 3). For diversity comparisons, we used species density (species-area) and species richness (species-individuals) Mao Tau rarefaction curves created for the ≥1.0 cm and ≥2.5 cm diameter cutoffs (including, but not limited to, those curves shown in Figure 2.2). For abundance comparisons, we used individuals-area "curves" (straight lines) obtained by quadrats randomization (see Methods). The values being compared are indicated with the same font (whether in **black bold** or **red bold**).

DATA FROM OTHER STUDIES (see Appendix 3)						**DATA FROM THIS STUDY**		
STUDY	**HABITAT**	**SAMPLED AREA (ha)**	**DIAMETER CUTOFF (cm)**	**# spp.**	**# ind.**	**species density[a] (# spp.)**	**species richness[b] (# spp.)**	**individuals density[a] (# ind.)**
Nabe-Nielsen (2001)	ridge	0.1	≥1.0	**44** (mean, *N*=4)	**94** (mean, *N*=4)	**53**	**40**	**153**
Nabe-Nielsen (2001)	ridge	0.1	≥2.5	**21** (mean, *N*=4)	**33** (mean, *N*=4)	**21**	**20**	**41**
Romero-Saltos, Macía, and Valencia (2001)	ridge	0.1	≥2.5	**20** (mean, *N*=10)	**37** (mean, *N*=10)	**21**	**21**	**41**
Burnham (2002)	ridge & valley	0.2	≥1.0	**99** (mean, *N*=6)	**342** (mean, *N*=6)	**87**	**96**	**324**
Burnham (2004)	ridge & valley	1.2	≥1.0	**254** (total of 6×0.2 ha)	**2053** (total of 6×0.2 ha)	**195**	**NA**[c]	**1919**

[a] Species density and individuals density were standardized to the same area sampled in other studies.

[b] Species richness was standardized to the same number of individuals sampled in other studies.

[c] Not enough individuals sampled in this study to make a valid comparison (but note that in 1919 ind. there were 195 spp.).

FIGURES

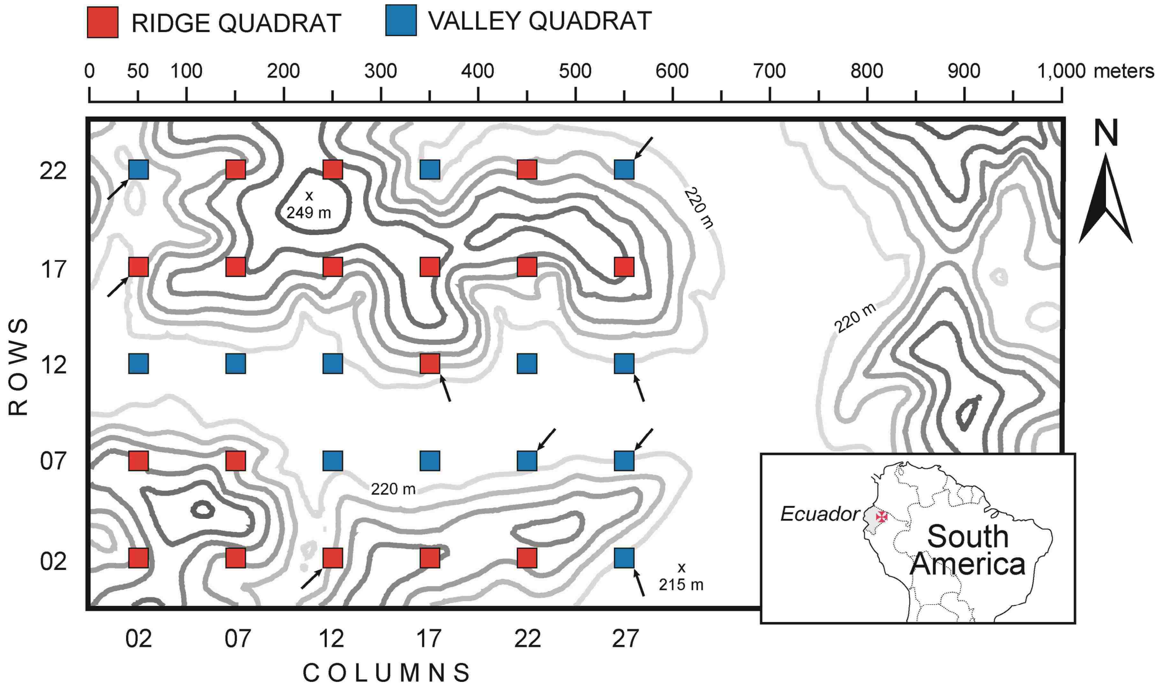

Figure 2.1. Topographic map of the 50-hectare Yasuní Forest Dynamics Plot (50-ha YFDP) and its relative location in Ecuador and in South America. The thirty non-contiguous 20×20 m quadrats (1.2 ha) sampled in this study formed a perfect rectangular grid in the western 500×600 m area of the YFDP. The habitat of each 20×20 m quadrat was classified, using topographic criteria, either as ridge (red square) or as valley (blue square). Quadrats can be identified by a combination of a column code and a row code that follows the tree census protocols (e.g. "27,22" for the quadrat at column 27 and row 22). Arrows indicate those quadrats which contain valley-ridge transitional 5×5 m subquadrats. The lowest and highest altitude points in the YFDP, at approximately 215 m and 249 m respectively, are also shown. Topographic contours represent 5 m altitude increments.

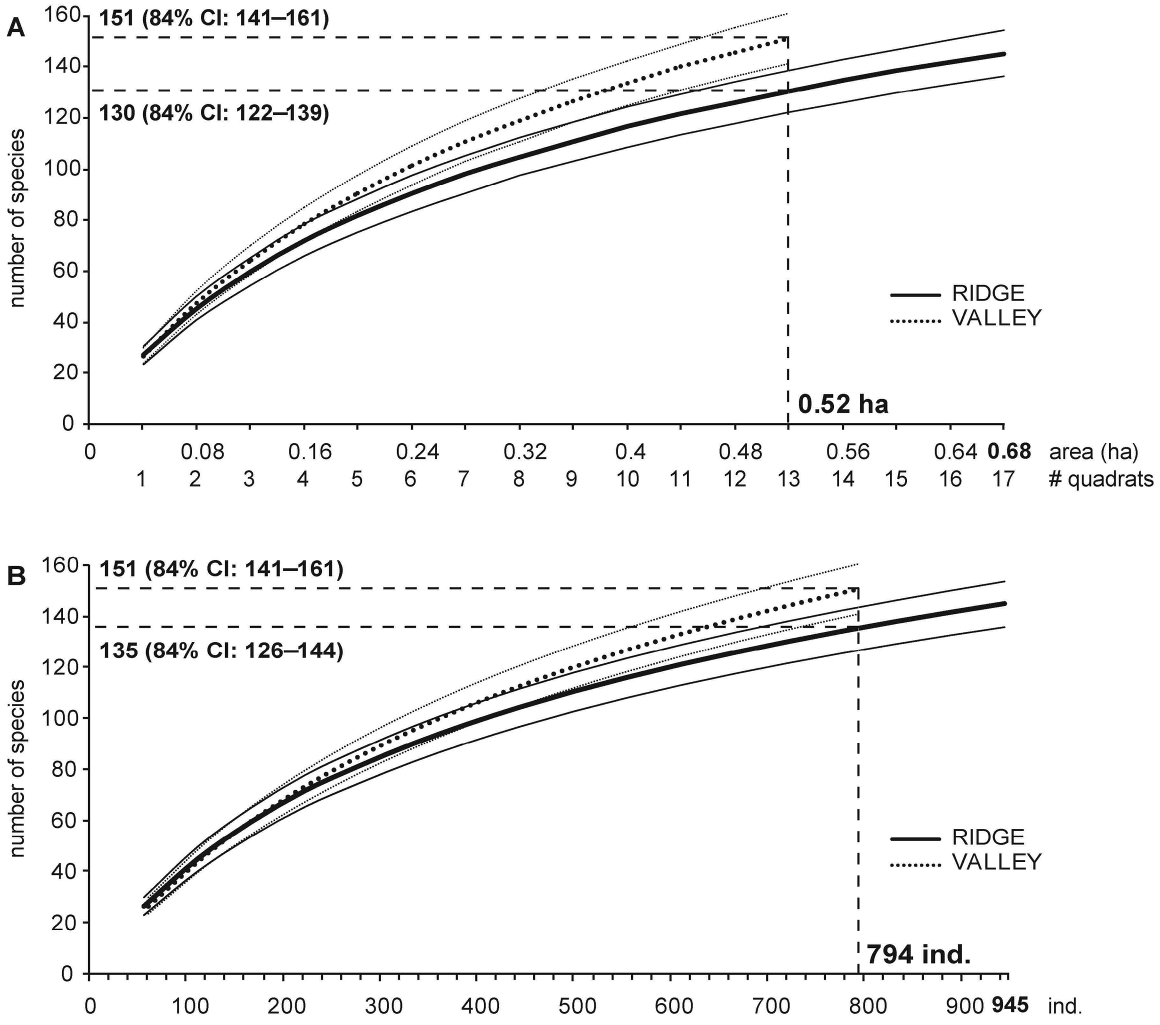

Figure 2.2. Mao Tau rarefaction curves with 84% confidence intervals (CI) for the lianas with diameter ≥1 cm in the ridge (continuous lines; *N*=17 quadrats) and the valley (dotted lines; *N*=13 quadrats) habitats of the YFDP. In this type of analysis, the 84% CI represent an α=0.05. (**A**) Species density curve (species vs. area); given the same sampled area (0.52 ha), the valley had significantly higher species density than the ridge (CI did not overlap). (**B**) Species richness curve (species vs. individuals); given the same number of individuals (794 ind.), the higher number of species of the valley was not significantly different from that of the ridge (CI overlap).

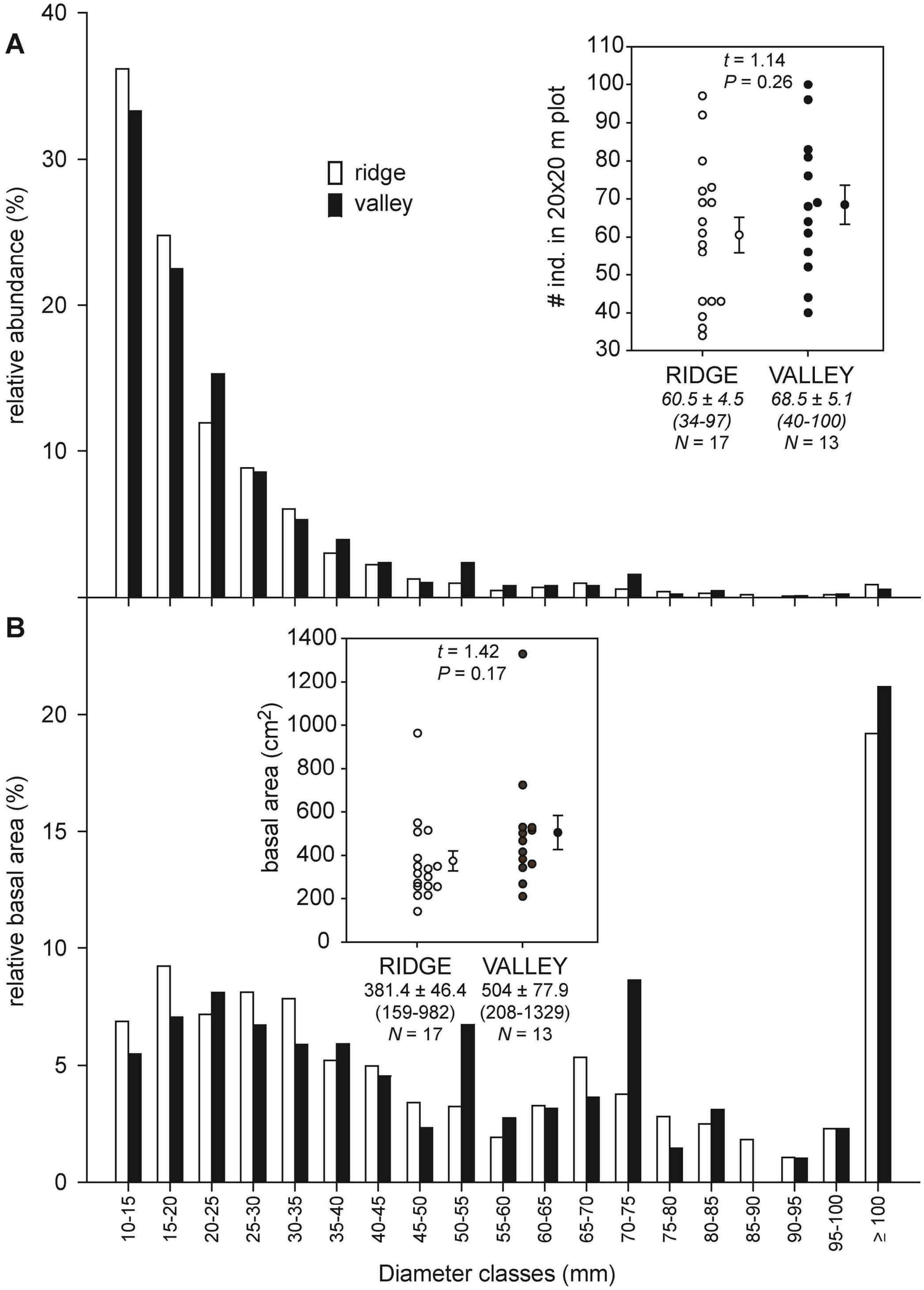

Figure 2.3. Abundance and basal area of lianas (diameter ≥1 cm) in the ridge (*N*=17 quadrats) and the valley (*N*=13 quadrats) habitats of the YFDP. (**A**) Relative abundance (%) by 5-mm diameter classes in ridge and valley habitats; the distributions did not differ significantly (Kolmogorov-Smirnov test, *D*=0.106, *P*=0.99). **Inset:** Number of individuals (# ind.) censused in ridge and valley quadrats; mean density per 20×20 m quadrat was not significantly different between habitats. Error bars represent ±1 standard error of the mean. (**B**) Relative basal area (%) by 5-mm diameter classes in ridge and valley habitats; the distributions did not differ significantly (Kolmogorov-Smirnov test, *D*=0.158, *P*=0.96). **Inset:** Basal area (cm^2) observed in ridge and valley quadrats; mean basal area per 20×20 m quadrat was not significantly different between habitats. Error bars represent ±1 standard error of the mean.

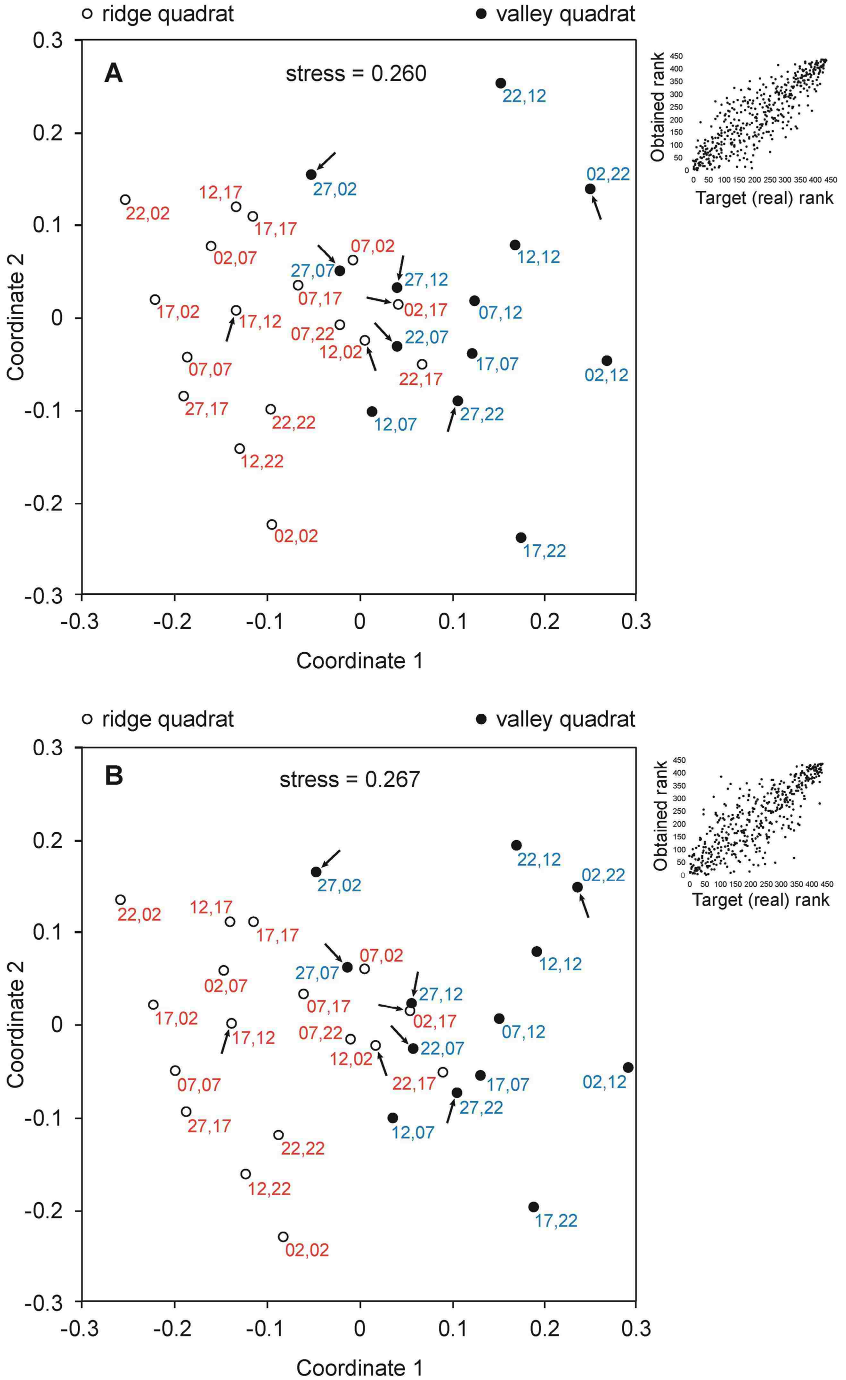

Figure 2.4. Non-Metric Multidimensional Scaling (NMDS) analyses using abundance data of liana species (diameter ≥1 cm) in thirty 20×20 m quadrats (1.2 ha) established in the ridge (*N*=17 quadrats) and the valley (*N*=13 quadrats) habitats of the YFDP. Open circles represent ridge quadrats, while closed circles represent valley quadrats. The codes next to each point identify each quadrat (red for ridge, blue for valley) and arrows indicate those quadrats that contained valley-ridge transitional zones (see Figure 2.1). The distances among quadrat coordinates in the diagram represent the rank-ordered (dis-)similarities in their species composition, according to the Bray-Curtis index. How well the distances in a NMDS two-dimensional diagram match the real dis-similarities among quadrats can be assessed by the stress index and the Shephard diagrams (upper right-hand corners of the graphs). To facilitate comparison, all axes use the same scale. (**A**) NMDS using the complete dataset (195 species, 1739 individuals; non-identified lianas excluded). (**B**) NMDS using a dataset of the the most common liana species, arbitrarily defined as those species with total abundance ≥5 individuals and frequency ≥2 quadrats (80 species, 1493 individuals; non-identified lianas excluded).

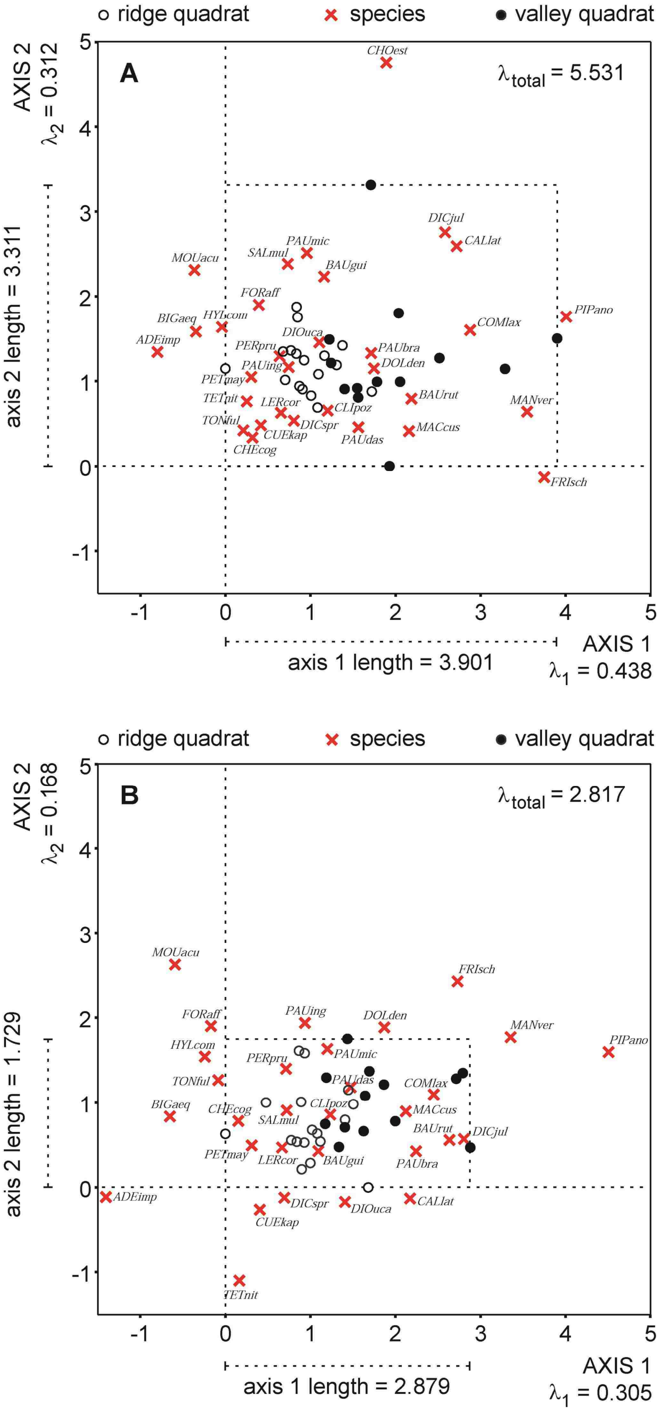

Figure 2.5. Detrended Correspondence Analyses (DCA) using abundance data of liana species (diameter ≥1 cm) in thirty 20×20 m quadrats (1.2 ha) established in the ridge (*N*=17 quadrats; 20×20 m each) and the valley (*N*=13 quadrats) habitats of the YFDP. Open circles represent ridge quadrats, while closed circles represent valley quadrats. Both DCA diagrams use the same axes scale for ease of comparison; units are "standard deviations of species turnover". In addition to quadrat scores (circles), the diagrams show species scores (red crosses) from the 31 most dominant species in either habitat (species acronyms in Table 2.3 and Appendix 2). The dashed rectangle in each DCA diagram depicts the quadrat scores diagram, on which the calculated axes lengths, a measure of species turnover in the system, are based. (**A**) DCA using the complete dataset (195 species, 1739 individuals; non-identified lianas excluded). (**B**) A conservative DCA using a subset of the most common liana species, arbitrarily defined as those species with total abundance ≥5 individuals and frequency ≥2 quadrats (80 species, 1493 individuals; non-identified lianas excluded).

CHAPTER 3: On the relation between plant functional traits and topographic habitat associations of lianas in a terra firme tropical rainforest, Yasuní, Amazonian Ecuador (4)

SUMMARY

In the Yasuní Forest Dynamics Plot (YFDP), in an attempt to understand why some species of lianas seem to be associated either with ridge habitat or valley habitat, or in fact not to be associated to a habitat at all, we analyzed the inter-specific variation and the intra-specific variation (phenotypic plasticity) of several quantitative traits in 43 species statistically classified into four species guilds of habitat association: 14 ridge species (R), 5 valley species (V), 20 generalist species (G) and 4 highly abundant species which statistically showed habitat association but were also widespread in the forest (2 WR and 2 WV species). Specifically, we asked: (1) for each trait, do species guilds differ in their trait values? and (2) for each trait, do species guilds differ in their intra-specific (between individuals) trait variation (phenotypic plasticity)? Traits measured included wood specific gravity [WSG], absolute diameter growth rate [AGR] by diameter classes, and several leaf traits mostly measured from understory shade leaves (specific leaf area [SLA], leaf dry matter content [LDMC], leaf thickness [LT], length to width ratio [L:W], individual-level leaf size range [LSR], leaf carbon [C], nitrogen [N], and phosphorus [P] concentrations, C:N and N:P ratios, and ^{13}C and ^{15}N isotopic signatures). SLA, LDMC, N concentration and P concentration values correlated among them, in accordance to what

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(4) Potential co-authors for publication: Esteban Gortaire[1], Leonel da S. L. Sternberg[2], Kyle Harms[3], Laura Salazar[4], Carolina Altamirano[1], Luis Espinoza, and Carlos Padilla[1]. [1]Escuela de Ciencias Biológicas, Pontificia Universidad Católica del Ecuador. Av. 12 de Octubre 1076 y Roca, Apartado postal 17-01-2184. Quito, Ecuador. [2]Department of Biology, University of Miami. 1301 Memorial Dr., Coral Gables, Florida 33146, USA. [3]Department of Biological Sciences, Louisiana State University. 202 Life Sciences Building, Baton Rouge, LA 70803, USA. [4]Albrecht-von-Haller-Institute for Plant Sciences, University of Göttingen, Untere Karspüle 2, D-37073 Göttingen, Germany.

is commonly predicted by theory. Among all traits analyzed, only SLA, leaf P concentration and WSG showed two or more significant, or almost significant, pairwise differences between inter-specific medians of trait values. Median phenotypic plasticity basically did not differ among species guilds of habitat association for almost all traits. The very limited sample size (number of individuals sampled per species) in the nutrient, WSG and AGR data may have hindered the uncovering of more differential patterns. In conclusion, although the few species guilds' pairwise differences observed shed some light on the underlying ecophysiological strategies that may explain the distribution of some liana species in the YFDP, the clearest pattern was really the absence of differential patterns for most traits among the species guilds of habitat association.

BACKGROUND AND HYPOTHESES

Living organisms thrive where, through evolution, they have become better fit. This paradigm is clear in extreme environments where adaptations of living organisms are obvious, but it may not be as clear along moderate environmental gradients where the adaptations can be subtle, if at all existent. What drives the distribution of plant species in a tropical forest? One hypothesis is that a plant species thrives where it is a good competitor, and that the hundreds of species in a tropical rainforest coexist because the conditions of Gause's Competitive Exclusion Principle are constantly violated (e.g., Palmer 1994, Wright 2002)—otherwise, only one species would persist (Gause 1937). Environmental homogeneity in time and space is one of such violated conditions: real environments are not immutable and are constantly producing environmental gradients. In a typical tropical forest, the abundance of a number of plant species strongly correlates with such environmental gradients, particularly soil gradients related to topography (e.g., Sollins 1998). One often tends to explain such distribution patterns by alluding to the niche concept—but the evolutionary diversification of specialized niches along environmental gradients probably explains relatively little of the great ecological problem of why so many woody species coexist in just a few hectares of lowland tropical rainforest (e.g., Wright 2002, Valencia et al. 2004c).

In the 50-ha Yasuní Forest Dynamics Plot (YFDP), in Amazonian Ecuador, the ridge-valley topographic signal is strong enough to statistically differentiate the tree, liana and palm communities along the topographic gradient (in terms of their species composition and/or species abundances), even if plants are sampled at the seedling stage and despite the hyperdiversity of the site (at least 1100 species of trees, 30 species of palms and 200 species of lianas; Svenning 1999a, Valencia et al. 2004c, Metz 2007, and Chapter 2). This statistically significant difference between the very diverse communities of ridge and valley is certainly driven by the differential abundances of some species along the gradient (in particular when comparing its extremes, i.e., upper ridge vs. valley). If abundant, such species have a stronger effect on the difference if they mostly occur in only one habitat; if rare (but not too rare as to become uninformative), they increase the variation in the system (Chapter 2). But why do such species partition the gradient in the first place, while the rest of species do not? One hypothesis is that they are the result of "niche differentiation", i.e., because of inter-specific competition (limiting similarity; MacArthur and Levins 1967), their traits evolved to become better adapted to either extreme of the topographic gradient (see e.g., Wright 2002, Kraft et al. 2007). Another hypothesis is that they are the result of "habitat filtering", i.e., a habitat filtered out those species that lacked a viable ecological strategy—reflected in their trait or life-history attributes—to survive in it (see e.g., Kraft et al. 2007). Either way, both hypotheses are related because niche differentiation may result in taxa that become so well adapted to a certain habitat or habitats that they lose the ability to successfully establish in other habitats, and thus become subject to habitat filtering. In the YFDP, roughly 40% of the tree and palm species show a statistically significant habitat association to either ridge or valley (Svenning 1999a, Valencia et al. 2004c), but because most tree species also do occur, infrequently, in the least "preferred" habitat, only 25% of the tree species are probably real topographic-habitat "specialists" (Valencia et al. 2004c). Among seedlings (mainly of trees and lianas), during yearly censuses for five years, up to 60% of the species showed significant associations to one or two of the following three habitats: ridge-top, mid-slope or valley (Metz 2007).

In the present study, we statistically identify the species of lianas in the YFDP that show a clear signal of habitat association and explore if such signal can be recovered in the expression of some quantitative functional traits measured in as many individuals of those species as possible—if so, this may ultimately help to explain the observed spatial distribution of the liana species in the YFDP. We compare the inter- and intra-specific trait variation of these species to that of "generalist" species, which were also statistically determined. For each trait measured, we specifically asked two questions:

(1) Do species guilds differ in their trait values? For this first question, we developed two hypotheses that differed based on the assumed level of phylogenetic conservatism at the family or genus level: (1) if the traits are assumed to be not too phylogenetically conserved, then we hypothesized that species traits values will change considerably within the same family and be more environmentally- than phylogenetically-controlled,

i.e. significant differences will be observed among species guilds, whether or not family composition differed among habitats, and especially between guilds from contrasting environments (ridge vs. valley); on the other hand, (2) if traits are phylogenetically conserved at the family or genus level, then we hypothesized that species trait values will be rather insensitive to the environment, i.e. significant differences will be observed among species guilds only if the composition of families or genera also differed among them. Phylogenetic conservatism, which was not directly measured in the present study, occurs when the trait variation within family or genus clades is lower than what can be expected by chance (see e.g., Swenson and Enquist 2007).

(2) Do species guilds differ in their intra-specific (between individuals) trait variation (phenotypic plasticity)? For this second question, based on the premise that plants should be adapted to the environment(s) where they occur in greatest abundance, we developed two hypotheses: (1) generalist or widespread species of lianas, in order to tolerate a variety of forest soils, will have, on average, higher relative intra-specific (inter-individual) trait variation—"phenotypic plasticity"—than species mostly restricted to a single habitat (ridge or valley species); and (2) because ridges are physically and vegetation-wise more homogenous than valleys (Chapter 2), valley species, on average, will have higher intra-specific variation than ridge species. We reasoned that higher phenotypic plasticity of valley species should be advantageous to tolerate the variety of valley types that apparently exist within the Yasuní terra firme forest (Chapter 2). The biogeophysical heterogeneity of valleys is probably determined by distinct regimes of soil water logging (proneness to flooding), which in turn should influence local soil-plant water and nutrient dynamics.

METHODS

STUDY AREA

The present study was conducted in Yasuní National Park, Amazonian Ecuador, in the 50-hectare Yasuní Forest Dynamics Plot (YFDP) (00°41' S, 76°24' W). Mean annual rainfall and mean monthly temperature are approximately 3000 mm and 25 °C, respectively. The ever abundant rainfall (mean monthly rainfall = 250 mm) follows a seasonal pattern with two rainfall peaks occurring around May and October. More than 90% of Yasuní National Park is terra firme (upland) hilly forest on Udult Ultisols that are somewhat clayey, acidic, and rich in iron and aluminum (Pitman 2000, Valencia et al. 2004a). The surface soil (0–5 cm) of the terra firme forest is, when compared to other terra firme areas in northwestern Amazonia, relatively rich in exchangeable bases (particularly Ca, Mg, and Na) and has an average texture of approximately 50% silt, 29% sand and 21% clay (data extracted from Tuomisto et al. 2003).

The YFDP is located on terra firme (upland) forest, with ridge formations up to 250 m altitude, separated by a valley with an altitude of 215–225 m that can be considered terra firme as well, except for some swampy areas (Valencia et al. 2004a). Some of the streams that crisscross the valley may occasionally overflow during the rainiest months. Intervening valleys are a common physiographic feature of the hilly terra firme forest of Yasuní, and under low drainage conditions they may become swamp forests; in the YFDP, there are some such swampy areas, but they are relatively small and non-continuous (and were not sampled in the present study).

The main physical differences between ridge and valley habitats are evidently related to the effect of topography on the hydrological regime: on average, drainage is probably lower in the valley, soil water content is probably higher in the valley (see e.g. Jirka et al.

2007) and soil oxygen concentration is probably lower in the valley (see e.g., Silver, Lugo, and Keller 1999). If these differences are marked, other soil characteristics such as pH, Al concentration, nutrients concentrations and organic matter concentration should be also different between ridge and valley habitats (see e.g., Tange, Yagi, and Sasaki 1998, Tuomisto et al. 2003, Kubota, Murata, and Kikuzawa 2004), but a thorough geochemical/geophysical description of YFDP's ridge and valley soils is not as yet available (the YFDP soil data reported by John et al. 2007 was apparently faulty; J. Dalling, pers. comm., H. Romero-Saltos, pers. obs.).

DEFINING SPECIES GUILDS OF HABITAT ASSOCIATION

Species guilds of habitat association (or non-association) were defined by using habitat randomization tests of the 80 most common species of lianas (diameter ≥1 cm) occurring in a sample of 17 ridge quadrats and 13 valley quadrats (20×20 m each), aligned as a perfect rectangular grid in the western 600×500 m area of the 50-ha Yasuní Forest Dynamics Plot. The points in the grid were separated by exactly 100 m (i.e., 80 m from one quadrat edge to the next). The 80 most common species set (out of 195 species found in total in the grid quadrats; see Chapter 2) comprised those species with total abundance ≥5 individuals and frequency (# quadrats where a species occurs) ≥2 quadrats. For each species, randomization tests were run using, as a response variable, two kinds of relative abundance data: (1) a test using a species overall relative abundance in each habitat *(# individuals of a species in a habitat* / *total # individuals of all species in that habitat*), and (2) a test using a species mean relative abundance per quadrat in each habitat (sum of [*# individuals of a species in a quadrat / total # individuals in that quadrat*] of all quadrats in a habitat / *# quadrats in that habitat*). The tests were basically

Monte Carlo tests (*sensu* Gotelli and Ellison 2004) with 1000 randomizations in which habitat categories (valley and ridge) were randomly shuffled among plots but the internal distribution of taxa in each plot was maintained. In each simulation (randomization), the observed relative abundance of a species was compared to its simulated distribution of relative abundance, and whether the observed value was greater than, lower than or equal to the simulated value was tallied. A one-tailed Monte-Carlo probability of habitat association was then calculated, for each species, as the *number of times the observed relative abundance was less than or equal to the simulated relative abundance* / 1000 (see Gotelli and Ellison 2004).

To decide if a species showed association to a habitat, we did not use the strict 0.05 probability cutoff because with it very few species showed habitat association and thus the sample size (# species) for the subsequent trait analyses (see below) was greatly reduced. Instead, a less conservative probability cutoff of 0.10 was used. The selection criteria used to classify the habitat association or non-association of a species were: (1) *ridge* species [R]: if $P_{\text{ridge}} \leq 0.10$ and frequency in valley habitat <6 quadrats (<≈50% of the valley quadrats), (2) *valley* species [V]: if $P_{\text{valley}} \leq 0.10$ and frequency in ridge habitat <8 quadrats (<≈50% of the ridge quadrats), (3) *true generalist* species [G]: if $0.30 \leq P \leq 0.70$ and with any frequency (a 0.30–0.70 probability range was assumed to mean that a species was more or less equally represented in both habitats), and (4) *widespread* species *with habitat association* [W]: if $\mathrm{P}_{\text{ridge}} \leq 0.10$ but frequency in valley ≥6 quadrats, the species was classified as widespread with ridge association [WR]; if $\mathrm{P}_{\text{valley}} \leq 0.10$ but frequency in ridge habitat ≥8 quadrats, the species was classified as widespread with valley association [WV]. Note that a $P \leq 0.10$ for one habitat almost always would correspond to a $P \geq 0.90$ for the other. Those species with P ranges between 0.10–0.30 and 0.70–0.90 were not formally classified (nor their traits analyzed) because we assumed that their habitat association (or non-association) to ridge or valley was not clear—these "transitional" species can be however considered as species with a trend to be associated to one habitat over the other. To somehow compensate the liberal approach on the probability cutoff (0.10), we applied a conservative approach to select the final set of species for the functional traits analyses: only those species that complied with the selection criteria in *both* randomization tests were selected. This resulted in 43 liana species selected for trait analyses, out of the 80 species analyzed for habitat association, and out of the 195 species found in total in the grid quadrats.

SAMPLING QUANTITATIVE FUNCTIONAL TRAITS

Given the nature of our research questions (see Introduction), in our study we focused only on those traits that can be measured quantitatively at the individual-level (i.e., traits such as dispersal syndrome are not analyzed). Although moderate destructive sampling probably has minimal impact on individual plant fitness (Cornelissen et al. 2003), we decided to minimize the impact on the plants within the YFDP because their long-term demographics are being carefully studied. We thus only sampled representative individuals and collected as few leaves as possible. To understand our sampling approach, the following background information is relevant: (1) field sampling campaigns occurred in 2006 and 2008; (2) in order to increase sample size, sampling of functional traits was not limited to the 30 grid quadrats, but also included two other areas: a 20×500 m ridge-valley-ridge transect inside the YFDP ("column 07"; unpublished dataset), and the terra firme forest around the YFDP within a radius of approximately 2 km (where mainly destructive sampling of wood specific gravity was undertaken); (3) because the lianas in the 20×500 m transect were censused in 2006 and re-censused in 2008 (data unpublished), some of the lianas sampled in that transect were 2008 recruits or had, by the second census, died; (4) functional trait data of the 43 species whose traits were analyzed represent a subset of an unpublished liana trait dataset of approximately 200 liana species from the YFDP; (5) not all traits were collected in all the forest areas sampled; (6) for obvious reasons, traits were not sampled in every single liana censused in the YFDP; and (7) although we collected most data in a systematic way, sometimes data were also gathered opportunistically (e.g., sampling sun leaves of lianas from the crown of recently fallen trees). Detailed sampling protocols for each functional trait are explained below.

Specific leaf area

Specific leaf area (SLA, fresh leaf area / dry mass, mm^2/mg) was measured in the 2006 and 2008 field campaigns for 589 lianas (578 censused in the YFDP), representing all the 43 species selected for trait analyses. Quadrats sampled for SLA included all the quadrats in the grid and in the transect. In every 20×20 m quadrat, usually one individual per species was sampled; when in taxonomic doubt, or when the species seemed to occur at low densities locally, several individuals were sampled, but this happened rarely (mean number of individuals sampled per species per quadrat = 1.2, mode = 1, range = 1–6). For every individual sampled, we collected healthy leaves that had apparently recently matured and hardened, and thus had few or no epiphylls. We usually collected two or three leaves per individual, including the largest leaf and the smallest leaf we could locate on the plant, if they met the health and matureness criteria above (but in 29% of the 589 lianas, only one leaf was sampled). Leaves collected were mostly shade leaves from the understory because in general it was impossible to collect sun leaves from the upper canopy. In the field, leaf dehydration was minimized by maintaining the leaves in plastic bags, with a wet cotton ball inside, stored in a cooler with ice. Once in the lab, leaves were scanned (in 2006) or digitally photographed (in 2008; leaves pressed with a pane of glass), and then their fresh area was measured from the digital images using ImageJ®. After leaves were dried for three days at a temperature of about 50–60 °C, their dry mass was measured with a Sartorius® digital balance (±0.001 g) while they were still warm (to minimize humidity absorption from the environment). Dry leaves were then stored for subsequent chemical analyses of carbon, nitrogen and phosphorus (see below). Individual-level SLA was estimated by averaging the SLA values of the leaves collected in the same individual; these SLA's were in general very similar to each other despite that leaves were often different in size and that so few leaves were collected per individual. Indeed, regression equations among SLA's of leaves from the same liana, of the species considered for our study, and based on lamina-based SLA, had all $P<0.001$, and were: for largest leaf (x) vs. smallest leaf (y): $y=0.90x+2.23$, $R^2=0.65$, $N=411$ leaf pairs; for largest leaf (x) vs. extra leaf (y): $y=0.90x+2.66$, $R^2=0.77$, $N=127$ pairs; and finally for extra leaf (x) vs. smallest leaf (y): $y=0.96x+0.54$, $R^2=0.70$, $N=124$ pairs. These regressions were based on lamina-based SLA and not on whole leaf-based SLA because whole leaf SLA was not always sampled (see below).

In 2006, fresh leaf area and dry mass were measured without petioles, rachises, pulvini, or other similar structures (which were all discarded), so that measurements were only based on the lamina. We took this approach because at the time we were using a small flat-bed scanner. However, in 2008, when we used high-resolution digital photography, we were able to measure both the fresh area and dry mass of the lamina (as in 2006) and the fresh area and dry mass of the whole leaf. This allowed us to correct lamina-based SLA (x) to whole leaf-based SLA (y) with the following equations based on highly significant linear regressions between the two variables (R^2>0.9, P<0.001): y=0.92x+0.44 for simple leaves; y=0.87x−0.12 for pinnate/trifoliate/or similar leaves; y=0.77x+0.85 for partly bipinnate leaves; y=1.09x−6.97 for true bipinnate leaves. These regressions are based on data from >1000 individuals and >200 species of lianas sampled for functional traits in the whole YFDP (unpublished), not only on data from the 43 species selected for trait analyses.

Data curation procedures, necessary to increase data quality, were mostly based on the identification of outliers. One approach involved comparisons among the SLA values of the few leaves collected from the same individual; because such SLA's were usually similar (see above), extreme outliers were easily detected by scatter-plotting. Another approach, but only applicable for compound leaves, was to compare the SLA of the largest leaflet, which was independently measured, to the SLA of the whole leaf; again, because these two variables were correlated, extreme outliers were easily detected by scatter-plotting (for the species with compound leaves in our study, the regression equation between leaflet SLA (y) and whole leaf SLA (x) was: y=1.03x+4.71, R^2=0.67, N=103 lianas, P<0.001). Most of the strange values detected were caused by data entry typos; the few extreme outliers that could not be explained by careful data inspection were taken out from the analyses, which usually resulted in a reduction in the number of leaves included in the calculation of average individual-level SLA.

Leaf dry matter content

Leaf dry matter content (LDMC, dry leaf mass / water-saturated fresh leaf mass, mg/g) was only measured in the 2008 field campaign for 285 lianas (282 censused in the YFDP), representing 41 of the 43 species selected for trait analyses. Quadrats sampled for LDMC only included those censused in 2008: the quadrats in the transect (second census) and five of the 30 grid quadrats (those in "column 27" of the YFDP). In every 20×20 m quadrat, usually one individual per species was sampled; when in taxonomic doubt, or when the species seemed to occur at low densities locally, several individuals were sampled, but this happened rarely (mean number of individuals sampled per species per quadrat = 1.24, mode = 1, range = 1–6). The leaves collected for LDMC measurements were the same collected for SLA measurements, i.e. usually two or three leaves per individual, including the largest leaf and the smallest leaf we could locate on the plant, if they met the health and matureness criteria (but in 11% of the 285 lianas, only one leaf was sampled). Because of the storage procedure in the field (see SLA protocol), and because most leaves were understory shade leaves growing in a forest that receives a lot of rainfall, we did not rehydrate the leaves in the lab. Leaves were weighed as soon as we returned from the field (fresh mass), digitally photographed (for SLA measurements; see above), dried for three days at a temperature of about 50–60 °C, and then weighed again (dry mass). Mass was measured to the nearest thousandth of a gram (±0.001 g) using a Sartorius® digital balance. Individual-level LDMC was estimated by averaging the LDMC measurements of the leaves collected in the same individual; these LDMC's were in general very similar to each other despite the fact that leaves were often different in size and that so few leaves were collected per individual. Indeed, regression equations among LDMC's of leaves from the same liana, of the species considered for our study, had all $P<0.001$, and were: for largest leaf (x) vs. smallest leaf (y): $y=0.98x+16.24$, $R^2=0.82$, $N=253$ leaf pairs; for largest leaf (x) vs. extra leaf (y): $y=0.89x+38.33$, $R^2=0.84$, $N=117$ pairs; and finally for extra leaf (x) vs. smallest leaf (y): $y=1.0x+5.08$, $R^2=0.85$, $N=117$ pairs.

As in SLA, we curated LDMC data with two approaches. One approach involved comparisons among the LDMC values of the few leaves collected from the same individual; because such LDMC's were usually similar (see above), possible data errors (extreme outliers) were easily detected by scatter-plotting. Another approach, applicable for compound leaves only, was to compare the LDMC of the largest leaflet, which was independently measured, to the LDMC of the whole leaf; again, because these two variables were correlated, extreme outliers were easily detected simply by scatter-plotting (for the species with compound leaves in our study, the regression equation between leaflet LDMC (y) and whole leaf LDMC (x) was: $y=0.52x+172.3$, $R^2=0.50$, $N=103$ lianas, $P<0.001$). Most of the strange values detected were caused by data entry typos; the few extreme outliers that could not be explained by careful data inspection were taken out from the analyses, which usually resulted in a reduction in the number of leaves included in the calculation of average individual-level LDMC.

Leaf lamina thickness

Leaf lamina thickness (LT, mm) was measured in the 2006 and 2008 field campaigns for 589 lianas (578 censused in the YFDP), representing all the 43 species selected for trait analyses. LT was measured in the same leaves in which SLA was measured. Leaf lamina thickness of fresh leaves was measured in the lab using a micrometer, which can detect differences in thickness of 1/100 mm. For compound leaves, LT was measured in the largest leaflet only. LT was measured near the tip, at the middle (and between the midrib and the lamina edge) and near the base of each leaf (or leaflet). Leaf veins were avoided whenever possible. Individual-level LT was estimated by averaging the LT values of the leaves collected in the same individual (an average of up to 9 measurements if three leaves were sampled); these LT's were in general very similar to each other despite that leaves were often different in size and that so few leaves were collected per individual. Indeed, regression equations among LT's of leaves from the same liana, of the species considered in our study, had all $P<0.001$, and were: for largest leaf (x) vs. smallest leaf (y): $y=0.94x+0.004$, $R^2=0.86$, $N=544$ leaf pairs; for largest leaf (x) vs. extra leaf (y): $y=0.92x+0.007$, $R^2=0.86$, $N=141$ pairs; and finally for extra leaf (x) vs. smallest leaf (y): $y=0.94x+0.008$, $R^2=0.90$, $N=141$ pairs.

Data curation involved comparisons among the LT values of the few leaves collected from the same individual; because such LT's were usually similar (see above), possible data errors (extreme outliers) were easily detected by scatter-plotting.

Length to width ratio of whole leaf

Length (L) and width (W) of leaves were measured in the 2006 and 2008 field campaigns for 584 lianas (573 censused in the YFDP), representing all the 43 species selected for trait analyses. The length to width ratio (L:W) of a leaf (length/width) is considered in the present study as a quantitative proxy for leaf shape (as if leaves were ovoids). Leaf length and width were measured in the same leaves in which SLA was measured. Leaf length included the petiole length. In some leaves, because of leaflets arrangement, loss of leaflets, or loss of leaf tips, the approximate location of the leaf tip had to be approximated. Individual-level L:W was estimated by averaging the L:W values of the leaves collected from the same individual; these L:W's were in general very similar to each other despite that leaves were often different in size and that so few leaves were collected per individual. Indeed, regression equations among L:W's of leaves from the same liana, of the species considered in our study, had all $P<0.001$, and were: for largest leaf (x) vs. smallest leaf (y): $y=0.91x+0.18$, $R^2=0.72$, $N=539$ leaf pairs; for largest leaf (x) vs. extra leaf (y): $y=0.86x+0.42$, $R^2 = 0.74$, $N=141$ pairs; and finally for extra leaf (x) vs. smallest leaf (y): $y=0.83x+0.44$, $R^2=0.60$, $N=141$ pairs.

Data curation involved comparisons among the L:W values of the few leaves collected from the same individual; because such L:W's were usually similar (see above), possible data errors (extreme outliers) were easily detected by scatter-plotting.

Individual-level leaf size range

Leaf size range (LSR, cm^2) at the individual level was defined as the difference in leaf lamina area between the largest and the smallest leaves from the same liana. LSR data were collected in the 2006 and 2008 field campaigns for 415 lianas (411 censused in the YFDP), representing all the 43 species selected for trait analyses. LSR is considered a proxy for within-individual variation of leaf size. Leaf size, defined as the fresh area of the leaf lamina (Cornelissen et al. 2003), was measured by analyzing the digital images of leaves obtained for SLA (see above). Lianas that had only one leaf sampled (169 lianas) were obviously excluded from LSR calculations. We have not used leaf size *per se* as a trait because we did not sample enough leaves to represent the average leaf size in a liana—a maximum of only three leaves were sampled from each liana, and because they often represented leaf size extremes, purposely sampled to estimate LSR, the leaves were not necessarily representative of the most common size of leaves in an individual.

Leaf carbon and nitrogen concentrations, and their stable isotope signatures

In 2007 and 2008, mass-based concentrations (%) of carbon (C) and nitrogen (N) in the leaves, along with relative abundances of ^{13}C and ^{15}N stable isotopes (δ^{13}C and δ^{15}N), were measured at the University of Miami, USA. These 113 lianas (104 censused in the YFDP), represent all the 43 species selected for trait analyses, and represent a subset of the 589 lianas whose SLA's were sampled and which had dry leaves in storage, but which could not all be chemically analyzed because of funding limitations. This subset was initially created by randomly selecting 2 individuals per species; however, because of lumping or separation of species by the time the liana taxonomy was completed, the end result was 1–7 individuals per species in the analyzed set of 113 lianas (mean = 2.63, mode = 2, median = 2, only two species had 1 individual analyzed, and only six species had 4–7 individuals analyzed).

For chemical analyses, the few leaves collected from each liana were finely ground together as a single composite sample. The day before sample preparation, the finely ground leaf material was dried overnight in an oven at 40 °C to get rid of as much humidity as possible. This extra-drying of leaf material was important because, for each liana, just about 5 mg of ground leaf material were used for analyses (exact weights were of course recorded for subsequent calculations). The weighed leaf material was placed into a small tin cup that was then rolled as a ball. The tin balls were loaded in an elemental analyzer (Eurovector, Milan, Italy) coupled with a continuous flow isotope ratio mass spectrometer (Isoprime, Elementar, Hannau, Germany). For isotopic relative abundances, results had an accuracy of ±0.1‰ (δ units).

Leaf phosphorus concentration

In 2007 and 2008, mass-based concentration (%) of phosphorus (P) in the leaves was measured at the University of Miami for the same ground leaf composite samples in which C(%) and N(%) were measured (113 lianas, 104 censused in the YFDP, representing all the 43 species selected for trait analyses). P was first extracted from the leaf tissue by the following procedure: first, a given mass of dry leaf tissue (in a crucible) was ashed at 600 °C for 6 hours (in a furnace), then the ash was digested with 5 ml of a 4% sulfuric acid solution for about 10 minutes, and finally solid impurities were filtrated out using glass fiber filter paper and washes of 4% sulfuric acid solution (on glass funnels). The resulting filtrate of 4% sulfuric acid solution + P (collected in graduated test tubes) had always a fixed volume of 25 ml. Although our intention was to ash about 500 mg of leaf material for every liana, often there was not enough leaf material (only 1–3 leaves were collected per liana) and so the weights of the dry leaf tissue (before ashing) had considerable variation (mean±1 SD=442.2±108.7 mg, median=464, minimum=66, maximum=612, *N*=113). The P concentration in the filtrate was measured using the Method 365.1 of the U.S. Environmental Protection Agency (USEPA 1983)—ultimately based on the classic colorimetric approach to measure P in aqueous solutions (Fiske and SubbaRow 1925)—accommodated for flow injection analysis (FIA) using a Flow Solution® 3000 instrument (Alpkem, OI Analytical, Texas, USA). The FIA instrument calculated the P concentration in the acid solution in ppm (X ppm = X mg P / 1000 ml filtrate); thus, the mass-based concentration of P (in %) was calculated as: {[mg of P in leaf tissue] / mg of leaf tissue analyzed} × 100 = {[(X mg P / 1000 ml filtrate) × 25 ml filtrate] / mg of leaf tissue analyzed} × 100.

In 2009-2010, after exploring the leaf nutrient data of >400 liana individuals and >200 liana species analyzed in the whole YFDP (unpublished data), including data from the 43 species selected for trait analyses, we noticed that our measured P concentration values were, in general, probably underestimated because many lianas had very high N:P ratios (mean±1SD=77.0±54.07, median=60.36, minimum=10.63, maximum=492.10) when compared to N:P ratios from other studies in lowland tropical rainforests, although in those studies very few lianas were represented (mean±1SD=14.8±7.91, median=14.21, minimum=6.27, maximum=73.33, Wright et al. 2004). This led us to send duplicate leaf samples for P analysis to two other university-affiliated labs in USA: the Soil and Plant Testing Laboratory at University of Missouri Extension (41 samples sent; one [rarely two] species per family sent) and the Agronomy Soil Testing Lab at Kansas State University (31 samples sent, from among the 41 samples). The samples sent to either Missouri or Kansas included 13 samples from the species selected for the present study. The results from Missouri and Kansas were very similar (y=1.07x+0.003, R^2=0.99, N=31, where y=Kansas result and x=Missouri result), despite their different method to extract P from the leaf tissue: in Missouri, leaves were ashed and then digested with 6N HCl (Miller 1997, Kalra 1998), while in Kansas, leaves were not ashed but instead a wet digest with sulfuric acid and hydrogen peroxide was used (Lindner and Harley 1942, Thomas, Sheard, and Moyer 1967). To measure P concentration in the extract, both labs used Inductively Coupled Plasma Atomic Emission Spectrometry (ICP). When the 41 values from Missouri/Kansas (31 of them averages between Missouri and Kansas) were plotted against the Miami data, we noticed that for Miami P concentration values >0.15 (%), there was relatively good agreement between the Missouri/Kansas and Miami measurements, meaning that when the P content in the leaf was relatively high, our method apparently worked well. On the other hand, for Miami values <0.15%, what was measured in Missouri/Kansas was consistently higher than what was measured in Miami, and followed a linear relation described by the following regression equation: $y=2.318x+0.026$, $R^2=0.82$, $P<<0.001$, $N=37$, where y = Missouri/Kansas value and x = Miami value. Given the high R^2 and very low P, we decided to correct all Miami values <0.15% with this equation, except those from samples sent to Missouri/Kansas, which of course kept the values measured in those labs.

Carbon-nitrogen ratio and nitrogen-phosphorus ratio

The ratio of carbon concentration to nitrogen concentration (C:N) and the ratio of nitrogen concentration to phosphorus concentration (N:P) were calculated in order to explore differences in nutrient stoichiometry among the species guilds of habitat association.

Wood specific gravity

Wood specific gravity (WSG, dry wood mass / fresh wood volume, g/cm^3) was measured in the 2006 and 2008 field campaigns for 157 lianas representing 39 species of the 43 species selected for trait analyses. Because to obtain a representative wood sample from the thin stem of most lianas may jeopardize liana survival, WSG was not measured in YFDP lianas, but in lianas along the terra firme trails of the nearby Yasuní Research Station. A liana was sampled only if it could be identified (or leaves could be collected for later taxonomic identification). Wood was usually extracted from the thickest area of the *main* stem, usually near the base, either by coring (large lianas, usually ≥5 cm of diameter), by sawing (medium-sized lianas), or by cutting (very small lianas). If coring, we used a small Haglöf increment borer to obtain cortex-to-pith wood cores approximately 5 mm wide; if sawing, we used a small manual saw to obtain triangular-shaped pieces of wood which included the pith (like a pie slice); if cutting, we used a hand pruner and buried the cut stem in the soil hoping the liana will regrow. Stem diameter at the point of collection was recorded (data not analyzed).

To measure WSG, the fresh volume of a wood sample was estimated, without cortex, using the Archimedes' principle (i.e., by sinking the fresh wood sample in a small container of water on top of a digital scale; because the density of water is ≈ 1 g/cm^3, the weight reading of the scale must be basically equal to the volume of wood). Dry weight of the wood sample was measured after drying the sample in an oven for 48 hours at 100 °C. A Sartorius® digital balance (±0.001 g) was used to make these measurements.

Stem diameter growth rate

Absolute stem growth rate (AGR, Δ diameter between censuses / Δ time between censuses, mm/yr) were calculated for 606 lianas representing 42 of the 43 species selected for trait analyses. These lianas represent a subset of the lianas initially censused in 2006 and re-censused in 2008 in a 20×500 m transect inside YFDP ("column 07"). To be included in the growth rate calculations, a liana had to meet the following criteria: (1) have a geometric mean diameter ≥ 1.0 cm in the first census (the geometric mean diameter is the geometric mean of the diameters of the longest and widest axes, at the point of diameter measurement [PDM] on a liana stem; the geometric mean diameter was the value used for growth rate calculations); (2) have the same PDM in the first and second censuses (sometimes the original PDM would be destroyed); (3) have a growth rate that is not an outlier (at the end, only one liana that had a growth rate of 11.91

mm/yr, probably a result of erroneous data recording, was excluded from the analysis); and (4) obviously, be alive in the two censuses (“survivor”).

To explore the change in absolute growth rate as the lianas age, for every species we separately analyzed the growth rates of the lianas in the following four diameter categories: 1.0–1.5 cm, 1.5–2.5 cm, 2.5–5.0 cm and ≥5.0 cm (defined using first census data). The first two categories were meant to represent young lianas that were probably actively growing (at least those facing ideal environmental conditions), while the last category was meant to represent old established lianas that probably were not growing as much (or so we assumed). Just a few species had individuals represented in all diameter categories. Because of this analysis by short-range diameter classes, we considered that the calculation of relative stem growth rate (RGR, Δ [ln diameter] / Δ time, 1/yr) was not necessary for the comparisons among species guilds. RGR is thus only reported (in an Appendix) but not analyzed.

COMPARING AMONG SPECIES GUILDS OF HABITAT ASSOCIATION

The present study posed two research questions for each trait (see Introduction): (1) Do species guilds differ in their trait values?, and (2) Do species guilds differ in their intra-specific (between individuals) trait variation (phenotypic plasticity)? To answer them, as explained above, we first classified liana species into four species guilds of habitat association or non-association (ridge species [R], valley species [V], true generalist species [G], and widespread species with habitat association [W]), and sampled 14 quantitative traits of as many individuals per species as possible (SLA, LDMC, LT, L:W, LSR, C, N and P concentrations, C:N and N:P ratios, relative isotopic abundance of ^{13}C and ^{15}N, WSG, and AGR), and then selected 43 species for trait analyses.

Data analysis for research question 1: Do species guilds differ in their trait values?

To answer question 1, the following approach was taken: First, a mean value was calculated for each of the 43 species by averaging the individual-level measured values (themselves averages of up to three leaves) of all individuals in the species. Second, the analysis itself consisted in comparing pairwise between species guilds via Mann-Whitney (non-parametric) tests in which each species-level mean value was considered a replicate (an independent statistical observation) (i.e., intra-specific [inter-individual] variation was disregarded). Mann-Whitney was used because species-level mean values were often not normally distributed, i.e. this statistical test compared medians, not averages, of the distributions of species-level mean values. *P* values of the six possible pairwise comparisons were Bonferroni-corrected; corrected and uncorrected *P* values for each pairwise comparison are reported in Results only if uncorrected $P \leq 0.10$.

Data analysis for research question 2: Do species guilds differ in their intra-specific (between individuals) trait variation (phenotypic plasticity)?

To answer question 2, the following approach was taken: First, to make the intra-specific (between individuals) variation of different species comparable (relative) so that statistical calculations can be done (e.g., the calculation of a median of intra-specific variation for all species in a species guild; see below), the intra-specific trait variation of each of the 43 species was expressed as a coefficient of variation (CV = standard deviation / mean; we did not express it as a percentage). A CV was calculated even if only two individuals had been sampled because very low numbers of sampled individuals per species were common particularly among the C, N, P, WSG and AGR data of the valley species (had we used the threshold of including only species with three or more individuals for the CV calculations, almost no valley species would have been represented in the analysis of these traits). Second, the analysis itself consisted in comparing pairwise between species guilds via Mann-Whitney (non-parametric) tests in which each CV, one per species, was considered a replicate (an independent statistical observation). Mann-Whitney was used because CV's were often not normally distributed, i.e., this statistical test compared the medians, not averages, of the distributions of species-level CV's. *P* values of the six possible pairwise comparisons were Bonferroni-corrected; corrected and uncorrected *P* values for each pairwise comparison are reported in the present study only if uncorrected $P \leq 0.10$.

CORRELATIONS AMONG TRAITS

Although it was not the aim of the present study to explore in detail how traits vary concomitantly with each other (e.g., if the aim had been to detect trade-offs), to support some aspects of the Discussion, we nonetheless created a matrix of Pearson correlations among all traits using data from 43 species whose traits were analyzed. For every trait, one value per species was used as an independent statistical observation (i.e., N = number of species); this value was the *mean* trait value of all measured individuals in a species. Because *P* values were not corrected for multiple comparisons, we assumed that correlations existed only if $P \leq 0.001$. The statistical program used was SPSS®.

RESULTS

SPECIES GUILDS OF HABITAT ASSOCIATION

To test for habitat association (or non-association), we focused the analyses on the 80 most common species out of the 195 found in the sample of 30 grid quadrats in the YFDP (see Chapter 2). The 80 most common species were defined as those with at least five individuals in all *and* occurring in at least two quadrats.

Tables 3.1 and 3.2 show the 66 species classified as ridge species (R, 18 species), valley species (V, 13 species), widespread species with habitat association (W, four species) and true generalist species (G, 31 species), according to the classification criteria used (see Methods). Fourteen species (not shown) remained unclassified because they did not show a clear signal of habitat association (or non-association) according to our criteria. To counteract the liberal criteria of this classification process (probability threshold of 0.10; see Methods), we used the following conservative criterion to select the species for functional trait analyses: both statistical tests of habitat association had to agree in order for a species to be selected (see Methods). This approach resulted in 43 species (of the 66) actually selected for the functional trait analyses, and which included: 14 R species (out of 18; Table 3.1), five V species (out of 13; Table 3.1), four W species (out of four; Table 3.1), and 20 G species (out of 31; Table 3.2). Had we used more strict (very conservative) criteria to select species with habitat association for analyses—or, for that matter, to classify habitat association—only a handful of species would have been selected; for example, using the criteria that P must be ≤ 0.05 in *both* statistical tests, and that frequency must be <6 valley quadrats (for R species) or <8 ridge quadrats (for V species), only nine R species and two V species would be selected (R species [acronyms]: *FORaff*, *ADEimp*, *DIOuca*, *HYLcom*, *SALmul*, *STRram*, *TETnit*, *MOUacu*, and *PETmay*; V species: *MANver* and *DOLden*; Table 3.1). The four species classified as W (*CLIpoz* and *CUEkap* with ridge association; *COMlax* and *MACcus* with valley association; Table 3.1) are among the five most common species in the YFDP forest (the other most common is *PETmay*, clearly an R species)—these four species are very widespread but anyhow seem to “prefer” (be relatively more abundant in) one habitat over the other.

Although we did not conduct a formal analysis of habitat association at the family level, in Tables 3.1 and 3.2 some trends were apparent for the most diverse families (recall though that the analyses were conducted in a subsample of the 195 species). Asteraceae, Bignoniaceae, Dilleniaceae and Fabaceae had species represented in at least three of the guilds (Fabaceae in actually all of them). Other diverse families that were also well represented across the topographic gradient, with species represented in two guilds including the generalist guild, were Sapindaceae, Connaraceae, Malpighiaceae and Menispermaceae; the latter three did not have valley species as such, but only generalist or ridge species. The families Convolvulaceae (with three species) and Dichapetalaceae (with two species) appeared only among the generalist guild. Perhaps the most striking pattern, however, is that of the Hippocrateaceae—in this family, which is among the most speciose in the YFDP (10 species; Chapter 2), almost all species were restricted to ridge habitat, and there were no true valley species.

QUESTION 1: DO SPECIES GUILDS DIFFER IN THEIR TRAIT VALUES?

Descriptive statistics for each of the 43 species whose traits were analyzed are shown in Appendices 3.1 and 3.2.

When *P*'s of the Mann-Whitney pairwise comparisons between species guilds were applied a Bonferroni correction, the only trait that still showed significant pairwise differences between species guilds was mass-based phosphorus concentration, P(%) (Figure 3.2A). If uncorrected *P*'s were used, only a few comparisons of median trait values between two species guilds would be significantly different ($P_{\text{uncorrected}} \leq 0.05$), while another handful of comparisons would show a trend toward a significant difference ($0.05 < P_{\text{uncorrected}} \leq 0.10$) (Figures 3.1A, 3.2A, and 3.3A). The comparisons that showed at least a trend to be significantly different (particularly if uncorrected *P* values were used) appeared in the SLA, LDMC, L:W, C(%), P(%), C:N, δ^{15}N and WSG traits, and were:

(1) R species had lower median SLA than V species (uncorrected/corrected *P*=0.06/0.35; Figure 3.1A) and G species (*P*=0.08/0.50). In addition, V species had higher median SLA than W species (*P*=0.02/0.12; Figure 3.1A).

(2) R species had higher median LDMC than G species (*P*=0.03/0.19; Figure 3.1A);

(3) R species had higher median L:W than G species (*P*=0.05/0.31; Figure 3.1A);

(4) V species had higher median C(%) than G species (*P*=0.06/0.37; Figure 3.2A);

(5) R species had significantly lower median P(%) than V species (*P*=0.005/0.03; Figure 3.2A) and G species (*P*=0.003/0.02; Figure 3.2A). In addition, V species had higher median P(%) than W species (*P*=0.07/0.40; Figure 3.2A).

(6) R species had higher median C:N than G species (*P*=0.06/0.34; Figure 3.2A);

(7) G species had higher median δ^{15}N than W species (*P*=0.02/0.13; Figure 3.2A); and,

(8) V species had lower median WSG than R species (*P*=0.06/0.38; Figure 3.3A) and W species (*P*=0.03/0.18; Figure 3.3A).

QUESTION 2: DO SPECIES GUILDS DIFFER IN THEIR INTRA-SPECIFIC (BETWEEN INDIVIDUALS) TRAIT VARIATION (PHENOTYPIC PLASTICITY)?

Basically, species guilds did not differ in their inter-specific *median* of intra-specific trait variation. No difference was significant after probabilities were Bonferroni-corrected. The comparisons that showed at least a trend to be significantly different (particularly if uncorrected *P* values were used) appeared in the LDMC, LT, C:N, δ^{13}C, $AGR_{1.0–1.5\ cm}$ and $AGR_{all\ lianas}$ traits, and were:

(1) G species had higher LDMC median intra-specific variation than R species (uncorrected/corrected P=0.03/0.17; Figure 3.1B);

(2) V species had higher LT median intra-specific variation than R species (P=0.05/0.28; Figure 3.1B) and W species (P=0.07/0.40; Figure 3.1B);

(3) R species had higher C:N median intra-specific variation than V species (P=0.06/0.35; Figure 3.2B);

(4) V species had higher δ^{13}C median intra-specific variation than G species (P=0.09/0.56; Figure 3.2B); and,

(5) W species had higher $AGR_{1.0–1.5\ cm}$ median intra-specific variation than R and G species (P=0.05/0.32 and P=0.08/0.46, respectively; Figure 3.3B). W species also had higher $AGR_{all\ lianas}$ median intra-specific variation than G species (P=0.08/0.49; Figure 3.3B).

CORRELATIONS AMONG TRAITS

Appendix 6 shows the Pearson correlation matrix using trait data of the 43 species selected for trait analyses (AGR's of the different diameter classes were excluded from the correlation matrix because these are not independent of $AGR_{all\ lianas}$). Because P values were not adjusted for multiple comparisons (e.g. by using a Bonferroni correction), we consider here that correlations existed only if $P\leq0.001$. Thus, positive correlations included SLA vs. N (r=0.50), N vs. P (r=0.50), N:P vs. C (r=0.58), N:P vs. N (r=0.58), while negative correlations included SLA vs. LDMC (r=−0.51), C:N vs. SLA (r=−0.53), C:N vs. N (r=−0.82), and C:N vs. P (r=−0.55).

DISCUSSION

ASSOCIATION (OR NON-ASSOCIATION) OF LIANA SPECIES TO TOPOGRAPHIC HABITATS

Criteria to define species habitat association are not written in stone

We have statistically identified species of lianas in the YFDP that (1) show a clear signal of habitat association to either ridge (18 "R" species; Table 3.1) or valley (13 "V" species; Table 3.1), (2) show no habitat association at all, i.e. they are true generalists (31 "G" species; Table 3.2), and (3) have a widespread distribution but yet also show association to either ridge (two "WR" species) or valley (two "WV" species) (Table 3.1). However, the criteria used to define species membership to these guilds were relatively arbitrary and represented a compromise between liberal (non-strict) and conservative approaches, as we discuss below.

First, to avoid drawing conclusions on species with very low number of individuals sampled, the analyses were conducted with the 80 most common species of lianas only (out of 195 species in all; see Appendix 5 of Chapter 2). This conservative approach does not imply that rare species—which represent almost 60% of the species in the YFDP liana community and which were defined as those with total abundance ≤4 individuals or total frequency = 1 quadrat—cannot be associated to a given habitat. It merely means that to decide whether a rare species is a specialist or a generalist, a larger sample size (both in area and individuals) would be needed. Out of the 80 species, 14 (17.5%) remained unclassified into the species guilds because they represented "transitional" species. These "transitional" species were neither G nor R/V species, but had a tendency to occur more abundantly in either habitat.

Second, we have defined habitat association (or non-association) of single species by using relative abundance. There is not, however, a single definition of relative abundance or, for that matter, of habitat association. For the habitat randomization tests, we used two definitions of relative abundance for each species: overall relative abundance and mean relative abundance per quadrat (see Methods). However, these did not always give the same conclusion: one species could be classified as having habitat association according to one definition, but not according to the other (Tables 3.1 and 3.2). Yet another alternative to define habitat association would be to use presence/absence data of a species in a quadrat (frequency data) and discard the per quadrat abundance data of a species; such approach may balance the importance of rare vs. common species by giving widespread but locally rare species as much weight as widespread but locally abundant species. It would be interesting to conduct such analysis using the whole dataset of 195 species to see if results agree with those conducted here using only the 80 most common species.

Third, instead of using the classic threshold *P* value of 0.05 to decide if a species showed significant association to a habitat, we used a liberal *P* threshold of 0.10. This increased the probability for a type I error—i.e., classifying a species as being associated to a habitat, when in reality it does not—but reduced the probability of a type II error—i.e., not classifying a species as being associated to a habitat, when in reality it does. The 0.30–0.70 probability range used to define a true generalist, which selected species more or less evenly distributed in both habitats, could be also considered a liberal choice (a stricter criterion would be to select a range closer to 0.50). Among the 31 species with habitat association (Table 3.1), 11 species could be considered real habitat "specialists" because they had test 1 and test 2 probabilities ≤ 0.05. All except one of these 11 species were also among the most dominant species in the YFDP (Table 3.1), so clearly these species had very low probabilities because of their large sample size (number of individuals). As explained in Methods, to somehow counteract the liberal 0.10 *P* threshold, we decided to analyze the traits of only those species (out of the 66 classified; Tables 3.1 and 3.2) for which the conclusions of both randomization tests agreed. This approach left us with 43 species (shadowed in Tables 3.1 and 3.2), from which 14 were R species but only five were V species. The trait expression of these 43 species are discussed in another section below (discussion on research question 1).

There were few V and W species, while G and R species were numerous

Why most species were G or R species, and why was it rare to be a V or W species? We think this pattern in the number of constituent species in each species guild is giving two clear messages, evolutionarily speaking. First, the appearance of specialized species of lianas in environments subjected to periodic soil water saturation and associated low soil O_2 concentration (Tange, Yagi, and Sasaki 1998, Silver, Lugo, and Keller 1999, Jirka et al. 2007), such as the valley in our study, seems a rare evolutionary event—although nutrient availability might be actually higher in the valley than in the ridge (by accumulation of nutrients via water-mediated erosion). Second, at the opposite extreme of being a true specialist, it seems also hard to evolve as a widespread and very dominant species (W species) probably because evolving the traits necessary to grow well in a variety of environments (not to mention environmental stochasticity) must be difficult—traits indeed cannot be infinitely flexible and so trade-offs must emerge at some point in order for a plant species to persist (“super” plant species don’t exist).

A brief discussion on the relative abundance of the W species (except *Clitoria pozuzoensis*) and of the most common true R species (*Petrea maynensis*) in another study in Yasuní, but which sampled habitats at the forest-type scale (Burnham 2002), can be read in Chapter 2—basically, that study found similar patterns as in our study, in particular with regard to the apparent association of *Machaerium cuspidatum* and *Combretum laxum*, the two most common species in the YFDP, to moister soil conditions in the valley than in the ridge.

Hippocrateaceae species were basically R species, while Fabaceae species appeared in all species guilds

Among the 80 most common species that were subjected to the tests of habitat association, seven were Hippocrateaceae. From these, six could be assigned a habitat association (or non-association): four were classified as R species, one as a WR species (*Cuervea kappleriana*; statistically, really an R species), and one as a G species (*Tontelea fuliginea*, but which had a stronger habitat association trend towards ridge than towards valley) (Tables 3.1 and 3.2). The non-classified species was *Cheiloclinium cognatum*, a species in between an R and a G species. Thus, among the species of Hippocrateaceae analyzed, none were associated to valley habitat, making it the only family, among those with highest species diversity (Chapter 1), with such an unusual pattern. Why do the “hippocrats” find it difficult to thrive in valley? To answer this question, field experiments in which eco-physiological measurements are monitored must be designed (e.g., reciprocal transplant experiments), but in the meantime, our current trait data (Figures 3.1, 3.2 and 3.3) pinpoint a few trends that hint what the underlying eco-physiological mechanisms for the strong ridge association of hippocrats might be. These are discussed in another section below.

In sharp contrast to Hippocrateaceae, the seven species of Fabaceae that entered in the habitat association analyses were spread out in all four species guilds (Tables 3.1 and

3.2). This is not surprising as Fabaceae is indeed one of the most biologically successful angiosperm families, the third most diverse after Asteraceae and Orchidaceae (Stebbins 1981). The innate capacity of most legumes to fix atmospheric nitrogen and the varied climbing mechanisms of legume lianas most probably contribute to the ubiquitousness of this plant family across the whole topographic gradient in the YFDP (along with other characteristic traits; Stevens 2001 onwards).

Habitat association of lianas in other studies

In lowland tropical rainforests, there are not many studies that have evaluated habitat association of lianas at the topographic scale (within the same forest). In Borneo, habitat "associations" of lianas were studied at the forest-type scale in three very distinct forest types—alluvial, sandstone hill, and kerangas—using the same statistical technique as in our study but using only mean relative abundance per quadrat as a definition for relative abundance (DeWalt et al. 2006). In that study, 71.4% of the 42 most common species of lianas analyzed (selected from 107 species) showed habitat association to at least one forest type. On the other hand, we found that only 43.8% of the 80 most common species analyzed (selected from 195 species) showed habitat association to either ridge or valley (Table 3.1). Note, however, that their study and ours did not strictly evaluate the same species distribution phenomenon (ours assessed topographic habitat association, while theirs assessed forest-type habitat association) and did not use the same statistical criterion to define habitat association (ours used a *P* threshold of 0.10 in a one-tailed test, while theirs used a *P* threshold of 0.05 in a two-tailed test). It would be interesting to test, with the same statistical technique used in the present study, if the levels of habitat association of lianas in Yasuní increase when analyzed at the forest-type level. The

Rabinowitz-type rarity analyses (Rabinowitz 1981) of the two landscape-level liana studies of Yasuní (Romero-Saltos, Valencia, and Macía 2001 and Burnham 2002) are a clue to what the result might be. The first study sampled terra firme, floodplain and swamp forests, and found that, among the 83 fully identified species of lianas (diameter ≥2.5 cm) with abundance >1 individual, 53.1% were restricted to one of the three forest types. The second study sampled terra firme and floodplain forests, and found that, among the 191 fully identified species of lianas (diameter ≥1 cm) occurring in at least two of 12 sites sampled, 33.5% were restricted to one of the two forest types. Note that the criteria to exclude a species from the rarity analyses were different in these two studies, although both criteria aimed to exclude the rarest species.

TRAITS VS. TOPOGRAPHIC HABITAT ASSOCIATION: DID HYPOTHESES HOLD?

The first approach to study whether there was any trait signal(s) associated with a guild of species defined by their common habitat association (or non-association) was to compare inter-specific trait medians (not means) among species guilds of the 43 liana species whose traits were analyzed (Figures 3.1A, 3.2A, and 3.3A). We developed two hypotheses to describe what we *a priori* expected (see Introduction), each predicting something different depending on the level of phylogenetic conservatism assumed (phylogenetic conservatism itself was not assessed in the present study; it would require mapping of trait evolution onto phylogenetic “supertrees” of all liana taxa in the community, see e.g., Swenson and Enquist 2007). Data indicate that there is *partial* support for the second hypothesis, which was based on the premise that traits are phylogenetically conserved and which stated that “significant differences will be observed among species guilds only if the composition of families or genera also differed among them". The support is partial because although the composition of families and genera was clearly not the same in the different species guilds (see Tables and Figures), differences were not always observed in all traits analyzed—as the second hypothesis implied—but in just a handful of traits (only seven pairwise comparisons were significant when using uncorrected *P* values; Figures 3.1A, 3.2A, and 3.3A), or just in P concentration if we apply the conservative Bonferroni correction of *P* values (mass-based P(%) was clearly significantly lower in R species than in V and G species; Figure 3.2A).

The second approach to study whether there was any trait signal associated with a guild of species defined by their common habitat association (or non-association) was to compare inter-specific medians of relative intra-specific trait variation—"phenotypic plasticity"—among species guilds of the 43 liana species analyzed (Figures 3.1B, 3.2B, and 3.3B). We developed two hypotheses to describe what we a priori expected (see Introduction), based on the premise that plants should be adapted to the environment(s) where they occur in highest abundance: first, we expected that generalist or widespread species will have higher phenotypic plasticity than specialist species; second, we expected that valley species will have higher phenotypic plasticity than ridge species. Our rationale was that a generalist or widespread species should be able to cope with a variety of (often unpredictable) environments, while a valley species should be able to cope with the intrinsic physical and vegetation-wise heterogeneity that valley environments seem to have in Yasuní, which is far greater than the one observed for ridges (see Introduction, and Chapter 2). Data analyses showed that only three of the 108 possible pairwise comparisons (6 pairwise comparisons × 18 trait comparisons) were significant when using uncorrected *P* values, and none were significant after *P* values were Bonferroni-corrected (Figures 3.1B, 3.2B, and 3.3B). The three pairwise comparisons that were significant when using uncorrected *P* values (LDMC and LT in Figure 3.1, and $\mathrm{AGR}_{1.0\text{-}1.5\ \mathrm{cm}}$ in Figure 3.3) conformed, more or less, to our predictions—but they were only three of the many statistical comparisons made and thus we conclude that there is not really support for either hypothesis in our dataset. This is in accordance to what was observed in a meta-analysis of leaf dry mass per unit area (LMA; Poorter et al. 2009), in which no difference in LMA plasticity was observed between species from wet and dry environments.

TRAITS VS. TOPOGRAPHIC HABITAT ASSOCIATION: BARELY ANY PATTERN?

Are the few observed differences, or lack thereof, giving any meaningful ecological message on the trait-topography relation in lianas in the YFDP? We discuss below a few of the results that might be relevant to this end.

SLA and P trends: potential explanations for the low values among R species

Our data followed the well-known correlations among SLA, LDMC, N concentration and P concentration, although the correlations among these traits were relatively weak ($r \approx 0.35$–0.51, Appendix 6; for a discussion on the functional meaning of these correlations, refer to e.g., Cornelissen et al. 2003, Wright et al. 2005, Westoby and Wright 2006, Poorter et al. 2009). The existence of these correlations assured us that the quality of our data was sufficient, despite the low sample size in nutrient traits with respect to the number of individuals sampled per species (Appendix 4). The interesting aspect of our data are not these well-known correlations but the observation that median SLA and median P concentration among the R species tended to be the lower than V and G species, and that the direction of the differences in the species guilds' pairwise comparisons of these two traits were exactly the same (Figures 3.1A and 3.2A; see Results). Behind these results, there is of course the concerted data trends of several species: low SLA's were measured in three of the four Hippocrateaceae species (all from different genera!) and in the climbing palm *Desmoncus orthacanthos* (Figure 3.1A), while low P concentrations were measured in all four Hippocrateaceae species and the two *Strychnos* (Loganiaceae) species (Figure 3.2A). V species, on the other hand, tended to have higher SLA's and higher P concentrations than R species, although still within the range observed in numerous G species (Figures 3.1A and 3.2A). Therefore, it seems that the species driving the statistically significant, or almost significant, pairwise differences in SLA and P concentration are, for the most part, the several Hippocrateaceae species and the rather few V species.

A recent review on the functional meaning of leaf dry mass per unit leaf area (LMA) (Poorter et al. 2009)—in which data from near 4000 plant species reported in hundreds of studies were synthesized—is useful to interpret the SLA patterns observed in our study because LMA is simply the inverse of SLA. Among the LMA trends emphasized in that review (in *italics* below), we think the following are relevant for the present study:

(1) In general, low LMA (high SLA) has been correlated to relatively high growth rate, in both herbaceous and woody plants. The few V species tended to have higher SLA's than most R species (Figure 3.1A), but the expected accompanying trend of higher AGR in V species was not observed (Figure 3.3A) probably because our AGR estimates come only from two censuses, two-years apart, of a 20×500 m area in the YFDP where valley habitat was barely represented, resulting in very few number of individuals of V species measured (except for *Doliocarpus dentatus*; Figure 3.3A, Appendix 5). Sampling

issues for AGR are further discussed below. In any case, in Chapter 2 we showed that there is a tendency for larger lianas (larger basal area) to occur in valley than on ridge, in particular among the V species *Piptadenia anolidurus* and *Doliocarpus dentatus*, and the WV species *Combretum laxum* and *Machaerium cuspidatum*. Thus, all things considered, we put forward the hypothesis that some species of lianas with a "preference" to thrive in valley habitat get larger in valley than on ridge because of high growth rates associated with low LMA (high SLA), in turn associated with higher leaf N and P concentrations (Appendix 6). V species may be effectively using P obtained from a source that is constantly renewed: the P being washed off from the ridge via downslope water-mediated soil erosion. On the other hand, most R species had low P concentration, perhaps reflecting low P availability in ridge soil. Reliable soil data from the YFDP is not however available at present to confirm these speculations on soil P content in ridge and valley soils (the YFDP soil data published by John et al. 2007 had several problems; J. Dalling, pers. comm., H. Romero-Saltos, pers. obs.).

(2) In general, high LMA (low SLA) means leaves with high total structural carbohydrates (TSC) and lignin (e.g., with more sclerenchyma in cell walls). R species tended to have low SLA's, in particular the Hippocrateaceae species and the climbing palm *Desmoncus orthacanthos* (Figure 3.1A). The dry leaves of these species appear rigid once dried probably because of their high content of TSC and lignin.

(3) In general, in species not adapted to "drought" conditions, LMA increases (SLA decreases) toward either extreme of the soil moisture gradient: the dry extreme and the waterlogging extreme. According to Poorter et al. (2009), this effect of soil moisture on LMA can be explained because leaves under "drought" stress tend to expand slower, so

cells in the fully expanded leaves end up more tightly packed and have even thicker walls. Keep in mind that for land plants not adapted to “drought” conditions, both extremes of the soil moisture gradient represent stressful situations: on the one hand, very low soil water content may surpass the permanent wilting point, while on the other hand, very high soil water content (inundated root system) can greatly reduce root conductance, making shoot and leaves effectively suffer from water stress because they are still under evaporative demand. Of course, these stressful conditions will have more of an impact on leaves developing during the stress period. In the present study, the dry extreme of the soil moisture gradient is not plausible because average monthly rainfall in Yasuní is well above 100 mm. Anyhow, ridge areas in general may have lower soil water content than valley areas, thus making the probably inherent (phylogenetically conserved) high LMA of hippocrats an advantage in ridge habitat. Regarding waterlogging, in our study there is not a signal of decreasing SLA (increasing LMA) among the only species that may have potentially faced waterlogging: the V species. This may be because most of the valley quadrats that we studied in the western half of the YFDP actually have relatively good drainage (indeed, most valleys in Yasuní, interspersed among the hills, are physiographically considered part of *terra firme* forest). LMA of V species may however increase in the individuals of these species growing in the valley area of the eastern half of the YFDP, which certainly has lower drainage than the western side because a few swampy areas have developed there. We will test this hypothesis when lianas in the eastern half of the YFDP are sampled.

(4) From an ecological perspective, low-LMA (high-SLA) species tend to realize a life strategy of fast resource acquisition and growth, while high-LMA (low-SLA) tend to

realize a life strategy of high resource conservation and persistence. This in turn implies that low-LMA species will tend to be better fit under high-resource conditions (productive habitats) whereas high-LMA species will tend to be better fit under adverse growing conditions (e.g., in oligotrophic habitats). In the present study, there was a tendency for V species to have high-SLA (low-LMA), but it was not significantly different from the median SLA observed in G species, although it was still higher than the median SLA of R species (Figure 3.1A). The large variation in SLA values among the G species, together with the limited number of V species found, precludes any hasty conclusion that the valley habitat in the YFDP might be more productive (i.e., that it is a high-resource environment) than the ridge habitat.

WSG: low in V species?

Although WSG was measured in very few individuals of the already small set of V species (0–2 individuals per species; Appendix 5), there is an apparent trend for V species to have relatively low WSG and low LMA (high SLA) than most species in other species guilds (Figures 3.3A and 3.1A). However, probably because of sampling drawbacks in our dataset (see discussion below), V species did not show high AGR (Figure 3.3A) as would be expected from theory (e.g., Swenson and Enquist 2007, Poorter et al. 2009). In any case, the trade-offs between WSG, LMA and GR (growth rate) that hold true for many tree species (particularly pioneer species) seem also supported in our liana dataset, at least partially. The observed trend that larger lianas of the species *Piptadenia anolidurus* and *Doliocarpus dentatus* occur in valley and not in ridge habitat (see Chapter 2) are consistent with the findings of low WSG and low LMA in these two V species (Figures 3.3A and 3.1A).

High phenotypic plasticity in AGR of W liana species?

In the analysis of inter-individual variation, i.e. phenotypic plasticity, the only apparent trend that might be ecologically meaningful is that concerning higher AGR inter-individual variation in the W species (*Clitoria pozuzoensis*, *Cuervea kappleriana*, *Combretum laxum* and *Machaerium cuspidatum*), observed in all diameter categories except that of lianas ≥5.0 cm (Figure 3.3B). This trend could represent a real adaptation of these very dominant species (all of them among the top five most abundant; the fifth being *Petrea maynensis*, a ridge specialist) to grow in many types of environments and thus explain, at least partially, why they have become so dominant. However, on the other hand, it could also simply be a sampling artifact: because there were more individuals sampled of these species, more different microhabitats affected the growth of the individuals positively or negatively, and thus the variation in AGR became higher. Given their high abundance, it is possible that W species, which statistically are really either R or V species (Table 3.1), appeared outside the habitat they "prefer" mainly as a result of mass effects (Shmida and Wilson 1985).

In general, the main pattern was the absence of differential patterns

Although we have thoroughly discussed the potential meaning of SLA (1/LMA) differential patterns for the apparent success of a handful of species in either ridge or valley, by no means SLA by itself can explain the performance of lianas in the YFDP topographic habitats. SLA is really part of a trait complex, which for the YFDP lianas we have just started to understand. The few statistical differences that we hardly recovered from the data get lost among the soaring message of our data: most traits did not really show any meaningful difference among species guilds of habitat association (or non-association). If most of the measured traits in our study do not seem to explain much about why certain species of lianas are associated to one topographic habitat over the other, or are not associated to any habitat at all, what can then explain this phenomenon? This is a question that must be tackled from different angles.

First, it is clear that our dataset at present suffers from several drawbacks which may be hindering any discernable relation between traits and species distributions. A particular problem with the current data is the low number of replicates (individuals sampled) in the C, N, P, WSG and AGR data (see Appendices). Further, AGR data comes only from two censuses, two-years apart, conducted in a 20×500 m transect that overlapped little with the 30 grid quadrats from which the leaf data was obtained (see Methods), and WSG was measured entirely from individuals outside the YFDP wherever they occurred, with no systematic sampling of ridge and valley habitats (see Methods). These sampling incongruities in our trait data must be solved in the future in order to obtain more conclusive patterns, if any. Yet, in dense and megadiverse tropical rainforests, such as Yasuní, to sample trait data at the individual level is a daunting task—in the 50-ha YFDP, among the woody plants with diameter ≥1 cm, there are approximately 300,000 trees (≈1100 species; R. Valencia and C. Hernández, pers. comm.) and an estimate of 70,000 lianas (≈200 species; see Chapter 2).

Second, there is certain doubt that the low number of species in the V guild represents a large enough sample size (number of species) to draw any conclusion. Our methodological approach to select species for trait analyses reduced the sample size of most species guilds, in particular the V species guild. The doubt thus arises of whether the trait "patterns" observed for the 43 species whose traits were analyzed will also hold if all 66 species from Tables 3.1 and 3.2 were analyzed, or if habitat association were to be evaluated for all 195 species registered in the 30 grid quadrats. We think, however, that re-analyses of the relation between liana traits and species guilds of habitat association should wait until more complete trait data is available from the YFDP and/or when lianas in the whole 50 hectares are censused. This will enable assessment of habitat association with other statistical techniques such as torus-translation (Harms et al. 2001) and a detailed evaluation of how individuals in the same species can change their trait values when faced with particular environments (we could have analyzed this in the present study, but did not because we think traits from not enough individuals were sampled to answer this question). Current available liana data from the YFDP come from an area of only two hectares in the western half of YFDP "dissected" into 25 non-contiguous 20×20 m quadrats and 25 contiguous 20×20 m quadrats (a 20×500 m transect)—they still just represent a broad image of what is happening in the whole 50-ha YFDP.

Third, the search for biological mechanisms that can explain the observed distribution of liana species in the YFDP can be advanced by altogether different approaches. For example, in a companion paper we explore the occurrence of different "whole-plant growth strategies" of lianas—defined by climbing mechanisms, presence or absence of creeping stems, and presence or absence of near-ground large branches—in the ridge and valley topographic habitats of the YFDP. Another approach that can advance our understanding of liana-environment relations is to compare traits of different liana species but control for their different evolutionary (phylogenetic) background—this can be done either statistically (e.g., Swenson and Enquist 2007), or by simply limiting the comparisons to species within the same genus or family (e.g., Cai et al. 2007). Such phylogenetic independent contrasts will allow to separate the effect of genetics from the effect of the environment on species' trait expression. Yet another comprehensive step would be to compare not only among liana species, but between growth forms: trees vs. lianas. We suspect that if such analyses were to be conducted with all ~1100 species of trees and ~200 species of lianas of the YFDP forest, leaf trait differences between trees and lianas that share a common phylogenetic background (assuming they exist) may well be as large as the differences among different genera or families (see Wright et al. 2005), effectively blurring any consistent difference in leaf traits between these two growth forms, which several authors have reported for other tropical forests, but often based on a limited sampling of the community (e.g., Kazda and Salzer 2000, Cai et al. 2009). Finally, trait- and phylogenetically-based tests of community assembly of the liana community at different spatial scales in the YFDP may shed light on the relative importance of the underlying evolutionary or ecological processes that shape the assembly of the community, such as niche differentiation, habitat filtering or stochasticity (see e.g., Kraft et al. 2007). Such analyses have the advantage that species are not classified into "functional groups"—or, for that matter, into "species guilds of habitat association" as in the present study—but are instead understood as distinct entities whose ecological strategies are described along continuum axes. In the YFDP, this type of analyses have already been conducted with the tree community (Kraft, Valencia, and Ackerly 2008, Kraft and Ackerly 2010) and have found that both habitat associations and niche differentiation processes shape the tree species co-occurrence patterns: a niche differentiation signal was found to be stronger at small spatial scales (certainly an effect of competition) while a habitat filtering signal was found at all spatial scales. A study of this nature but with lianas will represent the perfect opportunity to use the unpublished trait data of the approximately 200 species of lianas from the YFDP that has been already collected (although for many traits and species, the sample size is still limited)—after all, only a third of the liana species from which we have trait data appear in the TRY global database of plant functional traits (http://www.try-db.org).

CONCLUSION

In conclusion, although the few species guilds' pairwise differences observed shed some light on the underlying ecophysiological strategies that may explain the distribution of *some* liana species in the YFDP, the most striking pattern was really the absence of differential patterns for most traits among the species guilds of habitat association. Therefore, other ecological processes unrelated with trait expression, such as dispersal assembly, also probably influence the distribution of lianas in the ridge and valley habitats of the Yasuní Forest Dynamics Plot.

TABLES

Table 3.1. Liana species showing habitat association according to two kinds of randomization tests of 17 ridge quadrats and 13 valley quadrats in the YFDP, using abundance data of the 80 most common species (those with abundance ≥5 individuals and frequency ≥2 quadrats), from the 195 species registered in total (see chapter 1). As response variable, test 1 used overall relative abundance, while test 2 used mean relative abundance per quadrat. The tests gave Monte-Carlo probabilities (*P*) that served to classify a species' habitat association (or non-association). A species was classified (CLASS.) as a ridge species (R) if $P_{\text{ridge}} \leq 0.10$ and frequency in the valley habitat was <6 quadrats (< ~50% of the valley quadrats). A species was classified as a valley species (V) if $P_{\text{valley}} \leq 0.10$ and frequency in the ridge habitat was <8 quadrats (<~50% of the ridge quadrats). If, for a given habitat, $P \leq 0.10$, but frequency in the other habitat was ≥6 valley quadrats or ≥8 ridge quadrats, the species was classified as a widespread species with habitat association (W, with two subcategories: WR, with ridge association, and WV, with valley association). *P* and frequency values that complied with these selection criteria are shown in bold, but only those species that complied with the criteria in both randomization tests, indicated by **FT** and with its habitat association shadowed, were included in the functional traits analyses (conservative approach). Species that were among the 31 most dominant species (see Chapter 2) are indicated by **D**. Species acronyms (in **bold**) were formed by the first three letters of the genus (in UPPERCASE) and the first three letters of the epithet. Names within quotation marks are morphospecies. Family acronyms (in parentheses) were formed by a three-letter code. Species are ordered by family.

		P_{ridge}		P_{valley}					
FAMILY ***Species***	**CLASS.**	**TEST 1**	**TEST 2**	**TEST 1**	**TEST 2**	**RIDGE ABUND.**	**VALLEY ABUND.**	**RIDGE FREQ.**	**VALLEY FREQ.**
APOCYNACEAE (APO)									
***FOR**steronia **aco**uci*	R	**0.06**	0.17	0.93	0.83	9	2	6	**2**
***FOR**steronia **aff**inis* **FT,D**	R	**0.01**	**0.03**	0.99	0.97	13	1	7	**1**
ARECACEAE (ARE)									
***DES**moncus **ort**hacanthos* **FT**	R	**0.08**	**0.09**	0.93	0.95	6	1	4	**1**
ASTERACEAE (AST)									
***MIK**ania **hoo**keriana*	R	**0.08**	0.12	0.92	0.90	5	1	5	**1**
***MIK**ania **lei**ostachya* **FT**	V	0.96	0.98	**0.04**	**0.06**	1	6	**1**	4
BIGNONIACEAE (BIG)									
***ADE**nocalymna **imp**ressum* **FT,D**	R	**0.03**	**0.04**	1.00	1.00	24	0	5	**0**
***CAL**lichlamys **lat**ifolia* **D**	V	0.79	0.93	0.22	**0.07**	24	29	**5**	8
***FRI**dericia **sch**ummaniana* **D**	V	0.89	0.92	0.14	**0.08**	6	11	**4**	5
***MAN**soa **ver**rucifera* **FT,D**	V	1.00	1.00	**0.02**	**0.01**	0	11	**0**	5
***TAN**aecium **aff**ine* **FT**	V	1.00	1.00	**0.04**	**0.08**	0	5	**0**	3
BORAGINACEAE (BOR)									
***TOU**rnefortia **cor**iacea*	V	0.89	0.98	0.12	**0.07**	1	4	**1**	3
COMBRETACEAE (COM)									
***COM**bretum **lax**um* **FT,D**	WV	1.00	1.00	**0.01**	**0.01**	46	95	**8**	12
CONNARACEAE (CNN)									
***CON**narus **pun**ctatus*	R	**0.03**	0.18	1.00	1.00	5	0	3	**0**
DILLENIACEAE (DIL)									
***DOL**iocarpus **den**tatus* **FT,D**	V	0.99	1.00	**0.01**	**0.004**	2	10	**2**	7
***TET**racera **vol**ubilis*	R	**0.04**	0.17	1.00	1.00	7	0	3	**0**
FABACEAE (FAB)									
***BAU**hinia **rut**ilans* **D**	V	0.94	0.87	**0.07**	0.13	16	36	**7**	9
***CLI**toria **poz**uzoensis* **FT,D**	WR	**0.05**	**0.05**	0.95	0.95	53	29	15	**11**
***DIO**clea **uca**yalina* **FT,D**	R	**0.03**	**0.01**	0.97	0.99	12	2	8	**2**
***MAC**haerium **cus**pidatum* **FT,D**	WV	0.99	0.98	**0.02**	**0.02**	50	85	**16**	12
***PIP**tadenia **ano**lidurus* **FT,D**	V	1.00	1.00	**0.04**	**0.08**	0	11	**0**	3
HIPPOCRATEACEAE (HIP)									
***ANT**hodon **dec**ussatum* **FT**	R	**0.04**	**0.08**	1.00	1.00	6	0	4	**0**
***CUE**rvea **kap**pleriana* **FT,D**	WR	**0.01**	**0.003**	1.00	1.00	75	21	16	**6**
***HYL**enaea **com**osa* **FT,D**	R	**0**	**0.001**	1.00	1.00	15	2	10	**2**
***PER**itassa **pru**inosa* **FT,D**	R	**0.10**	**0.06**	0.90	0.94	13	4	7	**4**
***SAL**acia **mul**tiflora* **FT,D**	R	**0.05**	**0.03**	0.96	0.97	20	6	10	**5**
LOGANIACEAE (LOG)									
***STR**ychnos **mit**scherlichii* **FT**	R	**0.07**	**0.05**	0.94	0.96	5	1	4	**1**
***STR**ychnos **ram**entifera* **FT**	R	**0.03**	**0.02**	0.97	0.99	7	1	6	**1**
MALPIGHIACEAE (MLP)									
***TET**rapterys **nit**ida* **FT,D**	R	**0.03**	**0.04**	0.97	0.97	17	1	5	**1**
MENISPERMACEAE (MEN)									
***CUR**area **tec**unarum* **FT**	R	**0.04**	**0.09**	0.96	0.91	10	2	7	**2**
POLYGALACEAE (PGA)									
***MOU**tabea **acu**leata* **FT,D**	R	**0.01**	**0.02**	1.00	1.00	11	0	6	**0**
POLYGONACEAE (PGO)									
***COC**coloba **exc**elsa*	V	0.95	0.90	**0.06**	0.12	1	4	**1**	4
SAPINDACEAE (SPI)									
***PAU**llinia* "**cor**teza"	V	0.92	0.88	**0.08**	0.16	1	6	**1**	3
***PAU**llinia **das**ystachya* **D**	V	0.93	0.87	**0.07**	0.13	3	9	**3**	5
***PAU**llinia **ing**ifolia* **D**	V	0.92	0.88	**0.08**	0.12	4	9	**4**	5
VERBENACEAE (VER)									
***PET**rea **may**nensis* **FT,D**	R	**0.01**	**0.004**	0.98	1.00	97	30	15	**4**

Table 3.2. Liana species showing NO habitat association to either ridge or valley according to two kinds of randomization tests of 17 ridge quadrats and 13 valley quadrats in the YFDP, using abundance data of the 80 most common species (those with abundance ≥5 individuals and frequency ≥2 quadrats), from the 195 species registered in total (see chapter 1). As response variable, test 1 used overall relative abundance, while test 2 used mean relative abundance per quadrat. The tests gave Monte-Carlo probabilities (*P*) that served to classify a species' habitat association (or non-association). A species was classified (CLASS.) as a true generalist (G) if $0.3 \leq P \leq 0.7$ (i.e., it was more or less equally represented in both habitats), independent of its frequency in either habitat. *P* values that complied with these selection criteria are shown in **bold**, but only those species that complied with the criteria in both randomization tests, indicated by **FT** and with its habitat association shadowed, were included in the functional traits analyses (conservative approach). Species that were among the 31 most dominant species (see Chapter 2) are indicated by **D**. Species acronyms (in **bold**) were formed by the first three letters of the genus (in UPPERCASE) and the first three letters of the epithet. Names within quotation marks are morphospecies. Family acronyms (in parentheses) were formed by a three-letter code. Species are ordered by family.

		P_{ridge}		**P_{valley}**					
FAMILY ***Species***	**CLASS.**	**TEST 1**	**TEST 2**	**TEST 1**	**TEST 2**	**RIDGE ABUND.**	**VALLEY ABUND.**	**RIDGE FREQ.**	**VALLEY FREQ.**
ASTERACEAE (AST)									
***PIP**tocarpha **lec**hleri*	G	**0.30**	**0.33**	**0.70**	0.82	5	1	2	1
BIGNONIACEAE (BIG)									
***BIG**nonia **aeq**uinoctialis* **FT,D**	G	**0.46**	**0.46**	**0.54**	**0.57**	10	7	3	2
***STI**zophyllum **rip**arium* **FT**	G	**0.62**	**0.38**	**0.38**	**0.63**	5	5	4	3
BORAGINACEAE (BOR)									
***TOU**rnefortia **bic**olor* **FT**	G	**0.41**	**0.39**	**0.59**	**0.64**	3	2	3	2
CONNARACEAE (CNN)									
***CON**narus **pat**risii* **FT**	G	**0.32**	**0.32**	**0.68**	**0.70**	7	3	4	2
***ROU**rea **ama**zonica* **FT**	G	**0.58**	**0.46**	**0.43**	**0.56**	4	4	3	3
***ROU**rea **cam**ptoneura* **FT**	G	**0.44**	**0.38**	**0.57**	**0.63**	6	4	5	3
CONVOLVULACEAE (CNV)									
***DIC**ranostyles **hol**ostyla*	G	**0.40**	0.25	**0.60**	0.76	7	5	7	3
***MAR**ipa **pau**ciflora*	G	0.75	**0.55**	0.25	**0.49**	2	3	2	3
***MAR**ipa **per**uviana* **FT**	G	**0.67**	**0.68**	**0.33**	**0.33**	5	6	4	3
DICHAPETALACEAE (DIC)									
***DIC**hapetalum **fro**esii* **FT**	G	**0.41**	**0.70**	**0.59**	**0.45**	3	2	2	1
***DIC**hapetalum **spr**uceanum* **FT,D**	G	**0.69**	**0.51**	**0.32**	**0.49**	7	8	3	5
DILLENIACEAE (DIL)									
***TET**racera **wil**ldenowiana* **FT**	G	**0.33**	**0.47**	**0.66**	**0.54**	10	5	4	4
DIOSCOREACEAE (DIO)									
***DIO**scorea* "**ray**amarilla"	G	**0.31**	**0.32**	**0.69**	0.71	8	3	4	1
FABACEAE (FAB)									
***BAU**hinia **gui**anensis* **D**	G	0.19	**0.34**	0.81	**0.66**	29	13	10	6
***BAU**hinia* "**pel**uda" **FT**	G	**0.63**	**0.65**	**0.38**	**0.36**	6	6	4	3
HIPPOCRATEACEAE (HIP)									
***TON**telea **ful**iginea* **D**	G	**0.33**	0.20	**0.67**	0.80	17	10	9	3
ICACINACEAE (ICA)									
***LER**etia **cor**data* **FT,D**	G	**0.61**	**0.59**	**0.39**	**0.41**	11	10	7	6
MALPIGHIACEAE (MLP)									
***ECT**opopterys **soe**jartoi* **FT**	G	**0.40**	**0.41**	**0.60**	**0.64**	6	3	3	2
***HIR**aea **val**ida* **FT**	G	**0.37**	**0.47**	**0.63**	**0.67**	5	2	2	1
***MAS**cagnia **dis**similis* **FT**	G	**0.69**	**0.70**	**0.31**	**0.37**	2	3	2	2
MENISPERMACEAE (MEN)									
***ABU**ta **sol**imoesensis*	G	0.74	0.71	0.26	**0.39**	3	4	1	2
***SCI**adotenia **tox**ifera* **FT**	G	**0.59**	**0.66**	**0.41**	**0.36**	4	4	3	2
PASSIFLORACEAE (PAS)									
***PAS**siflora **spi**nosa*	G	0.28	**0.44**	0.72	**0.58**	4	2	4	2
RHAMNACEAE (RHA)									
***GOU**ania **lup**uloides*	G	0.73	0.81	**0.28**	**0.44**	1	5	1	1
SAPINDACEAE (SPI)									
***PAU**llinia **bra**cteosa* **D**	G	**0.41**	0.25	**0.59**	0.75	17	12	9	6
***PAU**llinia **obo**vata* **FT**	G	**0.43**	**0.56**	**0.57**	**0.44**	7	5	4	4
***SER**jania **pyr**amidata* **FT**	G	**0.68**	**0.70**	**0.32**	**0.31**	4	5	2	4
***THI**nouia **obl**iqua* **FT**	G	**0.59**	**0.50**	**0.42**	**0.53**	5	6	4	1
SOLANACEAE (SOL)									
***SOL**anum **bar**beyanum* **FT**	G	**0.65**	**0.70**	**0.35**	**0.44**	2	5	2	1
VERBENACEAE (VER)									
***AEG**iphila* "**exe**lata"	G	0.83	**0.64**	0.17	**0.38**	2	4	1	4

FIGURES

Figure 3.1. Intra- and inter-specific averages and variation of specific leaf area (SLA), leaf dry matter content (LDMC), leaf lamina thickness (LT), leaf length to width ratio (L:W; incl. petiole), and individual-level leaf size range (LSR) of the 43 liana species included in the functional traits analyses. Species were classified in the following species guilds on the basis of their habitat association (or non-association): *ridge* species (R), *valley* species (V), *true generalist* species (G), and *widespread* species *with habitat association* (W, with two subcategories: WR, with ridge association, and WV, with valley association). Variation is expressed as mean ± 1 standard deviation (SD). To compare among species guilds pairwise, non-parametric Mann-Whitney tests were used (i.e., medians were compared, but mean ± 1 SD error bars, not boxplots, were used for the figure to simplify appearance and to make the calculation of the coefficients of variation in **(B)** clearer). The uncorrected/Bonferroni-corrected *P* values of the pairwise comparisons are shown only if uncorrected $P \leq 0.10$. **(A) (research question 1)** For each species (filled circles with thin error bars), intra-specific (between individuals) mean ± intra-specific variation (± 1 SD); and, for each species guild (open circles with thick error bars), inter-specific mean (mean of species mean values) ± inter-specific variation (± 1 SD). Mean and SD for each species, in addition to range (minimum and maximum values) and sample size (*N*), are reported in Appendix 4. Species are ordered by family (for acronyms meaning, see Tables or Appendices). **(B) (research question 2)** For each species guild (open circles with thick error bars), mean intra-specific (between individuals) variation ± inter-specific variation, expressed as coefficients of variation (CV) to make the intra-specific variation comparable across different species. Because a coefficient of variation obviously cannot be calculated for species with $N=1$ individual sampled, only species with $N \geq 2$ individuals sampled were considered to test if intra-specific variation was different among species guilds.

Figure 3.1

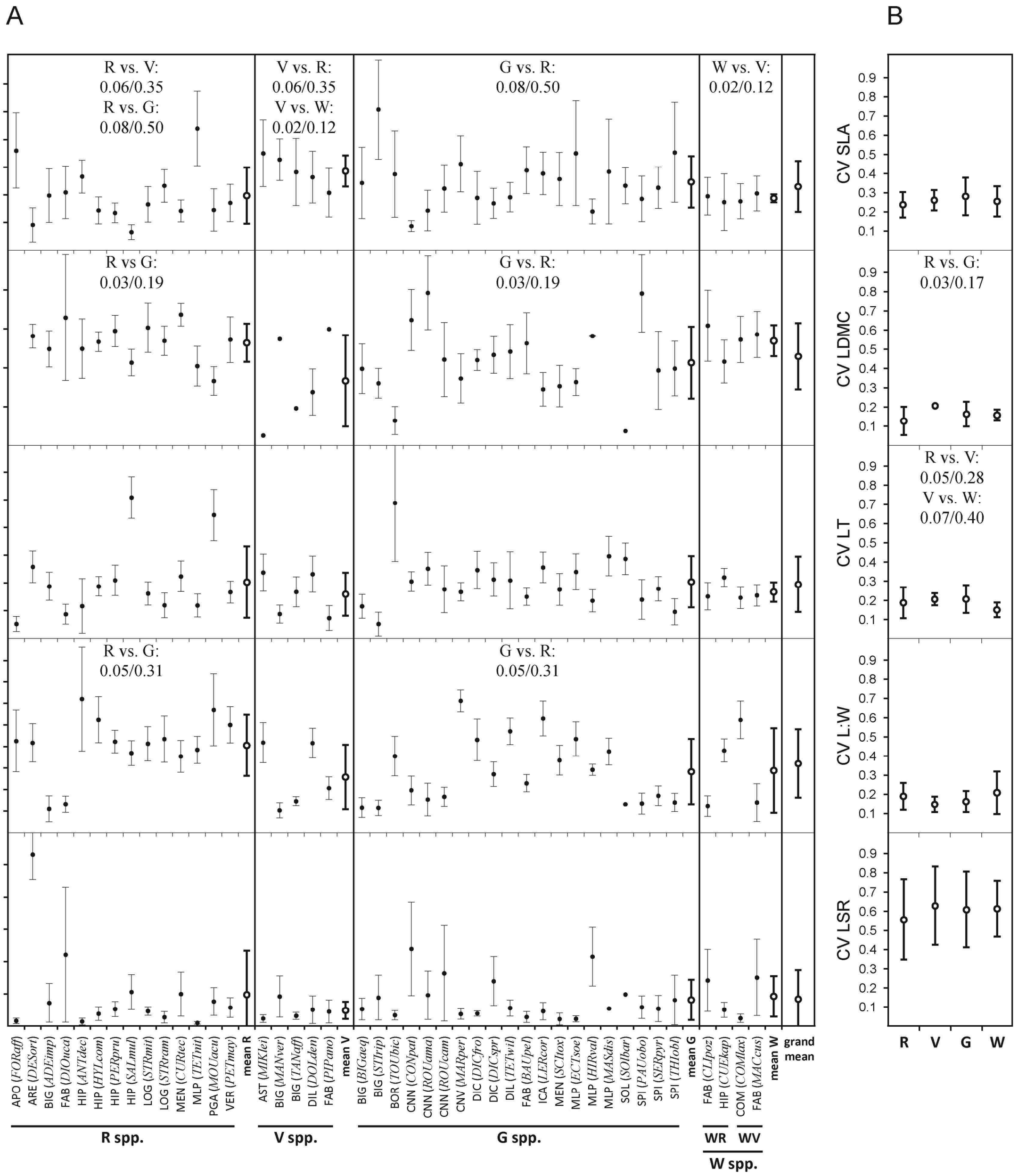

A
B
SLA (mm²/mg)
LDMC (mg/g)
LT (mm)
L:W
LSR (cm²)
R vs. V:
0.06/0.35
R vs. G:
0.08/0.50
V vs. R:
0.06/0.35
V vs. W:
0.02/0.12
G vs. R:
0.08/0.50
W vs. V:
0.02/0.12
R vs G:
0.03/0.19
G vs. R:
0.03/0.19
R vs. G:
0.05/0.31
G vs. R:
0.05/0.31
CV SLA
CV LDMC
R vs. G:
0.03/0.17
CV LT
R vs. V:
0.05/0.28
V vs. W:
0.07/0.40
CV L:W
CV LSR
APO (FORaff)
ARE (DESort)
BIG (ADEimp)
FAB (DIOuca)
HIP (ANTdec)
HIP (HYLcom)
HIP (PERpru)
HIP (SALmul)
LOG (STRmit)
LOG (STRram)
MEN (CURtec)
MLP (TETnit)
PGA (MOUacu)
VER (PETmay)
mean R
AST (MIKlei)
BIG (MANver)
BIG (TANaff)
DIL (DOLden)
FAB (PIPano)
mean V
BIG (BIGaeq)
BIG (STTrip)
BOR (TOUbic)
CNN (CONpat)
CNN (ROUama)
CNN (ROUcam)
CNV (MARper)
DIC (DICfro)
DIC (DICspr)
DIL (TETwil)
FAB (BAUpel)
ICA (LERcor)
MEN (SCItox)
MLP (ECTsoe)
MLP (HIRval)
MLP (MASdis)
SOL (SOlbar)
SPI (PAUobo)
SPI (SERpyr)
SPI (THIobl)
mean G
FAB (CLIpoz)
HIP (CUEkap)
COM (COMlax)
FAB (MACcus)
mean W
grand mean
R spp.
V spp.
G spp.
WR
WV
W spp.
R
V
G
W

Figure 3.2. Intra- and inter-specific average and variation of leaf carbon (C) concentration (%), leaf nitrogen (N) concentration (%), leaf phosphorus (P) concentration (%), leaf C:N ratio, leaf N:P ratio, leaf $\delta^{13}C$, and leaf $\delta^{15}N$ of the 43 liana species included in the functional traits analyses. Species were classified in the following species guilds on the basis of their habitat association (or non-association): *ridge* species (R), *valley* species (V), *true generalist* species (G), and *widespread* species *with habitat association* (W, with two subcategories: WR, with ridge association, and WV, with valley association). Variation is expressed as mean ± 1 standard deviation (SD). To compare among species guilds pairwise, non-parametric Mann-Whitney tests were used (i.e., medians were codmpared, but mean ± 1 SD error bars, not boxplots, were used for the figure to simplify appearance and to make the calculation of the coefficients of variation in **(B)** clearer). The uncorrected/Bonferroni-corrected *P* values of the pairwise comparisons are shown only if uncorrected $P \leq 0.10$. **(A) (research question 1)** For each species (filled circles with thin error bars), intra-specific (between individuals) mean ± intra-specific variation (± 1 SD); and, for each species guild (open circles with thick error bars), inter-specific mean (mean of species mean values) ± inter-specific variation (± 1 SD). Mean and SD for each species, in addition to range (minimum and maximum values) and sample size (*N*), are reported in Appendix 4. Species are ordered by family (for acronyms meaning, see Tables or Appendices). **(B) (research question 2)** For each species guild (open circles with thick error bars), mean intra-specific (between individuals) variation ± inter-specific variation, expressed as coefficients of variation (CV) to make the intra-specific variation comparable across different species. Because a coefficient of variation obviously cannot be calculated for species with $N=1$ individual sampled, only species with $N \geq 2$ individuals sampled were considered to test if intra-specific variation was different among species guilds.

Figure 3.2

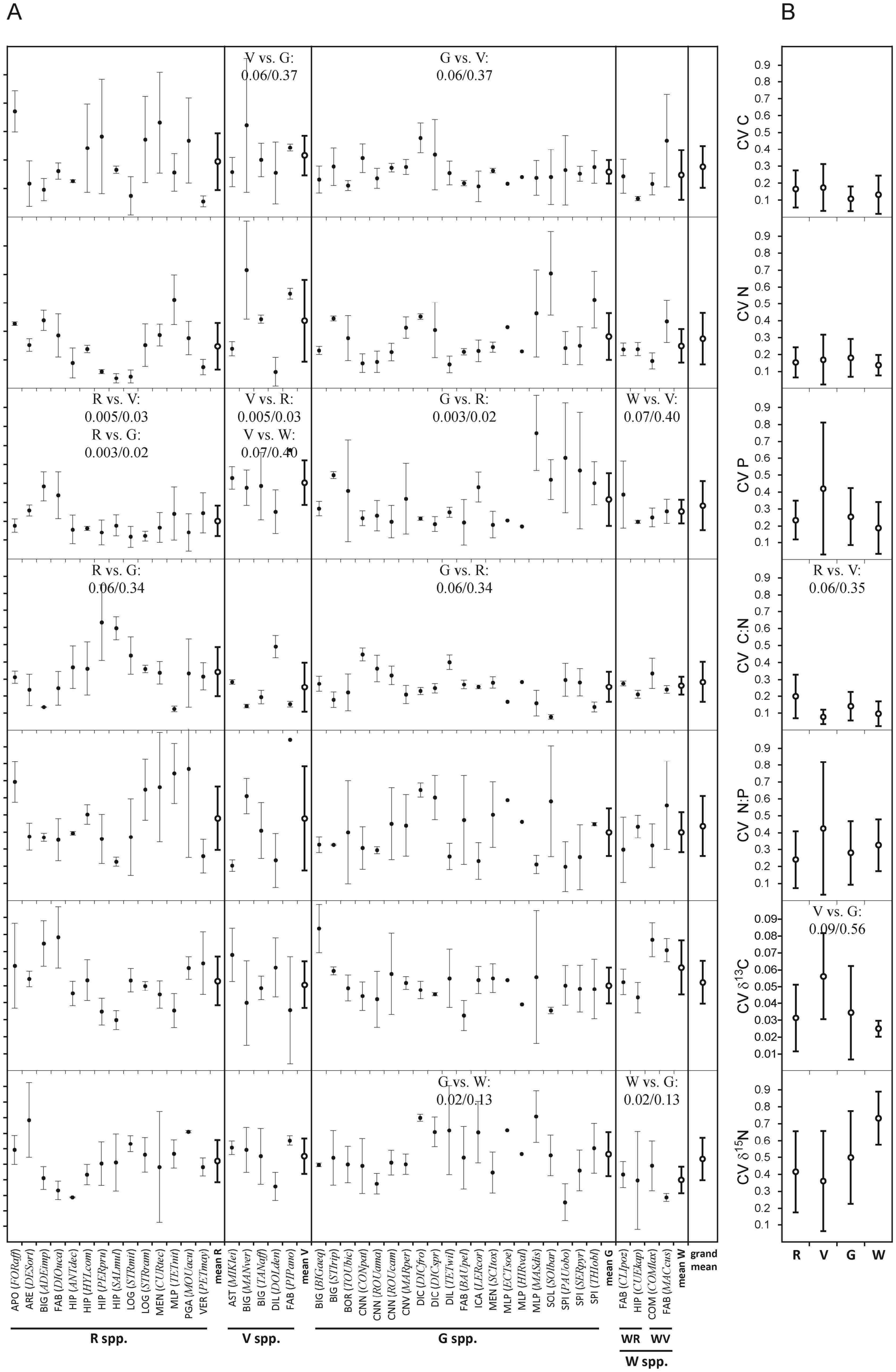
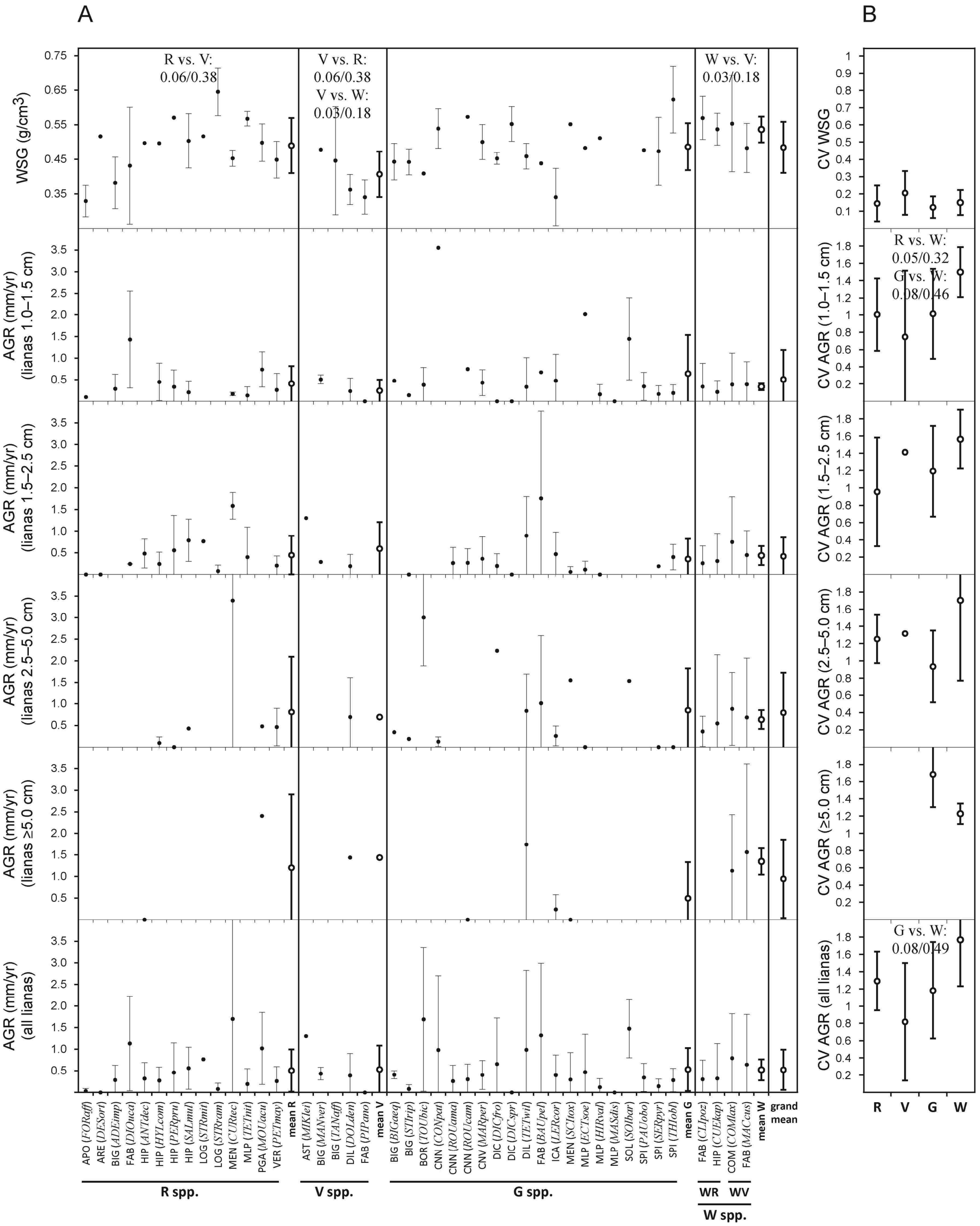

A
B
C (%)
N (%)
P (%)
C:N
N:P
δ^{13}C
δ^{15}N
V vs. G:
0.06/0.37
G vs. V:
0.06/0.37
R vs. V:
0.005/0.03
R vs. G:
0.003/0.02
V vs. R:
0.005/0.03
V vs. W:
0.07/0.40
G vs. R:
0.003/0.02
W vs. V:
0.07/0.40
R vs. G:
0.06/0.34
G vs. R:
0.06/0.34
G vs. W:
0.02/0.13
W vs. G:
0.02/0.13
CV C
CV N
CV P
CV C:N
R vs. V:
0.06/0.35
CV N:P
CV δ^{13}C
V vs. G:
0.09/0.56
CV δ^{15}N
APO (FORaff)
ARE (DESort)
BIG (ADEimp)
FAB (DIOuca)
HIP (ANTdec)
HIP (HYLcom)
HIP (PERpru)
HIP (SALmul)
LOG (STRmit)
LOG (STRram)
MEN (CURtec)
MLP (TETnit)
PGA (MOUacu)
VER (PETmay)
mean R
AST (MIKlei)
BIG (MANver)
BIG (TANaff)
DIL (DOLden)
FAB (PIPano)
mean V
BIG (BIGaeq)
BIG (STIrip)
BOR (TOUbic)
CNN (CONpat)
CNN (ROUama)
CNN (ROUcam)
CNV (MARper)
DIC (DICfro)
DIC (DICspr)
DIL (TETwil)
FAB (BAUpel)
ICA (LERcor)
MEN (SCItox)
MLP (ECTsoe)
MLP (HIRval)
MLP (MASdis)
SOL (SOIbar)
SPI (PAUobo)
SPI (SERpyr)
SPI (THIobl)
mean G
FAB (CLIpoz)
HIP (CUEkap)
COM (COMlax)
FAB (MACcus)
mean W
grand mean
R spp.
V spp.
G spp.
WR
WV
W spp.
R
V
G
W

Figure 3.3. Intra- and inter-specific average and variation of wood specific gravity (WSG) and absolute growth rate by diameter categories (AGR) of the 43 liana species included in the functional traits analyses. Species were classified in the following species guilds on the basis of their habitat association (or non-association): *ridge* species (R), *valley* species (V), *true generalist* species (G), and *widespread* species *with habitat association* (W, with two subcategories: WR, with ridge association, and WV, with valley association). Variation is expressed as mean ± 1 standard deviation (SD). To compare among species guilds pairwise, non-parametric Mann-Whitney tests were used (i.e., medians were compared, but mean ± 1 SD error bars, not boxplots, were used for the figure to simplify appearance and to make the calculation of the coefficients of variation in **(B)** clearer). The uncorrected/Bonferroni-corrected P values of the pairwise comparisons are shown only if uncorrected $P \leq 0.10$. **(A) (research question 1)** For each species (filled circles with thin error bars), intra-specific (between individuals) mean ± intra-specific variation (± 1 SD); and, for each species guild (open circles with thick error bars), inter-specific mean (mean of species mean values) ± inter-specific variation (± 1 SD). Mean and SD for each species, in addition to range (minimum and maximum values) and sample size (N), are reported in Appendix 5. Species are ordered by family (for acronyms meaning, see Tables or Appendices). **(B) (research question 2)** For each species guild (open circles with thick error bars), mean intra-specific (between individuals) variation ± inter-specific variation, expressed as coefficients of variation (CV) to make the intra-specific variation comparable across different species. Because a coefficient of variation obviously cannot be calculated for species with N=1 individual sampled, only species with $N \geq 2$ individuals sampled were considered to test if intra-specific variation was different among species guilds.

Figure 3.3


A
B
R vs. V:
0.06/0.38
V vs. R:
0.06/0.38
V vs. W:
0.03/0.18
W vs. V:
0.03/0.18
R vs. W:
0.05/0.32
G vs. W:
0.08/0.46
G vs. W:
0.08/0.49
WSG (g/cm^3)
AGR (mm/yr) (lianas 1.0–1.5 cm)
AGR (mm/yr) (lianas 1.5–2.5 cm)
AGR (mm/yr) (lianas 2.5–5.0 cm)
AGR (mm/yr) (lianas ≥5.0 cm)
AGR (mm/yr) (all lianas)
CV WSG
CV AGR (1.0–1.5 cm)
CV AGR (1.5–2.5 cm)
CV AGR (2.5–5.0 cm)
CV AGR (≥5.0 cm)
CV AGR (all lianas)
0.75
0.65
0.55
0.45
0.35
3.5
3.0
2.5
2.0
1.5
1.0
0.5
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
APO (*FORaff*)
ARE (*DESort*)
BIG (*ADEimp*)
FAB (*DIOuca*)
HIP (*ANTdec*)
HIP (*HYLcom*)
HIP (*PERpru*)
HIP (*SALmul*)
LOG (*STRmit*)
LOG (*STRram*)
MEN (*CURtec*)
MLP (*TETnit*)
PGA (*MOUacu*)
VER (*PETmay*)
mean R
AST (*MIKlei*)
BIG (*MANver*)
BIG (*TANaff*)
DIL (*DOLden*)
FAB (*PIPano*)
mean V
BIG (*BIGaeq*)
BIG (*STIrip*)
BOR (*TOUbic*)
CNN (*CONpat*)
CNN (*ROUama*)
CNN (*ROUcam*)
CNV (*MARper*)
DIC (*DICfro*)
DIC (*DICspr*)
DIL (*TETwil*)
FAB (*BAUpel*)
ICA (*LERcor*)
MEN (*SCItox*)
MLP (*ECTsoe*)
MLP (*HIRval*)
MLP (*MASdis*)
SOL (*SOlbar*)
SPI (*PAUobo*)
SPI (*SERpyr*)
SPI (*THIobl*)
mean G
FAB (*CLIpoz*)
HIP (*CUEkap*)
COM (*COMlax*)
FAB (*MACcus*)
mean W
grand mean
R spp.
V spp.
G spp.
WR
WV
W spp.
R
V
G
W

CHAPTER 4: Growth strategies of lianas in the forest understory of ridge and valley topographic terra firme habitats in the Yasuní Forest Dynamics Plot, Amazonian Ecuador (5)

SUMMARY

In the Yasuní Forest Dynamics Plot (YFDP) we assessed the apparent "strategies" that lianas with diameter ≥1 cm were using to grow in the understory of ridge and valley topographic habitats, as observed in a sample of 17 ridge quadrats and 13 valley quadrats (20×20 m each). An understory growth strategy was defined by the following categorical variables: whether a liana was free-standing or already climbing, climbing mechanism (twining, tendrils, branch-twining, scrambling or adhesive roots/tendrils) and understory appearance (creeping or not, and having large branches or not; applicable to climbing lianas only). We reasoned that if a particular growth strategy is significantly more common in either ridge or valley, and that growth strategy can be more or less consistently associated to a particular species, or to a group of species, then the growth strategy exhibited by such species may play a role in determining where in the forest such species can grow—which in turn would explain, at least partly, the observed community-level difference in liana community structure (species composition and their abundances) between ridge and valley.

We found 286 free-standing lianas (representing 46 species) and 1378 climbing lianas (representing 190 species) with diameter ≥1 cm in the YFDP (43 species shared). Twining and tendrilate species were the most numerous among both free-standing and

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climbing lianas. Branch-twining lianas, represented only by Hippocrateaceae, were relatively more numerous among free-standing lianas than among climbing lianas (17% vs. 5%), suggesting that the species of Hippocrateaceae tend to be free-standing even as old saplings. There were practically no scrambling species among the free-standing lianas, while species with adhesive roots or adhesive tendrils were very rare. Among the top most frequent species (frequency defined as the number of quadrats in which a species occurs), we found that free-standing individuals were important in determining the habitat association mainly of tendrilate and branch-twining species.

Given that the trees in the valley have slightly higher dynamism (higher mortality, recruitment and growth rates) than the trees in the ridge (although the difference is not significant), it is possible that small trellises for lianas are relatively more common in valley than in ridge. If so—and based on the patterns observed in past studies—we hypothesized that twining lianas will be relatively more abundant in ridge than in valley, and that tendrilate lianas will show the opposite pattern. Further, because the understory of the Yasuní forest is apparently denser than other lowland tropical rainforests, we hypothesized that scramblers will have similar relative abundance in ridge and valley. Finally, because more trees apparently fall in valley than in ridge, we hypothesized that creeping lianas will be relatively more abundant in valley than in ridge. In the present study, we found, in general, statistical support for these predictions (hypotheses), although with varied degrees of confidence.

We conclude that understory growth strategies of lianas can help to explain the distribution of liana species in a forest because they reflect the concomitant, time-cumulative, effects of forest successional processes, tree dynamics (mortality, recruitment and growth rates, and associated processes such as tree-fall rates) and broad forest physiognomy (particularly the relative abundance of appropriate trellises for lianas).

BACKGROUND AND HYPOTHESES

Lowland tropical rainforests from western Amazonia, such as those in Ecuador, are more dynamic than those in central or eastern Amazonia (e.g., Phillips et al. 2004). Tree-fall gaps in western Amazonian forests probably create a very heterogeneous mosaic of microhabitats (gaps and their associated successional pathways) which, however, become diluted when the forest is observed at the landscape scale—indeed, relatively few common tree and liana species tend to dominate western Amazonian forests (see e.g., Pitman et al. 2001, Romero-Saltos, Valencia, and Macía 2001, Burnham 2002, Macía and Svenning 2005). At the plot scale, the presence of a limited set of tree and liana species that are associated to particular habitats—such as swampy areas, valleys, ridgetops, or secondary forests—reinforces this apparent order or predictability (Valencia et al. 2004c; see also Chapter 3).

At very small spatial scales, lianas are perhaps the only growth form that apparently adapts (survives) well to dynamic forest microsites which are frequently impacted by tree-falls (review in Schnitzer and Bongers 2002). Adult lianas, in general, have several stem anatomical characteristics that give them flexibility but also toughness, allowing them to sustain structural strains imposed by random disturbances or, if need arises, to quickly recover from breakage or wounds (reviews in e.g., Fisher and Ewers 1991, Putz and Holbrook 1991, Isnard and Silk 2009). Thus, given their innate adaptability to ever-changing environments, lianas may be especially responsive to the dynamic three-dimensional architecture created by the fast growing, fast recruiting and fast dying trees in the western Amazonian forests (e.g., Malhi et al. 2004, Phillips et al. 2004). This "responsiveness" of lianas to local disturbance may be strong enough to influence their distribution and abundance at the local scale (e.g., Putz 1984, Baulfor and Bond 1993, Schnitzer 2005), in addition to the well-known environmental variables that control the distribution and abundance of plants in general (e.g., water availability, light, nutrients, CO_2 concentration).

How can we assess if a liana species can grow successfully in different tropical rainforest microhabitats with different degrees of architectural complexity or successional status? The most direct approach is of course experimental and would consist of planting liana species in architecturally distinct microhabitats while controlling for confounding factors (e.g., Putz 1984). A second, indirect, approach would be to assume that if a liana species under natural conditions in the forest is repeatedly not found, or rarely occurs, in many independent replicates of an architecturally-defined microhabitat, then (statistically) it can be concluded that the liana species in question does not grow in such microhabitat. Both approaches seem valid, but they depend on how the concept of "architectural complexity" of a forest microhabitat is defined. Traditionally, liana studies have implicitly defined architectural complexity from the point of view of the lianas, i.e. as the availability of suitable "trellises" (supports for climbing) for species guilds of lianas defined by their common climbing mechanism, i.e. the mechanism used to attach to a support (e.g., Putz 1984, DeWalt, Schnitzer, and Denslow 2000, Nabe-Nielsen 2001). Per se, trellis availability has rarely, if ever, been measured directly, but instead it has been assumed to be correlated with forest type, forest age, microhabitats in a forest, or tree size distribution (e.g., Putz 1984, DeWalt, Schnitzer, and Denslow 2000, Nabe-

Nielsen 2001). Climbing mechanisms have been defined in various ways, but the most common classification, more ecologically- than ontogenetically-based, has five categories (originally proposed by Putz 1984): (1) climbing by extreme circumnutation, i.e. by the continuous twining of the main stem axis or its equivalent (e.g., *Forsteronia*, Apocynaceae), (2) climbing by coiling tendrils which may have diverse ontogenetic origins (e.g., *Paullinia*, Sapindaceae), (3) climbing by lateral branches that twine once or a few times around the support (e.g., *Salacia*, Hippocrateaceae), (4) erratically climbing by using hooks, thorns, or spines, or simply by leaning, a broad strategy to which we refer in this study as "scrambling sensu lato" (e.g., *Machaerium*, Fabaceae), and (5) climbing by a "glue-to-your-support" strategy, i.e. by tiny adventitious adhesive roots (e.g. *Marcgravia*, Marcgraviaceae) or by tendril tips that do not coil but are adhesive and thus the liana in practice climbs as if it were a root-climber (e.g., some Bignoniaceae and Vitaceae). Although some species have evolved more than one climbing mechanism, it is usually feasible to determine in the field what primary or main climbing mechanism the species is using (Putz 1984).

The characterization of climbing mechanisms along with the characterization of trellis availability have revealed ecological trends that, along with other more general processes (e.g., habitat filtering, niche differentiation, stochasticity, enemy-mediated density dependence, among others), hint about the nature of the underlying factors that determine the observed distribution and abundance of lianas at the landscape (forest-type) or local scales. For instance, it is well known that tendrilate lianas—which can only attach to small-diameter trellises—decrease, whereas twiners increase, as a tropical rainforest ages (DeWalt, Schnitzer, and Denslow 2000, but see Koski 2009). This phenomenon is concomitant with a reduction of liana density as the forest matures (Putz 1984, DeWalt, Schnitzer, and Denslow 2000, Letcher and Chazdon 2009, Madeira et al. 2009) which in turn, at least within the terra firme *ridge* forest of Yasuní, is positively correlated with a reduction in the number of small trees (Nabe-Nielsen 2001). In the terra firme ridge forest of Yasuní, it has also been shown that scrambling lianas prefer thinner host trees than lianas with other climbing mechanisms, and the thicker a liana, the thicker its host tree, independent of the liana's climbing mechanism (Nabe-Nielsen 2001). These and other studies (e.g., Baulfor and Bond 1993) have demonstrated that the availability of appropriate trellises is important in determining the distribution of lianas in a forest.

In the 50-ha Yasuní Forest Dynamics Plot (YFDP), the community of lianas in ridge habitat is different from that in valley habitat in terms of diversity and species composition (and/or species abundances; Chapter 2). The community difference between these two topographically-defined habitats is largely driven by those common species that partition the topographic gradient. In Chapter 3, we statistically identified such species and showed that the inter-specific median values of only three functional traits were statistically different between the ridge species guild and the valley species guild: leaf mass per area, leaf phosphorus concentration and wood specific gravity. However, because of the nature of the habitat association analyses, such pattern was based on the comparison of only 14 ridge species against five valley species (Chapter 3), i.e. it used just 10% of the 195 species of lianas found in the thirty 20×20 m non-contiguous quadrats sampled in the YFDP (Chapter 2). Clearly, the difference between ridge and valley liana communities in the YFDP calls for more comprehensive approaches, such as the present study.

In this study, in a further attempt to understand the reasons why the community of lianas in ridge habitat is different from that in valley habitat in the terra firme forest of the YFDP (Chapter 2), we quantify, in these two topographically-defined habitats, the frequencies of: relatively large free-standing lianas (diameter ≥1 cm, treelet-like, i.e. lianas that are not yet climbing), lianas that are already climbing, different climbing mechanisms (defined above), and different "understory appearances". Understory appearance—a concept by imagination (Ford 2000)—is defined by whether or not a liana has near-ground or on-ground branches (i.e., branches emerging from the main stem at a height ≤3 m approximately) and by whether or not its main stem, and/or any of its branches, are creeping (presence of stolons or runners).

We propose that the ability to be free-standing as an old sapling, climbing mechanism, and understory appearance represent whole-plant functional traits that can define the time-cumulative strategy of how a liana grew or is growing in the understory of a forest. Such understory growth strategies may reflect relatively long-term ecological processes that putatively affect the distribution and abundance of lianas in a forest. Within this framework, in this study we specifically explore the following topics in the YFDP lianas (hypotheses appear in *italics*):

(1) Free-standing vs. climbing lianas: We describe the community of free-standing lianas in the YFDP and contrast it with the community of climbing lianas, including the relative proportions of species with different climbing mechanisms in these two communities. We also characterize the climbing mechanism and size (diameter) distribution of each of the most frequent species (frequency = # quadrats a species occurs in) of free-standing lianas and of climbing lianas. This allows us to explore how the relative abundance of growth stages in each most frequent species of lianas played a role in determining its habitat association (as defined in Chapter 3). This is important because the most frequent and/or common species are the ones largely responsible for the statistical difference in species composition, and/or their abundances, between ridge and valley (see Chapters 1 and 2).

(2) On twining lianas: Twining lianas tend to become increasingly more common as a forest matures (DeWalt, Schnitzer, and Denslow 2000). On average, in the terra firme forest of the YFDP, tree biomass in the valley, compared to the ridge, has higher (although not significantly) relative mortality rate (2.83 vs. 2.30 %/year), recruitment rate (0.18 vs. 0.15 Mg/ha/year), and relative growth rate (2.86 vs. 2.36 %/year), although these differences are not statistically significant (Valencia et al. 2009). Also, above-ground biomass is at least 50% higher in ridge compared to that of valley (Valencia et al. 2009). Thus, it is possible that there is a higher abundance of young forest patches in valley than in ridge, and thus we hypothesize that, among climbing lianas, *twining lianas should be relatively more common in ridge than in valley*.

(3) On tendrilate lianas: Regarding tendrilate lianas, we set forth to explore which of two contradictory hypotheses is best reflected in the data. First, let's recall that trees in valley apparently tend to die and recruit faster than in ridge (higher dynamism; Valencia et al. 2009). If these slightly higher rates are caused in part by a slightly higher tree-fall rate (and associated successional processes) in valley—as has been observed in other studies in lowland Neotropical rainforests (e.g., Ferry et al. 2010), but not yet explicitly measured in the YFDP—it is possible, among other effects, that more small trellises for lianas exist in valley than in ridge. Thus, among climbing lianas, we hypothesize that such putatively higher abundance of small trellises in valley habitat should *increase the relative abundance of tendrilate lianas in valley* (e.g., Putz 1984), as indeed has been observed in young forests (e.g., DeWalt, Schnitzer, and Denslow 2000). Second, alternatively, tendrilate lianas may be also responding to the abundance of small trees and shrubs, which one may think should provide sufficiently small trellises for tendrilate lianas. In the YFDP, small trees ($1 \leq DBH \leq 10$ cm)—and in fact trees in general—tend to be increasingly more abundant from valley to upper ridge (Valencia et al. 2004c; tree data from the 30 quadrats sampled in this study confirm the positive correlation between small trees and elevation, $r=0.62$, $P<0.001$). Thus, if small trees are important for the occurrence of climbing tendrilate lianas, we hypothesize that *tendrilate lianas should be relatively more common in ridge than in valley*, which is the opposite of what the first hypothesis stated.

(4) On branch-twining lianas: In Yasuní, branch-twining lianas are characteristic of only a single family: Hippocrateaceae. Therefore, the distribution of branch-twining lianas should follow that of the species in Hippocrateaceae. In Chapters 1 and 2, we showed that this family was, among the most species-rich, the only family whose species mostly occurred in ridge than in valley. Thus, undoubtedly, we expect that *branch-twining lianas must be proportionally more abundant in ridge than in valley*.

(5) On scrambling lianas: In Yasuní, scrambling lianas (sensu lato) tend to grow on thinner trellises than lianas with other climbing mechanisms (Nabe-Nielsen 2001). Scramblers in general also seem to proliferate where there is a dense, closed, arrangement of supports, independent of their diameter (e.g., in vegetation tangles; Putz 1984). In a lowland tropical rainforest such as Yasuní, where the understory is supposedly denser than in other lowland tropical rainforests in the world (Pitman et al. 2002, S. Davies [CTFS-STRI], pers. comm.), we hypothesized that the *relative abundance of scramblers should be similar between ridge and valley* (although they might be slightly more abundant in valley if the higher dynamism there increases the abundance of thinner trellises).

(6) On understory appearances: Because in Yasuní creeping lianas have on average more rooting points than non-creepers (unpublished data), they may have a better chance to survive tree-falls than non-creepers because undamaged stem portions on the ground may resprout if still attached to nearby and intact rooting points (e.g., Peñalosa 1984, Alvira, Putz, and Fredericksen 2004). This putative advantage of creepers in forests with high tree mortality would be enhanced if a liana also produces near-ground branches or on-ground branches (stolons). Of course, it could also be that creepers become more abundant in a forest area not because they are more resilient to falling trees, but because tree-falls keep creating creeping lianas by breaking them or slipping them off from their host trees (cause and effect cannot be separated). In any case, in the YFDP the valley habitat is apparently more dynamic than the ridge habitat (see above; Valencia et al. 2009), and thus, among climbing lianas, we hypothesized that *creeping lianas—particularly if they have stolons or near-ground branches—should be relatively more abundant in valley than in ridge*.

(7) On the interaction between climbing mechanism and understory appearance: To complement the search for differential patterns between ridge and valley habitats with respect to the frequencies of different climbing mechanisms and understory appearances among climbing lianas, we assess if the expected differences can still be detected when a given comparison is conducted with the lianas in a given combination of climbing mechanism and understory appearance. We hope that this high-resolution evaluation of understory growth strategies among climbing lianas will allow us to gain understanding of the growth mechanisms behind the patterns that are expected at a lower resolution (i.e., the *hypotheses* above, where we just focus on a climbing mechanism without taking into account understory appearance, and vice versa). As a further step, we also gain insight by broadly characterizing the size (in diameter classes) of the individuals of the most frequent species of climbing lianas in the different combinations of climbing mechanisms and understory appearances.

In short, we postulate in this study that the distinct environmental conditions and the distinct tree dynamics in the ridge and valley habitats of the YFDP differentially influence the growth strategies that lianas can use in the forest understory, which in turn may partly explain the differences in species composition, species abundances, and species diversity observed between these two dissimilar liana communities (Chapter 2).

METHODS

STUDY AREA

This study was conducted in Yasuní National Park, Amazonian Ecuador, within the 50-hectare Yasuní Forest Dynamics Plot (YFDP; 1000×500 m; 00°41' S, 76°24' W). Mean annual rainfall and mean monthly temperature in the area are approximately 3000 mm and 25 °C, respectively (Chapter 2). Because mean monthly rainfall is 250 mm, Yasuní is considered a non-seasonal forest (Chapter 2). The YFDP is associated with an ever expanding network of large-scale permanent plots that monitor millions of trees in several tropical and temperate countries (Valencia et al. 2004a). Yasuní National Park, of approximately 10,000 km^2, is known to harbor very high levels of plant and animal alpha diversity (Bass et al. 2010), and lianas certainly are not the exception (Nabe-Nielsen 2001, Romero-Saltos, Valencia, and Macía 2001, Burnham 2002, Burnham 2004). The YFDP is located on terra firme (upland) forest, with ridge formations (up to 250 m altitude) towards the northern, southern and eastern areas, separated by a relatively wide valley (ca. 215–225 m altitude). Except for a few small swampy areas in the valley, ridge and valley are considered terra firme forest (Valencia et al. 2004c). A few permanent streams crisscross the valley; they may occasionally overflow and temporarily flood part of the valley during the rainiest months.

Past studies have shown that ridge and valley habitats of the YFDP are statistically dissimilar in terms of tree, liana and palm species composition or species abundances (Svenning 1999a, Valencia et al. 2004c, Chapter 2). While the diversity of tree species between ridge and valley is not significantly different—although a tendency towards higher diversity in valley exists—lianas show higher species diversity in valley than on ridge (Valencia et al. 2004c, Chapter 2). In the valley, the average density of trees and basal area per hectare is lower than on the ridge, whereas liana density is similar in both habitats (Valencia et al. 2004c, Chapter 2). Because trees with relatively large diameters occur more commonly on ridge than in valley—tree biomass is, in fact, at least 50% higher on ridge—mean canopy height is probably higher on ridge than in valley (Valencia et al. 2004c, Valencia et al. 2009; see also Svenning 1999a).

More than 90% of Yasuní is terra firme (upland) hilly forest growing on Ultisols soils that are somewhat clayey, acidic and rich in iron and aluminum (Pitman 2000, Valencia et al. 2004a). The surface soil (0–5 cm) of the terra firme is, when compared to other terra firme areas in northwestern Amazonia, relatively rich in exchangeable bases (particularly Ca, Mg, and Na) and has an average texture of approximately 50% silt, 29% sand and 21% clay (Tuomisto et al. 2003). The biogeochemical characteristics of the topographically distinct ridge and valley habitats of the YFDP have not been well studied, but differences are expected. The main physical differences should evidently be related to the effect of topography on the hydrological regime: on average, drainage is probably lower in the valley, soil water content is probably higher in the valley (see e.g. Jirka et al. 2007) and soil oxygen concentration is probably lower in the valley (see e.g., Silver, Lugo, and Keller 1999). If these differences are marked, other soil characteristics such as pH, Al concentration, nutrient concentrations and organic matter concentration should also be different between ridge and valley habitats (see e.g., Tange, Yagi, and Sasaki 1998, Tuomisto et al. 2003, Kubota, Murata, and Kikuzawa 2004), but a reliable geochemical/geophysical description of the YFDP's ridge and valley soils is not yet available.

SAMPLING DESIGN AND DATA ANALYSES

To evaluate the frequencies of different understory growth strategies of lianas in the ridge and valley habitats of the YFDP—as defined by free-standing/climbing status, climbing mechanism and understory appearance (see Introduction)—we used a subset of 1378 climbing lianas and 286 free-standing lianas, out of the total of 1919 lianas with diameter ≥1.0 cm (195 species) sampled in 17 non-contiguous ridge quadrats and 13 non-contiguous valley quadrats (each 20×20 m; Chapter 2). Excluded from this study were 176 climbing lianas not identified to family (usually very tall lianas with leaves that were practically inaccessible even by climbing nearby trees) and 79 lianas that were neither climbing nor free-standing (usually fallen branches with roots and leaves, but which were not yet climbing). The 176 unidentified (and non-collected) climbing individuals were excluded because their climbing mechanism was unknown or, even if directly observed or inferred, could not be unequivocally matched to a taxon. The 79 lianas that were neither climbing nor free-standing were not included because many of these lianas are very prone to die (unpublished recensus data) and because in this study we focus on the climbing and free-standing growth stages only.

Lianas were sampled from 2006 to 2008 following an in-house sampling protocol that is complementary to that of Gerwing et al. (2006), but which, for a number of reasons, is somewhat different from what was independently proposed by Schnitzer, Rutishauser, and Aguilar (2008) also as a complement to Gerwing et al. (2006) (see Appendix 1 of Chapter 2). Our Gerwing/Romero (G/R) protocol defines a Point of Diameter Measurement (PDM) in a liana by codifying, alphanumerically, its "understory appearance" (see Introduction) below an approximate height of 3 m, in addition to other characteristics used for the application of the G/R protocol, such as the distance along the stem from the main rooting point to the point where the first branch emerges, the presence of thick adventitious roots, the presence of a voluble main liana stem fully encircling a host stem, among other characteristics (see Appendix 1 of Chapter 2).

The data registered in the field for every one of the climbing and free-standing lianas included in this study were: (1) diameter at the PDM; (2) free-standing/climbing status; (3) PDM code in the G/R protocol (a proxy of understory appearance; see above); (4) whether it had any understory branch(es) ≥1 cm in diameter, <1 cm in diameter, or both (at at height <3 m approximately); and (5) its apparent climbing mechanism if easily observable (see Introduction). Climbing mechanisms registered at the individual level were later assessed for consistency within species; for data analyses, the same primary climbing mechanism was assigned to every individual of a species, so free-standing lianas also had their future climbing mechanism assigned. To assign an understory appearance to every liana sampled, we used information from numerals (3) and (4) above. The understory appearances used in this study focused on the presence/absence of *large* understory branches (diameter ≥1 cm) and on the creeping/not creeping status of liana stems (incl. branches); thus, there are four possible understory appearances, as used in this study: creeping with *large* branches, creeping with no *large* branches, not creeping with *large* branches, and not creeping with no *large* branches. Note that although the concept of understory appearance can be applied to climbing or free-standing lianas (in fact, 20 out of the 286 free-standing lianas crept a little), for the purpose of this study we applied it to climbing lianas only. To clarify our approach towards the understanding of understory growth strategies of climbing lianas in the YFDP, a graphical representation of the 16 possible combinations of climbing mechanisms and understory appearances (excepting the adhesive roots/tendrils climbing mechanism), as used in this study, is shown in Figure 4.1. However, not shown in the Figure is the possibility, indeed repeatedly observed in the field, that a branch, not the main stem, is the stem that creeps (those cases were nonetheless classified along with those lianas in which the main stem creeps).

The most frequent species of lianas among the free-standing lianas and among the climbing lianas were selected by the following criteria: in the free-standing lianas dataset, we selected those species occurring in at least ≈25% of either ridge quadrats (≥4 quadrats) or valley quadrats (≥3 quadrats), while in the climbing lianas dataset, we selected those species occurring in at least ≈50% of either ridge quadrats (≥8 quadrats) OR valley quadrats (≥6 quadrats). The low frequency threshold (25%) used for free-standing lianas was chosen because of the relative paucity of free-standing lianas in the forest. To describe size (diameter) distribution in each of the most frequent species, the percentage of individuals in each of the following diameter classes was calculated with respect to the total number of individuals in the species (free-standing + climbing individuals): 1.0–1.5 cm, 1.5–2.5 cm, 2.5–5.0 cm, and ≥5.0 cm. The first two classes were meant to represent young lianas that were probably actively growing in the forest (at least those facing ideal environmental conditions), while the last class was meant to represent very old established lianas (or so we assumed).

To test the hypotheses about differences in the proportion of climbing mechanisms and understory appearances from climbing lianas in ridge vs. valley (see Introduction), we considered a quadrat as an independent replicate. In each quadrat, the proportion of climbing lianas having a given climbing mechanism (out of five possible; see above), a given understory appearance (out of four possible; see above), or a given combination of climbing mechanism and understory appearance (out of 16 possible, see Figure 4.1; adhesive tendrils/adventitious roots climbing mechanism excluded), was calculated with respect to total number of climbing lianas in the quadrat (excluding unidentified lianas). For every comparison, the ridge sample (*N*=17 quadrats) was compared to the valley sample (*N*=13 quadrats) using a two-sample *t*-test and a Mann-Whitney non-parametric test; we conservatively decided to use both statistical tests for every comparison because the data used in a given comparison were not always normally distributed.

To complement the analysis above, we conducted an analysis that is similar in nature but in which climbing lianas were separated into four diameter classes: 1.0–1.5 cm, 1.5–2.5 cm, 2.5–5.0 cm, and ≥5.0 cm. The goal was to identify the size range (in diameter) of the lianas that were driving the postulated differences between ridge and valley in terms of climbing mechanisms and understory appearances. As above, we considered a quadrat as the independent replicate or sampling unit. In each quadrat, among the lianas of a given diameter class, the proportion of lianas of a given climbing mechanism or understory appearance was calculated with respect to the total number of climbing lianas of the given diameter class in the quadrat (excluding unidentified lianas). Ridge vs. valley comparisons by diameter classes in each of the 16 possible combinations of climbing mechanism and understory appearance (Figure 4.1) were not conducted. As above, for every comparison, the ridge sample (*N*=17 quadrats) was compared to the valley sample (*N*=13 quadrats) using both a two-sample *t*-test and a Mann-Whitney non-parametric test. Finally, for every comparison of ridge climbing lianas vs. valley climbing lianas of a given diameter class, we also identified which frequent species contributed at least two individuals in the datasets being compared; this way, we broadly (visually) characterized the size distribution of the most frequent species of climbing lianas across the different climbing mechanisms and understory appearances.

VEGETATION COVER: DENSIOMETER MEASUREMENTS

As a very broad proxy of forest successional status, we used measurements of vegetation cover (canopy openness) made with a convex densiometer. Densiometer readings were taken at the four corners of every 5×5 m subquadrat, each measurement taken with the densiometer facing towards the center of a subquadrat. Thus, for each

20×20 m quadrat, we obtained 64 densiometer readings. By using natural statistical breaks, we classified the densiometer data in three categories: “low” vegetation cover (62.5–87.5% of cover), “typical” cover (87.5–93.75%), and “high” cover (93.75–100%). Then, by assuming each densiometer reading best represented a forest area of 2.5×2.5 m (6.25 m^2), for each 20×20 m quadrat we calculated the forest area represented by the three vegetation cover categories (out of 400 m^2).

RESULTS AND DISCUSSION

We postulated that the real and presumed physical and ecological differences between the ridge and valley habitats in the YFDP (see Introduction and Methods) must have an effect on the growth strategies lianas use in the understory of these forest habitats, constraining at the same time what species can grow where, and thus partly explaining why the liana community structure (species composition and their abundances) in ridge is different from that in valley habitat (Chapter 2). Such strategies were defined in terms of frequencies of free-standing lianas, climbing lianas, different climbing mechanisms and different understory appearances (see Introduction and Methods).

FREE-STANDERS VS. CLIMBERS

General comparison

In this study, we analyzed a subset of 1664 lianas (193 species) from the dataset of 1919 lianas (195 species) with diameter ≥1 cm that were registered in 17 ridge quadrats and 13 valley quadrats in the YFDP (each 20×20 m; Chapter 2): 286 were free-standing lianas (46 species) and 1378 were climbing lianas (190 species). Forty-three species were shared between free-standing and climbing lianas, i.e. three species only appeared as free-standing lianas—*Strychnos mitscherlichii* (five individuals), *Paullinia clathrata* (one individual) and *Aegiphila elata* (one individual)—and 147 species had no free-standing individuals. Therefore, free-standing lianas represented approximately 15% of the liana individuals with G/R diameter ≥1 cm in the YFDP, but had they not been sampled, alpha diversity would have not changed significantly. The 15% value is difficult to compare to other studies that included free-standing lianas because the number of free-standing lianas ≥1 cm of diameter were not explicitly reported (e.g., Putz 1984, Mascaro, Schnitzer, and Carson 2004). This study is the first in Yasuní that has systematically sampled free-standing lianas at the community level. Past studies did not sample them (Nabe-Nielsen 2001, Romero-Saltos, Valencia, and Macía 2001, Burnham 2002, Burnham 2004) probably because of potential confusion with young individuals of tree species—but in the YFDP, given the taxonomic experience the project has accumulated since 1995 (Valencia et al. 2004a), this potential confusion became a minor problem despite high levels of species diversity.

Climbing mechanisms in free-standing and climbing lianas were represented in similar proportions, particularly for twining and tendrilate lianas. In the 46 species of free-standing lianas—from which 33 species contained no more than three free-standing individuals—approximately half (48%) were twining species (representing 38.1% of the free-standing individuals) and about a third (30%) were tendrilate species (representing 33.9% of the free-standing individuals). Interestingly, in the 190 species of climbing lianas, the proportions were similar as those of the free-standing lianas: 52% were twining species (representing 49.8% of the individuals) while 32% were tendrilate species (representing 25.9% of the individuals); these percentages among climbing lianas were very similar to those observed by Nabe-Nielsen (2001) in mature terra firme ridge forests in Yasuní, and by Santos, Kinoshita, and Rezende (2009) in fragmented seasonal semideciduous forest in southeastern Brazil. There were relatively more branch-twining species among the free-standers than among the climbers, 17% vs. 5%, suggesting that the species of Hippocrateaceae—the only family with this type of climbing mechanism in our dataset—tend to be free-standing even as old saplings (diameter ≥1 cm). Scramblers (sensu lato) were represented by relatively few species and individuals in both growth stages (among free-standing lianas: two individuals, two species; among climbing lianas: 197 individuals, 18 species). *Acacia tenuifolia* and *Piptocarpha lechleri* were the two scrambling species among the free-standers, each represented by only a single individual—thus, in Yasuní scramblers practically never can be free-standing! (at least not with a diameter ≥1 cm). This can be either interpreted as scramblers being very effective in finding suitable supports while they are still very young, or as scramblers lacking the wood ontogenetic adaptations necessary to develop as self-supporting when young (for some biomechanical and evolutionary perspectives on this issue, see e.g., Kennard 1998, Gallenmüller et al. 2001, Gallenmüller, Rowe, and Speck 2004, Rowe, Isnard, and Speck 2004, and Lahaye et al. 2005). Finally, root climbers did not exist among free-standing lianas, and only three species existed among climbing lianas, all in the Marcgraviaceae. This family, in addition to liana species, includes several species of secondary woody hemiepiphytes (which superficially may look like lianas).

Most frequent and most common species among free-standers and climbers

The majority of the most common species (defined by number of individuals) in each growth stage were also among the most frequent species (defined by number of quadrats in which they occurred) (Table 4.1). Further, the 10 most abundant species among the free-standing lianas were mostly the same as the 10 most abundant species among the climbing lianas, although ranked differently (Table 4.1). Among climbing lianas, *Machaerium cuspidatum* and *Combretum laxum*—both species with valley association, but also widespread (Chapter 3)—were the two most abundant (Table 4.1). On the other hand, among free-standing lianas, *Cuervea kappleriana* and *Petrea maynensis*—both species with ridge association (Chapter 3)—were the two most abundant, although they were also among the top five most abundant among climbing lianas (Table 4.1). *Callichlamys latifolia*, a species with valley association (Chapter 3), and *Bauhinia guianensis*, a generalist species (Chapter 3), had a higher rank position in abundance among free-standing lianas than among climbing lianas. All things considered, we conclude that the observed difference in community structure (species composition and their abundances) between the whole liana communities of ridge and valley (Chapter 2) seems also reflected among the free-standing lianas (in fact, using data from free-standing lianas only, an ANOSIM test gave a significant difference between ridge and valley: $R_{ANOSIM} = 0.24$, $P<0.01$, Bray-Curtis used as distance measure).

Table 4.1 illustrates a number of patterns in the occurrence and size distribution of free-standing and climbing lianas of the most frequent species within each growth stage, and within each habitat. First, free-standing individuals were relatively rare among the six frequent species of twining lianas, from which only *Petrea maynensis* had free-standing individuals that were as common as their climbing counterparts, in particular in the smallest diameter class: 1.0–1.5 cm. Therefore, the strong ridge association shown by this species (Chapter 3), one of the most dominant in the YFDP (Chapter 2), is very dependent on the relatively high abundance of free-standing individuals, which constitute 36.5% of the individuals in this species, almost all with a diameter ≤2.5 cm. Second, as opposed to what was observed with the twining species, free-standing individuals were relatively common among the most frequent species of tendrilate and branch-twining lianas. In fact, free-standing individuals constituted approximately half of the total number of individuals in the following four species: *Callichlamys latifolia*, *Bauhinia guianensis*, *Cuervea kappleriana* and *Tontelea fuliginea*. Thus, the habitat association shown by these dominant species in the YFDP (Chapter 2) is largely influenced by the distribution of their free-standing lianas. Third, as can be expected, it is very rare for a free-standing liana to reach a diameter greater than 2.5 cm. Fourth, it is peculiar that, among the most frequent species, the three species with the highest relative abundance of climbing lianas with diameter ≥5 cm are all twining species: *Combretum laxum* (a valley specialist), *Doliocarpus dentatus* (a valley specialist) and *Dioclea ucayalina* (a ridge specialist); these very large lianas are most probably associated with very large host trees (Nabe-Nielsen 2001) which one would expect are more common in mature forests, thus reaffirming the trend that twining species tend to increase in abundance in mature neotropical forests (DeWalt, Schnitzer, and Denslow 2000). Fifth, and finally, three species did not have any free-standing liana at all: *Doliocarpus dentatus* (a valley species), *Dioclea ucayalina* (a ridge species) and *Machaerium cuspidatum* (a valley species). *M. cuspidatum*, in particular, merits attention because it is the most abundant species among climbing lianas in the YFDP (Table 4.1) (or the second most abundant, after *Combretum laxum*, if all the 1919 sampled lianas are considered; Chapter 2).

Although the lack of free-standing individuals in *Machaerium cuspidatum* per se is not surprising because scrambling species were very rare among free-standing lianas in general, this result serves as a springboard to discuss why this species became ubiquitous in Yasuní. *M. cuspidatum* is a widespread and locally common species that occurs in terra firme, floodplain and swamp forests, although it tends to be relatively more abundant in terra firme valleys and in relatively well-drained floodplains (Nabe-Nielsen 2001, Romero-Saltos, Valencia, and Macía 2001, Burnham 2002, Burnham 2004, Chapters 1 and 2; Table 4.1). In addition to the life-history traits emphasized by other researchers but which may not necessarily be unique to the species (e.g., seedling shade-tolerance, high seedling growth rate in areas with high-light intensity although with lower seedling survivorship there, higher rate of vegetative reproduction in flood-prone soils where seedlings mortality is high, low mortality of large adults in tall mature forest, low mortality of juveniles in low, usually young, forest, among others; Nabe-Nielsen 2002, Nabe-Nielsen and Hall 2002, Nabe-Nielsen 2004), we postulate that *M. cuspidatum* became so successful in Yasuní simply because its specific climbing mechanism is more effective in attaching to a variety of supports, in a variety of microenvironments, than that of many other species. *M. cuspidatum* climbs by long, thin, flexible, usually leafless, branches (modified inflorescences?) which towards their tips have many tiny hooks pointing down and which can anchor strongly to basically any surface (pers. obs.). This is rather an uncommon strategy among scramblers, which instead tend to produce spines or thorns throughout the stem (e.g., *Piptadenia, Dioscorea*), sometimes very large (e.g., *Celtis iguanaea*), or hooks in pairs, but which are further separated along the stem and not as small as those of *M. cuspidatum* (e.g., *Randia*). Because scramblers tend to proliferate where the vegetation is dense (Putz 1984), the relatively denser understory of the Yasuní plot, compared to other tropical rainforests in the world (Pitman et al. 2002, S. Davies, CTFS-STRI, pers. comm.), probably also influences the success of this liana species. The slightly higher forest dynamism of the valley compared to the ridge in the YFDP (Valencia et al. 2009) should also influence the distribution of this species locally if the phenomenon results in slightly higher availability of small trellises in valley, to which scramblers show a clear tendency to attach (Nabe-Nielsen 2001).

CLIMBING MECHANISMS AND UNDERSTORY APPEARANCES IN RIDGE VERSUS VALLEY: TESTING THE HYPOTHESES

On the basis of proven and hypothesized biogeophysical and tree dynamics differences between ridge and valley (see Introduction and Methods), we developed a number of hypotheses about differences in the proportion of climbing mechanisms and understory appearances between climbing lianas occurring in ridge vs. those occurring in valley (see Introduction). We explored these hypothesized differences for every combination of climbing mechanism and understory appearance, for every climbing mechanism independent of understory appearance, and for every understory appearance independent of climbing mechanism (Table 4.2). We also explored if the expected differences could still be detected if the comparisons had been conducted only with lianas in different diameter classes (Figures 4.2 and 4.3, and on which the occurrence of the most frequent species were manually “mapped” onto them; see Methods). The hypothesized differences were formally tested via Mann-Whitney tests (non-parametric) and *t*-tests (parametric) (see Methods), which almost always gave similar *P* values (Table 4.2), meaning that patterns were robust independent of the underlying distribution of the data.

Hypothesis about twining lianas: ***Because of a lower occurrence of young forest patches in ridge than in valley, we hypothesized that twining lianas should be relatively more common in ridge than in valley.***

As predicted, twining lianas were relatively less abundant in valley than in ridge, although the trend is not strong (compare averages 0.52 vs. 0.45; Mann-Whitney's *P*=0.039, while *t*-test's *P*=0.08; Table 4.2). With some reservations, and assuming twining lianas are good indicators of the late successional status of a forest (DeWalt, Schnitzer, and Denslow 2000, Schnitzer and Bongers 2002), we thus infer that the forest on the ridge has been relatively less subjected to disturbances (e.g., tree-falls) than the forest in the valley. This assertion is somewhat supported by densiometer readings of the 30 quadrats sampled in this study. After categorizing the data into low (relatively open), intermediate and high forest cover (see Methods), we found that the average and median low forest areas per valley quadrat were slightly higher than those per ridge quadrat, although the difference was rather minimum and not significant (averages: 16.3 vs. 15.1 m^2; medians: 6.3 vs. 0 m^2; total area of a quadrat: 400 m^2; see also Svenning 2000). When twining lianas were decomposed into the four understory appearances, a statistical difference between ridge and valley was not detected at any of the understory appearances, although there is a slight trend for twining lianas to be relatively more abundant in ridge than in valley when they are not creeping and have large branches (Table 4.2). Similarly, when twining lianas were expanded by diameter classes, there were no significant differences between per-quadrat ridge and valley proportions in any of the diameter classes analyzed (Figure 4.2). When comparing the ridge and valley proportions of non-creeping twining lianas as a whole (whether with large branches or not; analysis not shown in Table 4.2), we did find a significant difference between them (ridge vs. valley averages: 0.33 vs. 0.25; ridge vs. valley medians: 0.31 vs. 0.23; $P \approx 0.03$ for Mann-Whitney test and *t*-test). Thus, *non-creeping* twining lianas are the ones driving the relatively higher abundance of twining lianas in ridge compared to valley (Table 4.2). This makes sense because, as it was also hypothesized (see Introduction, and hypothesis (5) below), non-creeping lianas were expected to be relatively more common in ridge than in valley given the slightly slower tree dynamics (Valencia et al. 2009) and the presumably lower tree-fall rate in the ridge habitat (Ferry et al. 2010).

Hypotheses about tendrilate lianas (contrasting hypotheses): ***Because putatively higher tree-fall rates in valley than in ridge may provoke higher abundance of small trellises in valley, which are suitable for tendrilate lianas, we hypothesized that the relative abundance of tendrilate lianas in valley should be higher than in ridge; however, in sharp contrast, tendrilate lianas could be relatively more common not in valley but in ridge if small trees, which increase in abundance from valley to upper ridge, are being used by tendrilate lianas as trellises.***

Among tendrilate lianas, we set forth to explore which of these two competing hypotheses was best supported by our data. We found support for the first hypothesis, i.e., tendrilate lianas were significantly more abundant in valley than in ridge, and this marked difference was being driven by the creeping tendrilate lianas (with and without large branches), not by the non-creeping tendrilate lianas, although non-creeping tendrilate lianas were actually more common than creeping tendrilate lianas in both habitats (Table 4.2). Further, the clear difference between ridge and valley is driven by the lianas from the size categories of 1.5–2.5 cm and ≥5.0 cm, i.e. by young but established lianas and by the very old *Bauhinia rutilans* lianas (Figure 4.2). The cause for this difference, as we hypothesized, might be that the availability of small trellises—caused by higher tree-fall rates and to which tendrilate lianas are particularly sensitive (Putz 1984, Schnitzer and Bongers 2002)—is higher in valley than in ridge, which is something expected if trees are dying and recruiting a little faster in valley (Valencia et al. 2009), even though the density of trees in general is lower in valley (Valencia et al. 2004c, Valencia et al. 2009). Tree-fall rates have not been empirically studied in the YFDP, but given the indirect evidence, we expect them to be higher in valley than in ridge, similarly to what was observed in the French Guianan forests which also, as in the YFDP, showed a marked reduction of biomass in bottomlands (Valencia et al. 2009, Ferry et al. 2010). The presence of small trees, which in the YFDP become increasingly more abundant as one walks from valleys to ridgetops (Valencia et al. 2004c), has apparently little effect on the local distribution of tendrilate lianas (see also Ewango 2010)—in other words, it is the intrinsic tree dynamics of a forest, not its static architecture, what apparently matters.

About branch-twining lianas: ***Because Hippocrateaceae species are the only ones that climb by branch-twining, and they mostly occur in ridge, branch-twining lianas must of course be significantly more abundant in ridge than in valley.***

This result was certainly anticipated based on the observed distribution of the majority of species in Hippocrateaceae, the only family that branch-twines to climb. Indeed, the difference in the relative proportions of branch-twiners in ridge vs. valley was highly significant for all but one understory appearance: creeping with no large branches (Table 4.2). This understory appearance, anyhow, is very rare among Hippocrateaceae

(Table 4.2), indicating that in this family creeping and the existence of large branches (probably stolons) normally occur together. The clear significant difference between ridge and valley in the per-quadrat proportions of branch-twiners is maintained for all diameter classes <5 cm (Figure 4.2), although it is considerably stronger (higher *P* value) for small lianas that are presumably actively climbing (1.0–1.5 cm). Thus, whatever the underlying factors that control the distribution of Hippocrateaceae, these are acting strongly since the plants are very small. The "preference" for ridge habitat of many members of this family is correlated with relatively low mass-based leaf phosphorous concentration, high leaf mass per area (low specific leaf area), high leaf dry matter content and high wood specific gravity (see Chapter 3). In addition, Hippocrateaceae commonly tend to be free-standing even as old saplings (see above). The conjunction of all these traits certainly plays a role in determining the spatial distribution of Hippocrateaceae species in the YFDP forest, but it would be interesting to explore if these traits also occur in other Neotropical forests, and how these apparent evolutionary adaptations came about.

Hypothesis about scramblers: ***Because the understory of Yasuní is apparently denser than other tropical lowland rainforests in the world, we hypothesized that scramblers should occur at similar relative abundances in ridge and valley, although they might be slightly more abundant in valley because of putatively higher abundance of small trellises there.***

There is clear support for this hypothesis in our dataset (Table 4.2). In addition, scramblers, which contained many less species than twining or tendrilate lianas (see above), showed a tendency to occur more frequently in valley, but only among creeping lianas (Table 4.2). When the ridge-valley comparisons were made by diameter classes, there was no difference between habitats at any of the diameter classes (Figure 4.2), meaning scramblers are widely distributed in the YFDP. In Yasuní, within ridge terra firme forest, scramblers showed a clear tendency to attach to relatively thin trellises (Nabe-Nielsen 2001); this is also probably true in valley habitat as well. As mentioned already, thin trellises might be slightly more frequent in valley than in ridge because of higher tree dynamism in valley forest (Valencia et al. 2009). Although such presumed higher abundance of trellis availability in valley seems unimportant for the distribution of most scramblers, it might anyhow help to explain why *Machaerium cuspidatum*, the most common scrambling species, but also the most common species among climbing lianas, occurs in greater abundance in valley than in ridge (Chapters 1 and 2).

Hypothesis about understory appearance: ***Either because the valley has a higher tree-fall rate than the ridge, which may cause more lianas to creep or fall to the ground, or because lianas that creep in general might be more resilient to falling trees than those that do not creep, we hypothesized that creeping lianas—particularly if they have stolons or near-ground branches—should be relatively more abundant in valley than in ridge.***

Although the average and median values shown in Table 4.2 follow what was expected—i.e., higher proportions in valley than in ridge for creeping lianas, and higher proportions in ridge than in valley for non-creeping lianas—the only significant difference between ridge and valley was detected with those creeping lianas that had no large branches (compare 0.12 in ridge vs. 0.21 in valley; Table 4.2). However, when creeping lianas as a whole (lianas with and without large branches considered together) and non-creeping lianas as a whole were compared (not shown in Table 4.2), the ridge vs. valley differences in the average and median per-quadrat proportions became significant (P=0.02–0.03 for all Mann-Whitney tests and t-tests) and followed the expected trends: for creeping lianas, higher relative abundance in valley, and for non-creeping lianas, higher relative abundance in ridge. Therefore, in general, the presence/absence of large branches was the only variable that was insensitive to the habitat, whereas creeping/non-creeping appearance and climbing mechanisms seemed to "react" to the environment. In other words, lianas with large branches, whether creeping or not, were more or less evenly distributed in the two habitats (Table 4.2). This is in a way similar to what was observed in Costa Rica where multi-stemmed individuals of lianas showed no trend with forest age, as opposed to trees which became significantly less multi-stemmed (at DBH level) in old-growth forests (Letcher and Chazdon 2009). The detected ridge vs. valley difference among the creeping lianas with no large branches was caused by the lianas in the size range from 1.5 to 5.0 cm (Figure 4.3), and was most probably driven by the presence of individuals from three frequent species with strong valley association (see Chapter 3): *Combretum laxum*, *Bauhinia rutilans* and *Machaerium cuspidatum* (Figure 4.3). In addition, it is evident from Figure 4.3 that when lianas are young (diameter <2.5 cm), they mostly are not creeping and have no large branches, while when they become old (diameter ≥5.0 cm), they are mostly found creeping and with large branches, although evidently just a few liana species can reach such large size (e.g., among the most frequent species: *Combretum laxum*, *Dioclea ucayalina*, *Machaerium cuspidatum*, and *Doliocarpus dentatus*).

CONCLUSION

We postulated that distinct environmental conditions and distinct tree dynamics in the ridge and valley habitats of the YFDP constrain the growth strategies that lianas can use in the forest understory of these two topographically-defined habitats. Because many liana species have clearly defined or distinct growth strategies, the interaction between environment and growth strategy may partly explain the differences in species composition, species abundances, and species diversity observed between these two dissimilar liana communities (Chapter 2). We found that, in general, the growth strategy patterns observed were in line with our predictions (hypotheses), which were literature-based or rationally developed. We conclude that understory growth strategies of lianas, assessed at a point in time in the long history of a forest, can help to explain the distribution of liana species because they reflect the concomitant, and time-cumulative, effects of forest successional processes, tree dynamics (mortality, recruitment and growth rates, and associated processes such as tree-fall rates) and general forest physiognomy (particularly the relative abundance of appropriate trellises for lianas).

TABLES

Table 4.1. Climbing mechanisms, relative abundances (%) and absolute abundances (ABS. ABUND., # individuals) of the most frequent species in 17 ridge quadrats (R) and 13 valley quadrats (V) sampled in the YFDP (each quadrat: 20×20 m). Among the free-standing lianas, the species selected as most frequent were those occurring in at least ≈25% of either the ridge quadrats (≥4 quadrats) OR the valley quadrats (≥3 quadrats). Among the climbing lianas, the species selected as most frequent were those occurring in at least ≈50% of either the ridge quadrats (≥8 quadrats) OR the valley quadrats (≥6 quadrats). For each species, the percentage of individuals in each category was calculated with respect to the total number of individuals of the species (free-standing + climbing individuals). In each species, the largest percentage and those within a 5% range from it appear **underlined and in bold**, the lowest *non-zero* percentage and those within a 5% range from it appear in **red bold**, and zero values appear as blanks. Absolute abundances of free-standing and climbing lianas, as well as habitat association (from Chapter 3), are also shown. Species were sorted by primary climbing mechanism, and then alphabetically by family and scientific name. Species acronyms (in **bold**) were formed by the three first letters of the genus (in UPPERCASE) and the first three letters of the epithet. The 15 species listed represented 79% of the 286 free-standing lianas found in this study (46 species/morphospecies, all identified at least to family) and 44.6% of the 1378 climbing lianas found in the 30 quadrats sampled (representing 190 species/morphospecies, all identified at least to family). The 176 unidentified/non-collected climbing lianas and the 79 lianas that were neither climbing nor free-standing were excluded from this study (see Methods).

	A frequent species...		RELATIVE ABUNDANCE (%) BY DIAMETER CLASSES (cm) of free-standing lianas								RELATIVE ABUNDANCE (%) BY DIAMETER CLASSES (cm) of climbing lianas										
			1.0–1.5		1.5–2.5		2.5–5.0		≥5.0		1.0–1.5		1.5–2.5		2.5–5.0		≥5.0				
Climbing mechanism *Species* (Family)	**...among free-standing lianas?**	**...among climbing lianas?**	**R**	**V**	**R**	**V**	**R**	**V**	**R**	**V**	**R**	**V**	**R**	**V**	**R**	**V**	**R**	**V**	**ABS. ABUND. among free-standing lianas^{1}**	**ABS. ABUND. among climbing lianas^{1}**	**HABITAT ASSOCIATION^{2}**
Main axis twining																					
COM*bretum* ***lax****um* (Combretac.)	yes	yes	**3.8**	8.3	**1.5**	**0.8**		**0.8**			6.0	9.8	6.0	**22.6**	9.0	12.8	7.5	11.3	20^{T}	113^{T}	WV
DOL*iocarpus* ***den****tatus* (Dilleniac.)	no	yes									8.3	**33.3**		8.3	8.3	8.3		**33.3**	0	12	V
CLI*toria* ***poz****uzoensis* (Fabac.)	yes	yes	**4.9**	**1.2**	11.1	**2.5**					12.3	9.9	**22.2**	**17.3**	13.6	**4.9**			16^{T}	65^{T}	WR
DIO*clea* ***uca****yalina* (Fabac.)	no	yes										**7.1**	**28.6**		**28.6**	**7.1**	**28.6**		0	14	R
LER*etia* ***cor****data* (Icacinac.)	no	yes			**4.8**						**23.8**	**9.5**	**4.8**	14.3	14.3	**23.8**	**4.8**		1	20	G
PET*rea* ***may****nensis* (Verbenac.)	yes	yes	13.6	**5.9**	11.9	**1.7**	**3.4**				14.4	**5.1**	**22.0**	8.5	11.0	**2.5**			43^{T}	75^{T}	R
Tendrils																					
CAL*lyclamys* ***lat****ifolia* (Bignoniac.)	yes	yes	**3.8**	**11.5**	**13.5**	**13.5**	**3.8**	**3.8**		**1.9**	**5.8**	7.7	**11.5**	7.7	**5.8**	**9.6**			27^{T}	25^{T}	V

	A frequent species...		RELATIVE ABUNDANCE (%) BY DIAMETER CLASSES (cm) of free-standing lianas								RELATIVE ABUNDANCE (%) BY DIAMETER CLASSES (cm) of climbing lianas										
			1.0–1.5		1.5–2.5		2.5–5.0		≥5.0		1.0–1.5		1.5–2.5		2.5–5.0		≥5.0				
Climbing mechanism *Species* (Family)	**...among free-standing lianas?**	**...among climbing lianas?**	**R**	**V**	**R**	**V**	**R**	**V**	**R**	**V**	**R**	**V**	**R**	**V**	**R**	**V**	**R**	**V**	**ABS. ABUND. among free-standing lianas[1]**	**ABS. ABUND. among climbing lianas[1]**	**HABITAT ASSOCIATION[2]**
__BAU__hinia __gui__anensis (Fabac.)	yes	yes	**28.6**	**4.8**	11.9	**4.8**					**7.1**		14.3	21.4	**7.1**				21^{T}	21^{T}	G
__BAU__hinia __rut__ilans (Fabaceae)	yes	yes	8.7	**4.3**	8.7	**2.2**	**2.2**	**2.2**			**2.2**	**4.3**	**6.5**	**23.9**	**4.3**	**23.9**	**2.2**	**4.3**	13^{T}	33^{T}	V
__PAU__llinia __brac__teosa (Sapindac.)	yes	no	10.3	17.2	**3.4**	**3.4**					13.8	10.3	**27.6**	**3.4**	**3.4**	**6.9**			10^{T}	19	G
__PAU__llinia __mic__roneura (Sapindac.)	yes	no	**14.3**		**14.3**	**14.3**					**7.1**		**14.3**	**7.1**	**14.3**	**7.1**	**7.1**		6^{T}	8	towards R
Branch twining																					
__CUE__rvea __kapp__leriana (Hippocratac.)	yes	yes	**19.8**	**2.1**	**21.9**	6.3	**4.2**	**2.1**			12.5		12.5	10.4	7.3	**1.0**			54^{T}	42^{T}	WR
__SAL__acia __mult__iflora (Hippocrateac.)	no	yes	**7.7**		**3.8**						**23.1**	**3.8**	**19.2**	15.4	**23.1**	**3.8**			3	23^{T}	R
__TON__telea __ful__iginea (Hippocrateac.)	yes	no	**4.0**	**8.0**	**12.0**	**12.0**	**4.0**	**8.0**			**8.0**		**8.0**	**8.0**	**16.0**		**8.0**	**4.0**	12^{T}	13	G
Scrambling (s.l.)																					
__MAC__haerium __cus__pidatum (Fabac.)	no	yes									12.2	**15.3**	**6.9**	**19.8**	13.0	**18.3**	**5.3**	**9.2**	0	131^{T}	WV
																			226	**614**	
																		Other species:	**60**	**764**	
																			286 free-standing lianas in all	**1378 climbing lianas in all**	

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[1] T = Species among the top 10 most common among the lianas in that growth stage.

[2] From Chapter 3. R = ridge species, V = valley species, G = generalist species, WR = widespread species with ridge association, WV = widespread species with valley association

Table 4.2. Proportions, per-quadrat, of primary climbing mechanisms and understory appearances among **climbing** lianas in ridge (N=17 20×20 m quadrats) and valley (N=13 quadrats) habitats of the YFDP. Proportions were calculated with respect to the total number of climbing lianas in a quadrat (but excluding unidentified lianas). Mean, median [in brackets] and range (in parentheses) are shown. Statistical differences between ridge and valley groups were assessed via Mann-Whitney (U) and t-tests. To gain readability, the statistics U and t are not shown and P-values are categorized as: $P \leq 0.001$(***, extremely significant difference), $0.001 < P \leq 0.01$ (**, highly significant difference), $0.01 < P \leq 0.05$ (*, significant difference), $0.05 < P \leq 0.10$ (NS*, no significant difference, but almost), $P > 0.10$ (NS, no significant difference). P-values of the U test and the t-test in general fell within the same range; when they did not, the P-value category of the t-test is shown below that of the U test. The rare root- and adhesive-tendril climbers are not shown.

			CLIMBING MECHANISM														
		twining			**tendrils**			**branch-twining**			**scrambling (sensu lato)**			**ALL CLIMBING MECHANISMS**			
		ridge		**valley**	**ridge**		**valley**	**ridge**		**valley**	**ridge**		**valley**	**ridge**		**valley**	
UNDERSTORY APPEARANCE **creeping**	**with large branches**	0.11 [0.10] (0.02–0.27)	NS	0.12 [0.10] (0.02–0.21)	0.03 [0.03] (0–0.12)	*	0.07 [0.08] (0–0.16)	0.03 [0.02] (0–0.11)	** *	0.01 [0] (0–0.03)	0.02 [0.02] (0–0.11)	NS* *	0.05 [0.04] (0–0.15)	0.20 [0.20] (0.05–0.39)	NS	0.24 [0.25] (0.03–0.41)	**The data in this box is expanded by diameter classes in Figure 4.3**
	no large branches	0.07 [0.05] (0–0.24)	NS	0.09 [0.08] (0–0.23)	0.03 [0.02] (0–0.11)	*	0.06 [0.05] (0–0.21)	0.002 [0] (0–0.02)	NS	0.004 [0] (0–0.03)	0.02 [0] (0–0.09)	* NS*	0.05 [0.04] (0–0.16)	0.12 [0.11] (0.03–0.28)	*	0.21 [0.21] (0.05–0.43)	
not creeping	**with large branches**	0.13 [0.12] (0–0.37)	NS NS*	0.07 [0.07] (0–0.13)	0.07 [0.06] (0–0.17)	NS	0.07 [0.07] (0–0.14)	0.05 [0.05] (0–0.14)	*	0.02 [0.02] (0–0.05)	0.02 [0] (0–0.13)	NS	0.03 [0.03] (0–0.11)	0.27 [0.29] (0.03–0.53)	NS	0.20 [0.17] (0.05–0.33)	
	no large branches	0.20 [0.19] (0.05–0.43)	NS	0.18 [0.16] (0.04–0.41)	0.08 [0.06] (0–0.30)	NS	0.10 [0.09] (0.02–0.22)	0.06 [0.05] (0–0.23)	** *	0.02 [0] (0–0.08)	0.06 [0.05] (0–0.14)	NS	0.05 [0.05] (0–0.10)	0.41 [0.37] (0.12–0.73)	NS	0.35 [0.33] (0.13–0.73)	
ALL APPEARANCES		0.52 [0.55] (0.23–0.66)	* NS*	0.45 [0.43] (0.36–0.56)	0.21 [0.18] (0.13–0.36)	**	0.30 [0.30] (0.20–0.42)	0.15 [0.14] (0–0.41)	*** **	0.05 [0.04] (0–0.14)	0.12 [0.10] (0.02–0.25)	NS*	0.18 [0.20] (0.05–0.33)	**1**		**1**	
		The data in this box is expanded by diameter classes in Figure 4.2															

FIGURES

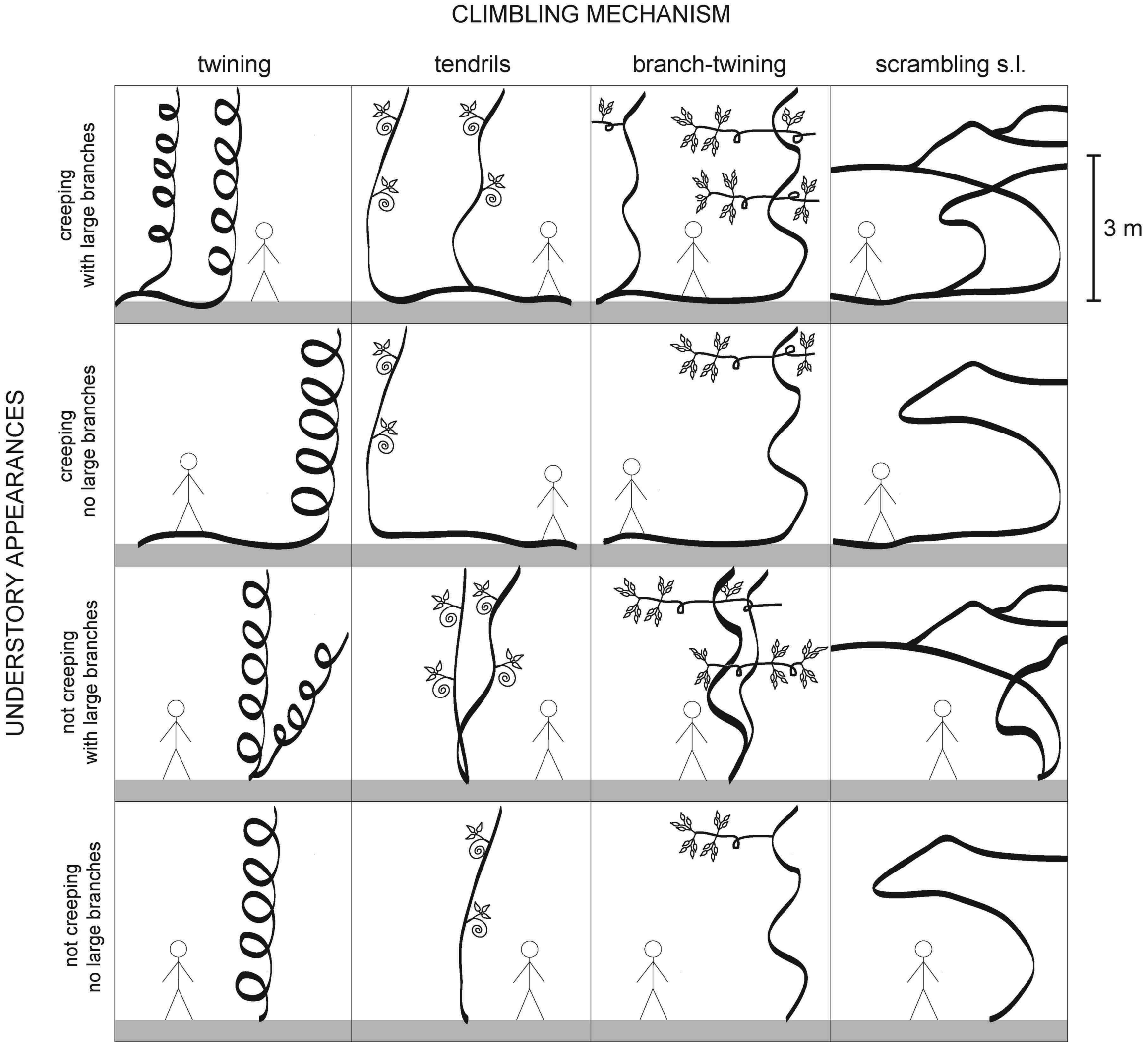

Figure 4.1. Sixteen schematic graphical examples of whole-individual growth strategies of climbing lianas in the low forest understory, as used in this study. The "trellises" (supports for climbing) used by the lianas are not shown. These strategies result from the combination of four climbing mechanisms (twining, tendrils, branch-twining and scrambling sensu lato) and four understory appearances defined by the presence/absence of creeping stems and the presence/absence of large branches (branches ≥1 cm in diameter) near ground-level. Our "scrambling s.l." category includes climbers with hooks or spines and sprawlers in general. A creeping stem can either be the main stem or a branch, but creeping branches are not shown in this Figure to gain clarity (also, note that a non-creeping liana may have underground runner stems nonetheless). Root-climbers and adhesive-tendril climbers are not shown. Many aspects in the figure are not drawn to scale nor are biologically precise. Understory appearance was characterized from what could be observed up to an approximate height of 3 m.

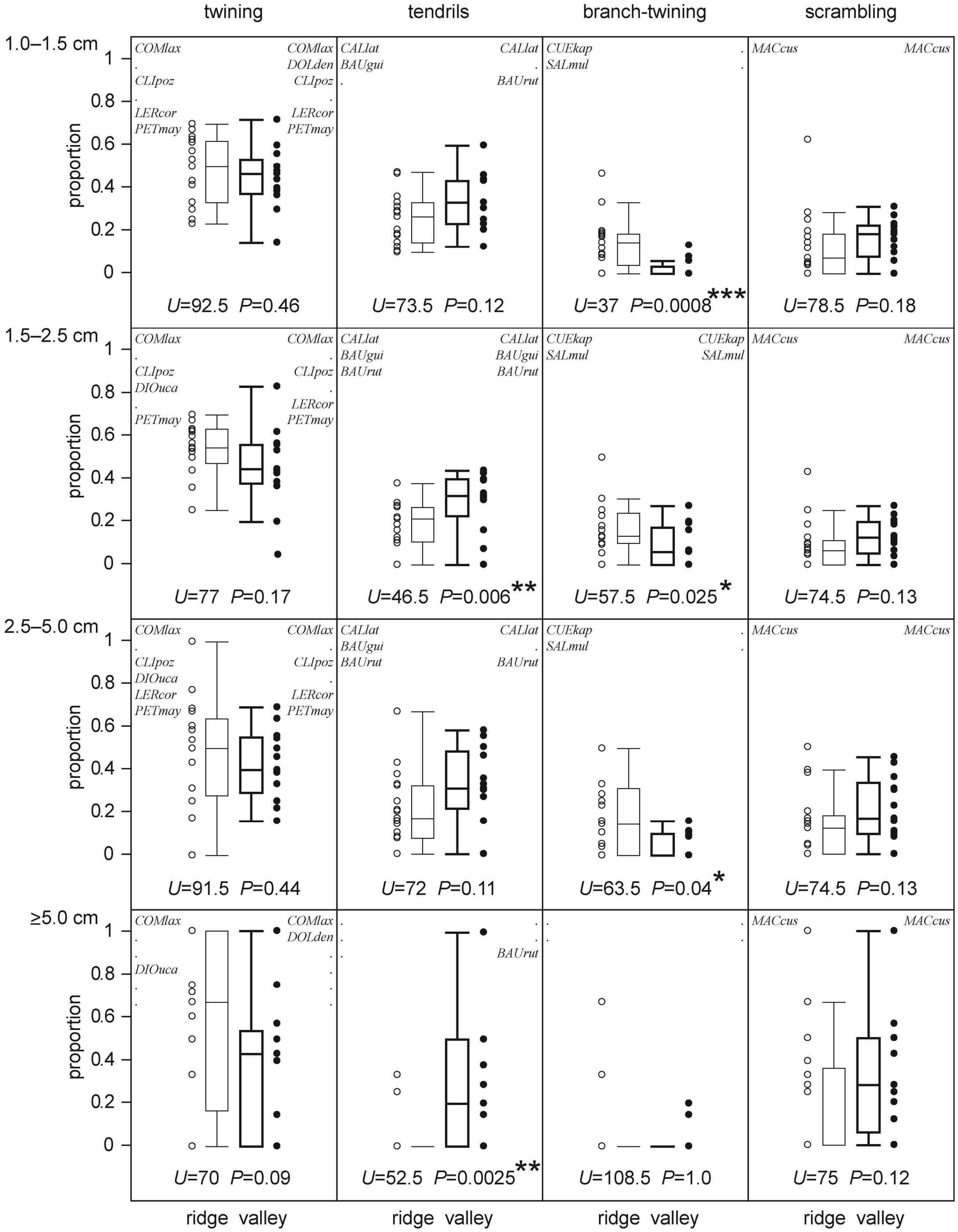

Figure 4.2. Proportions of primary climbing mechanisms by diameter classes among **climbing** lianas in ridge (*N*=17 20×20 m quadrats) and valley (*N*=13 quadrats) habitats of the YFDP. Root-climbers and adhesive-tendril climbers are not shown because they were very rare. The proportion of lianas of a given climbing mechanism in a given diameter class, in a given quadrat, was calculated with respect to the total number of climbing lianas of the given diameter class in the quadrat (but excluding unidentified lianas). Statistical differences between ridge and valley groups were evaluated via Mann-Whitney and *t*-tests, but because the *P* ranges of both tests were always similar, only Mann-Whitney results (*U*) are shown. Thin-lined boxplots and their corresponding open circles represent ridge quadrats, while thick-line boxplots and their corresponding filled circles represent valley quadrats. When a frequent species among the climbing lianas ("C" species of Table 4.1) had at least two individuals in a given diameter class in a given habitat, its acronym is shown in the Figure (acronyms ordered as in Table 4.1). *P*-values are categorized as: $P \leq 0.001$(***, extremely significant difference), $0.001 < P \leq 0.01$ (**, highly significant difference), $0.01 < P \leq 0.05$ (*, significant difference), $P > 0.05$ (no significant difference).

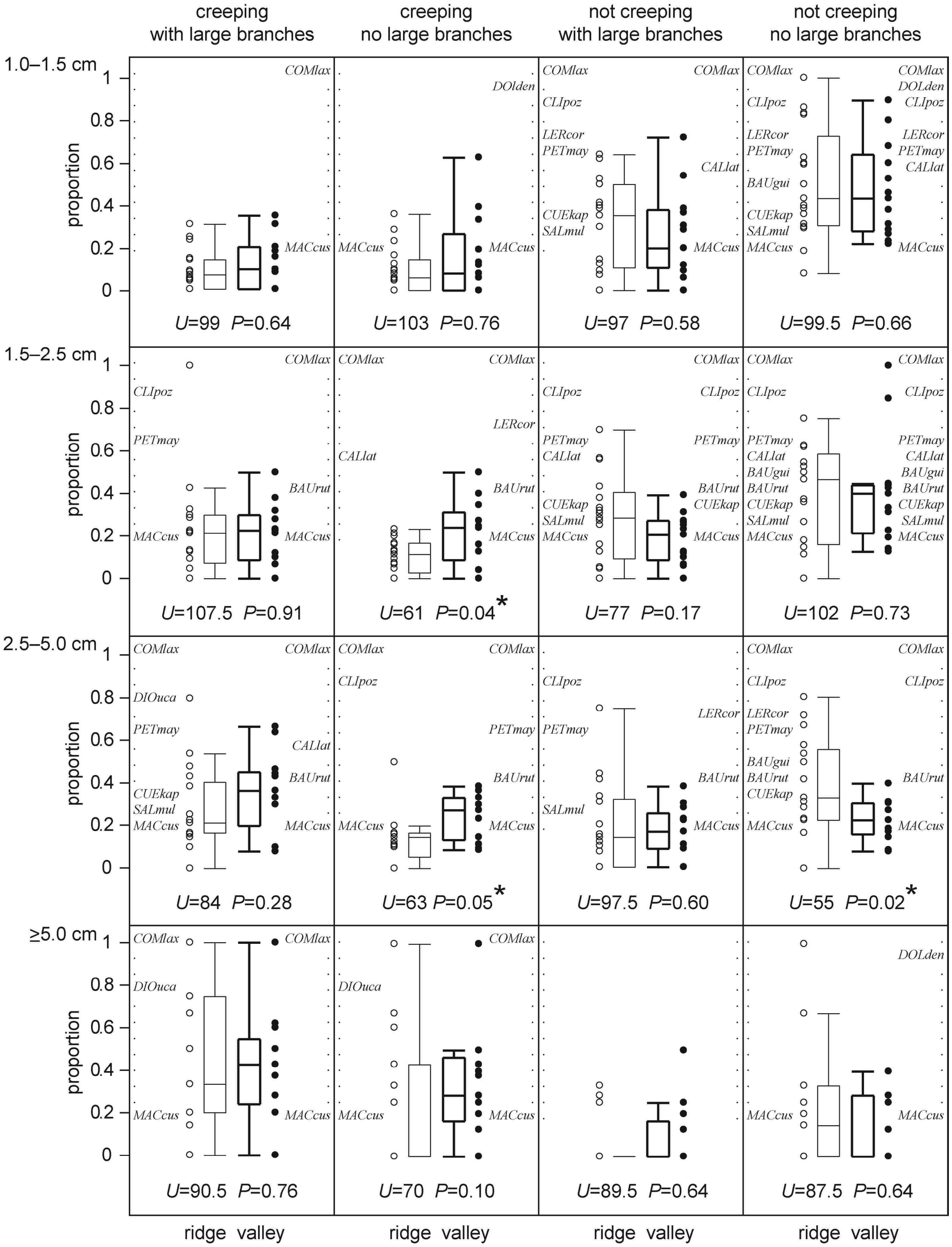

Figure 4.3. Proportions of understory appearances by diameter classes among **climbing** lianas in ridge (N=17 20×20 m quadrats) and valley (N=13 quadrats) habitats of the YFDP. Root-climbers and adhesive-tendril climbers are not shown because they were very rare. The proportion of lianas of a given understory appearance in a given diameter class, in a given quadrat, was calculated with respect to the total number of climbing lianas of the given diameter class in the quadrat (but excluding unidentified lianas). Statistical differences between ridge and valley groups were evaluated via Mann-Whitney and t-tests, but because the P ranges of both tests were always similar, only Mann-Whitney results (U) are shown. Thin-lined boxplots and their corresponding open circles represent ridge quadrats, while thick-line boxplots and their corresponding filled circles represent valley quadrats. When a frequent species among the climbing lianas ("C" species of Table 4.1) had at least two individuals in a given diameter class in a given habitat, its acronym is shown (acronyms ordered as in Table 4.1). P-values are categorized as: $P \leq 0.001$(***, extremely significant difference), $0.001 < P \leq 0.01$ (**, highly significant difference), $0.01 < P \leq 0.05$ (*, significant difference), $P > 0.05$ (no significant difference).

CHAPTER 5: Conclusion

In the Yasuní Forest Dynamics Plot (YFDP), I have demonstrated that the liana community (diameter ≥1 cm) in ridge habitat is different from the community in valley habitat in at least two respects: community structure (understood as the composition and abundance of species) and species diversity. Why does this difference exist? If one assumes it is the environment that controls the distribution of plants, this pattern is not surprising given the suspected biogeochemical differences that certainly exist between ridge and valley (from valley to ridgetop, there is an altitudinal difference of 20–30 m). But there is a diametrically opposite alternative: one can assume what controls the distribution of plants are plants themselves (e.g., via competition) or the activity of animals (e.g., via dispersal and herbivory). This classic ecological dilemma is unsolvable because the truth, as many studies have shown, lies somewhere in the middle and it is always relative to the system, the spatiotemporal scale under study, and the amount of information available. Given the paucity of information about the lianas within the YFDP, in this dissertation I tackled the problem of explaining the ridge vs. valley difference by focusing on one specific part of the conundrum: the relationship between the differential spatial distribution and abundance of liana species in ridge and valley habitats *and* the functional traits they exhibit, or express, in these habitats. In other words, my over-arching question was: To what extent is the observed spatial distribution of lianas in the YFDP forest explained by the characteristics of the different species?

The functional traits sampled in the present study were classified into two groups: quantitative traits (continuous variables) and qualitative traits (categorical variables). The quantitative traits included those commonly measured in plants: specific leaf area (SLA), leaf dry matter content (LDMC), leaf morphometry (lamina thickness, length:width ratio, leaf size), leaf carbon (C), nitrogen (N), and phosphorus (P) concentrations, leaf ^{13}C and ^{15}N isotopic signatures, wood specific gravity (WSG) and stem growth rate (in diameter). The qualitative traits, on the other hand, were particular to lianas and described the strategy used by a liana, as a whole plant, to grow in the understory of the forest; these included: whether a liana was growing as a free-stander or as a climber, its climbing mechanism (twining, tendrils, branch-twining, scrambling [sensu lato], and adhesive roots/tendrils) and its understory appearance (creeping liana with large understory branches [usually stolons], creeping liana with no large understory branches, non-creeping liana with large understory branches, and non-creeping liana with no large understory branches).

I found that because the trait expression patterns of a group of related species (species within the same family or genus) is often different from the expresssion patterns of another group of related species, the generalization of trait expression to the whole ridge or valley commnunities must be made cautiously. In fact, not all traits showed a distinctive pattern between ridge and valley. In the subset of common species that had a clear habitat association to either ridge or valley, I found that ridge species had a lower SLA and leaf P concentration, but higher WSG, than valley species. The other traits did not show any clear differential pattern, although there is a trend for LDMC to be higher among ridge species (expected, given the low SLA among them). In addition, I found that the ability to be free-standing as an old sapling (diameter ≥1 cm) is only typical of very few liana species, while in the rest it occurs sporadically (and rarely among twining lianas and practically never among scrambling lianas). I also found that tendrilate lianas and creeping lianas were significantly more common in valley, while branch-twining lianas and main stem-twining lianas were significantly more common on ridge. The presence or absence of understory branches in lianas occurred randomly and did not show any particular pattern associated with habitat.

The patterns above mentioned constitute the main "discoveries" of this doctoral dissertation and those for which I sought to find an explanation in the Discussion sections of the different data Chapters. I focused mostly on the role of the environment (particularly soil characteristics and canopy openness) and the observed tree dynamics (mortality, recruitment and growth rates), and offered some rational arguments why these may be relevant to explain the observed distribution of lianas in the YFDP. I hope this treatise on the lianas of the Yasuní Forest Dynamics Plot motivates more in-depth studies about the distribution problem (why some species of lianas are differentially distributed along the ridge-valley topographic gradient) and the diversity problem (why so many species coexist in such a reduced space).

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APPENDICES

APPENDIX 1

The "Gerwing/Romero" (G/R) and "Basal" protocols to locate the Point(s) of Diameter Measurement (PDM) of a liana as used in the Yasuní Forest Dynamics Plot (YFDP)—and how or why the G/R protocol, or similar others (Schnitzer, Rutishauser, and Aguilar 2008), became relatively impractical.

Introductory remarks

The "Gerwing/Romero" (G/R) protocol to locate the Point(s) of Diameter Measurement (PDM) of a liana is mostly based on the recommendations of Gerwing et al. (2006), but complemented with instructions for those special cases whose PDM's were not defined in that publication. Schnitzer, Rutishauser, and Aguilar (2008)—to whom we sent a draft of our G/R protocol in November 2006—have also defined PDM's for such special cases, and here we refer to their protocol as the "Gerwing/Schnitzer" (G/S) protocol. We did not make any attempt to incorporate the G/S protocol into our G/R protocol because it was published when our field work was almost finished, and because we thought (and still do) that the G/R protocol has arguably better qualities although probably is more labor-intensive (particularly because of our system of sampling/tagging near-ground branches; see description of the G/R protocol below). As a result, the G/R PDM's and the G/S PDM's may sometimes differ considerably, although most often they coincide (see accompanying figure at the end of this Appendix, modified with permission from the publisher ELSEVIER).

The G/S protocol was developed for the first (full) inventory of lianas in the 50-ha Barro Colorado Island Forest Dynamics Plot in 2007, while the G/R protocol was developed for the first (partial) inventory of lianas in the 50-ha Yasuní Forest Dynamics Plot in 2006–2008 (this dissertation). However, the original versions of these G/R and

G/S protocols were developed for the censuses of lianas in the Forest Dynamics Plots in Africa (e.g., Kenfack et al. 2005, cited in Schnitzer, DeWalt, and Chave 2006). Despite the broad application of these similar protocols in several studies, the G/R protocol was not used to locate PDM's during the 2008 field campaign in the YFDP, but only to codify the growth stage (free-standing/climbing/neither) and general appearance of a liana near ground level (see below how the G/R protocol works). What protocol did we use instead to locate PDM's on lianas in 2008, and why did we reduce the application of the G/R protocol to the description of liana appearances only? To answer these questions, a short account of our field experience with the G/R protocol is necessary.

At the beginning of 2008—while conducting the first census of the five quadrats in column 27 (see Methods) and the second census of the liana community in the whole column 07 (unpublished data)—we realized that the application of the G/R protocol to locate PDM's was prone to two recurring problems: (1) it sometimes absurdly excluded lianas from the sample, especially when in conjunction with a diameter cutoff criterion; and (2) it tended to cause confusion, during a recensus, in the location of PDM's of ramets originating from lianas censused in the past. Let's exemplify these problems. An absurd exclusion from the sample occurred, for example, when we encountered two young free-standing *Bauhinia guianensis* lianas, of about the same age and height (<2 m) and growing next to each other. One had no branches at all (the leaves came out directly from the primary stem) while the other had a single small branch appearing at <130 cm from the rooting point. When the G/R protocol was applied, the *Bauhinia* with no branches was excluded from the sample because it did not reach a diameter ≥1 cm at the G/R PDM on the main stem (130 cm from the rooting point), while the branching

Bauhinia was included in the sample because it reached the 1 cm diameter cutoff at the G/R PDM (20 cm below the branch). The inclusion of only one of the *Bauhinia*’s just didn’t make sense because the two lianas looked basically the same. Regarding the potential confusion in locating PDM’s of ramets that originate from lianas sampled in a previous census, we recall, as an example, the case of a liana whose main stem in the first census crept several meters from its rooting point before ascending towards the canopy. Following the G/R protocol, the PDM was located at 130 cm above the point on the stem that last touched the ground. By the time of the second census, this creeping stem had broke off between the original rooting point and the PDM and two independently rooted lianas, i.e. ramets (clones), had been created. For such a case, we thought it was most logical to keep the old tag on one of the ramets, and to consider the other as a new (vegetative) recruit to be censused and tagged (or should we create two new tags?). But then the question arose as to which ramet should maintain the original tag. Again, we thought it was logical that the liana still attached to the original rooting point should keep the original tag, but that was *not*, given the circumstances, the liana with the original tag attached (and associated PDM)—the G/R protocol had tricked us and made evident the incongruousness between method and (our) logic.

Our solution to the complications above explained, and various others that we painstakingly faced, was rather elementary. In 2008, instead of applying the G/R protocol to locate PDM’s, we decided to use a much simple, practical and inclusive method: the “Basal” protocol. This protocol simply dictates that the PDM should be located at any point along a liana stem with minor or no growth irregularities, preferably within the first tens of centimeters (at 20 cm if possible) from the presumable original rooting point of a liana, preferably before the first branch independent of its diameter, and if possible away from adventitious roots. When this broad Basal protocol can not be easily applied or results in a nonsense measurement (e.g., when the diameter in the basal area of a stem is much lower than in other stem areas and thus it is not representative, or when a liana has multiple branches originating from almost the same point at ground level, etc.), the "Basal" PDM should be simply located at any visible, but not deformed, *representative* area of the *main* stem, and the arbitrary location should be explained in the datasheet. From our experience, to decide the location of a "representative" area is usually commonsense—i.e., there is not really a need for convoluted protocols (like the G/R or the G/S protocols).

Because a Basal protocol—or other similar protocol—is more inclusive, it increases the measured diversity, abundance, and basal area of a liana community, as well as the estimated biomass (Schnitzer, DeWalt, and Chave 2006). At the YFDP, however, measurements of basal area and estimates of biomass at the *individual* level, are not apparently very affected, according to what we observed in a random sample of 217 lianas where both diameters were measured ($y=1.024x-0.087$, where y=G/R diameter and x=Basal diameter; $R^2=0.852$; see Data Analyses section). In a long-term study of forest dynamics, like that in the 50-ha YFDP, to include more individuals in the sample is certainly a plus because demographic rates will better reflect reality (be more accurate). For this reason—not to mention the added benefit of unambiguity during its application in recensuses (see example above)—we plan to continue using the "Basal" protocol for sampling lianas in the YFDP. In general, it is after all a straightforward method, just like the Diameter at Breast Height (DBH) is for trees. An alternative for sampling a community more completely is of course the use of a lower diameter cutoff (Gerwing et al. [2006] suggest 0.5 cm) or no diameter cutoff at all (e.g., Nabe-Nielsen 2001). Although in certain tropical rainforests such approach can easily duplicate the number of individuals sampled (e.g., Romero-Saltos 1999), in the Yasuní terra firme forest, liana abundance estimates from different studies were very similar whether lianas <1 cm were included or not (Nabe-Nielsen 2001, Burnham 2002; see Results section). In any case, even if lianas <1 cm were abundant in the YFDP area, because of the large-scale and detailed sampling scheme, the costs of sampling them will probably outdo the benefits.

Comparisons between YFDP and other studies that use different protocols should be possible as long as one always measures, in addition to the Basal diameter, the diameters at PDM's based on the G/R or G/S protocols. Sometimes, the PDM's of these different protocols will coincide, in particular the G/R and G/S PDM's. To clarify, we prepared a Figure (shown at the end of this Appendix) based on different graphical examples of lianas that appeared in Gerwing et al. (2006) and Schnitzer, Rutishauser, and Aguilar (2008), and which are reproduced here with permission of the publisher ELSEVIER. The G/R PDM's are depicted by **green lines**, while the Basal PDM's are depicted by **red lines**. The alphabetical codes of branch PDM's and other special PDM's in these two protocols are tagged with **green uppercase letters**. The G/S PDM's are shown as black lines, along with the black uppercase letters used by Gerwing et al. (2006) and Schnitzer, Rutishauser, and Aguilar (2008) to identify each case. Cases I, L and N are lianas that would not be sampled under the G/S criteria but that would be sampled under our more inclusive G/R criteria. To exemplify the use of the G/R "liana appearance" system, below each liana we also indicate its corresponding "appearance" code (see below).

The “Gerwing/Romero” (G/R) protocol: a key of liana appearances

General guidelines—To successfully apply the G/R protocol to locate the Point(s) of Diameter Measurement (PDM) of a liana, it is necessary to keep in mind the following guidelines:

(1) Locate on the ground the presumable original rooting point of a liana and consider it the reference to apply the G/R PDM location criteria. Specially in prostrate lianas, the original rooting point may not necessarily be the principal (thickest) rooting point which sometimes may be even located several meters from the original one. In contrast to this protocol, Gerwing et al. (2006) and Schnitzer, Rutishauser, and Aguilar (2008) stressed that the principal, not the original, rooting point should be the one used as a reference to apply their protocols (and if a liana is prostrate, they even proposed that the principal rooting point should be the last substantial rooting point before the stem ascends for the last time). However, from our own field experience (unpublished recensus data), to use the original rooting point instead of the principal rooting point—and, actually, to use a “Basal” PDM instead of the G/R PDM—makes it much easier to resolve potentially confusing situations during recensuses (see above).

(2) Measure the initial reference distances (40 cm and 130 cm) from the original rooting point and following any curvature of the stem. In fact, always follow the stem curvature to measure any distance along a stem.

(3) Decide which stem is acting as the main stem from which the present branches developed. This is important to apply the criteria effectively and to properly measure and tag branches (see guideline # 9). The distinction between main stem and branches may not be always obvious, e.g. when the oldest stems are thinner than the younger stems, or

when the liana has determinate growth. A thick branch that in practice has become a continuation of the main stem, i.e. its diameter is similar to that of the main stem and is growing in the same direction, could be effectively be considered not a branch anymore. We however leave this decision up to the researcher's criteria.

(4) Do not confuse leafless, aerial, vertical branches whose tips have rooted, with true aerial roots. Node scars, present only in branches, should help to distinguish them.

(5) Remember that stolons or "runners" (creeping stems) coming out from the main stem are, indeed, branches.

(6) Consider all reachable branches (i.e., at a person's reach, say <3 m height) for the application of the criteria, independent of their diameter. This contrasts with what was suggested by Schnitzer, Rutishauser, and Aguilar (2008) who recommended that branches under a given cutoff diameter should be ignored. We disagree with such recommendation because a branch with diameter <1 cm will probably have a diameter ≥1 cm in the next census and may provoke confusion if the original PDM mark disappears. This potential confusion may be avoided if, as we recommend, all branches independent of their diameter are taken into account for the application of the criteria because then the location of the original PDM could be approximated if the original mark is lost (unless of course the branches fall). When a branch is taken as a reference, we recommend to mark it (paint it) along with the PDM on the main stem.

(7) Remember that leaf petioles, no matter how long or thick, are not "branches". This is particularly relevant in lianas with leaves with long petioles that grow directly from the main stem (e.g., some *Bauhinia*).

(8) Realize that a host stem can be any stem (live or dead), not only a tree trunk.

(9) For multi–stemmed lianas (including “multi–stranded” lianas), the G/R protocol simply dictates that all all primary and secondary branches greater than the diameter cutoff (e.g., ≥1 cm in this study) and at a person’s reach (approximately <3 m height) should be measured and tagged. This also applies to those “strands” resulting from the rupture of a single stem (as in some *Bauhinia*). A branch PDM should be located at 5–20 cm from the branching point, i.e. it is basically a “Basal” PDM. The branches should be tagged with the same tag number as the main stem but followed by a letter or set of letters that uniquely identifies them (i.e., A, B, C... etc. for primary branches; AA, AB... BA, BB... CA... etc. for secondary branches; see accompanying figure). In addition, creeping or rooted branches should be again measured as they ascend to the canopy for the last time. For such PDM’s, in this study we added an “ –S” code to the tag (from the Spanish word “Sube”; see accompanying figure). For long-term monitoring, we argue that liana branches should be sampled whenever possible because some (many?) lianas tend to produce ramets from them, especially if the branches form roots.

(10) To complement the “appearance” codes (see below), classify the lianas into three “growth stage” categories: climbing liana, free–standing non–climbing liana (treelet–like), or neither of them (e.g. a fallen branch that has rooted and leafed but it is not yet climbing). If a liana that is “neither climbing nor free–standing” is also a “ground–to–ground” liana forming an “arch”, include it in the sample and describe it as such (as opposed to what Schnitzer, Rutishauser, and Aguilar 2008 recommend).

(11) Realize that our G/R PDM criteria are not strict and that the PDM can be moved to a more suitable place if the researcher has logical reasons to do so (e.g., when the G/R PDM falls on a deformed place of the stem, or in other special cases that we have failed

to anticipate). In such a case, an explanation in the field datasheet should suffice. The important thing is to always mark (paint) the PDM and attach the tag next to it.

The G/R protocol—In the Gerwing/Romero (G/R) protocol, the general "appearance" of a liana is described by a classification key, in which the codes within a square □ are the end points of the classification. It is at these end points that G/R instructions to locate the Point(s) of Diameter Measurement (PDM) are given (in blue). The classification of "appearances" is not perfect (foolproof), but worked well for the great majority of lianas in the Yasuní Forest Dynamics Plot.

1 Creeping liana (i.e., a liana with often multiple rooting points, with a creeping [or almost creeping] main stem OR branch; creeping can be along the soil or along any other surface) with original rooting point clearly defined (Note: free–standing lianas with, usually short, creeping stems are included under this criterion)

11 Branches at a person's reach; main stem with or without aerial adventitious roots

11a In the first 130 cm, main liana stem is *completely aerial* and has branches (creeping or not)

11a1 First branch present at less than or at 40 cm. Measure main stem at halfway between first branching point and ground level (attach main tag here). If applicable, measure also the main stem at 130 cm from the last point touching the ground as the stem finally ascends (a duplicate of the main tag, but with "M-S" code should be attached here). In addition, measure and tag every accessible branch (with diameter greater than the diameter cutoff) at 5–20 cm from the branching point; if applicable, also measure branches at 130 cm from the last point touching the ground as they ascend for the last time (a duplicate of the main branch tag, but with "-S" code should be attached here).

11a2 First branch present between 40 and 130 cm. Measure main stem at 20 cm below first branching point (attach main tag here). If applicable, measure also the main stem at 130 cm from the last point touching the ground as the stem finally ascends (a duplicate of the main tag, but with "M-S" code should be attached here). In addition, measure and tag every accessible branch (with diameter greater than the diameter cutoff) at 5–20 cm from the branching point; if applicable, also measure branches at 130 cm from the last point touching the ground as they ascend for the last time (a duplicate of the main branch tag, but with "-S" code should be attached here).

11b In the first 130 cm, main liana stem is *completely aerial* and does NOT have any branches. Measure main stem at 130 cm from the original rooting point (attach main tag here). If applicable, measure also the main stem at 130 cm from the last point touching the ground as the stem finally ascends (a duplicate of the main tag, but with "M-S" code should be attached here). In addition, measure and tag every accessible branch (with diameter greater than the diameter cutoff) at 5–20 cm from the branching point; if applicable, also measure branches at 130 cm from the last point touching the ground as they ascend for the last time (a duplicate of the main branch tag, but with "-S" code should be attached here).

11c In the first 130 cm, main liana stem is creeping at any point. Measure main stem at a representative point, preferably where the liana is thicker and the main tag is relatively visible. We suggest, if possible, to measure at 20 cm below or above the first branching point, even if that results on a tag at ground level. Do not take into account at what distance from the original rooting point such first branch is. If applicable, measure also the main stem at 130 cm from the last point touching the ground as the stem finally ascends (a duplicate of the main tag, but with "M-S" code should be attached here). In addition, measure and tag every accessible branch (with diameter greater than the diameter cutoff) at 5–20 cm from the branching point; if applicable, also measure branches at 130 cm from the last point touching the ground as they ascend for the last time (a duplicate of the main branch tag, but with "-S" code should be attached here).

12 Branches above a person's reach, OR liana without branches

121 Without well developed, woody, aerial adventitious roots

121a In the first 130 cm, main liana stem is NOT creeping. Measure main stem at 130 cm from the original rooting point (attach main tag here). If applicable, measure also the main stem at 130 cm from the last point touching the ground as the stem finally ascends (a duplicate of the main tag, but with "M-S" code should be attached here).

121b In the first 130 cm, main liana stem is creeping at any point. Measure main stem at 130 cm from the last point touching the ground as the stem finally ascends (attach main tag here).

122 With well developed, woody, aerial adventitious roots reaching the soil

122a In the first 130 cm, main liana stem is NOT creeping. Measure main stem at 50 cm after the last aerial adventitious root (attach main tag here).

122b In the first 130 cm, main liana stem is creeping at any point. Measure main stem at 50 cm after the last aerial adventitious root (attach main tag here).

2 Non–creeping liana (not even with creeping branches) with original rooting point clearly defined

21 Branches present at less than or at 130 cm

211 First branch present at less than or at 40 cm; if the main liana stem is voluble, it does NOT circumnutate the host stem at less than or at 40 cm. Measure main stem at halfway between first branching point and ground level (attach main tag here). Measure and tag every accessible branch (with diameter greater than the diameter cutoff) at 5–20 cm from the branching point.

211V First branch present at less than or at 40 cm, and with a voluble main stem that fully circumnutates the host stem starting at less than or at 40 cm. Measure main stem at 130 cm from the original rooting point (attach main tag here). For practicality, the diameter at breast height can be measured instead. Measure and tag every accessible branch (with diameter greater than the diameter cutoff) at 5–20 cm from the branching point.

212 First branch present between 40 and 130 cm; if the main liana stem is voluble, it does NOT circumnutate the host stem at less than or at 40 cm. Measure main stem at 20 cm below first branching point (attach main tag here). Measure and tag every accessible branch (with diameter greater than the diameter cutoff) at 5–20 cm from the branching point.

212V First branch present between 40 and 130 cm, and with a voluble main liana stem that fully circumnutates the host stem starting at less than or at 40 cm. Measure main stem at 130 cm from the original rooting point (attach main tag here). For practicality, the diameter at breast height can be measured instead. Measure and tag every accessible branch (with diameter greater than the diameter cutoff) at 5–20 cm from the branching point.

22 Branches present at more than 130 cm

22N First branch NOT at a person’s reach

22NV **(or 22N1)** Main liana stem is voluble and fully circumnutates the host stem starting at less than or at 130 cm. Measure main stem at 130 cm from the original rooting point (attach main tag here). For practicality, the diameter at breast height can be measured instead.

22N2 Main liana stem reaches host stem after 130 cm, OR liana does not have a host plant

22N21 Either without any adventitious roots, OR with small adventitious roots not reaching the soil, OR with well developed and woody adventitious roots reaching the soil but growing from the main stem at less than 130 cm. Measure main stem at 130 cm from the original rooting point (attach main tag here).

22N22 With well developed and woody adventitious roots reaching the soil and growing from the main stem above 130 cm. Measure main stem at 50 cm after the last aerial adventitious root (attach main tag here).

22S First branch at a person’s reach

22SV **(or 22S1)** Main liana stem is voluble and fully circumnutates the host stem starting at less than or at 130 cm. Measure main stem at 130 cm from the original rooting point (attach main tag here). For practicality, the diameter at breast height can be measured instead. Measure and tag every accessible branch (with diameter greater than the diameter cutoff) at 5–20 cm from the branching point.

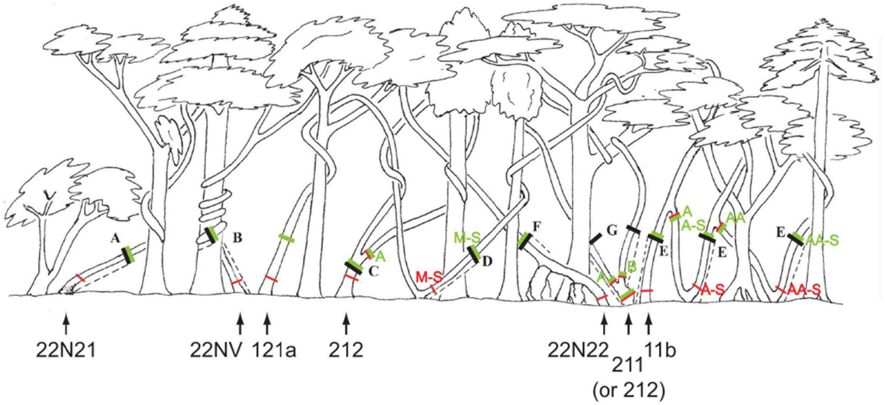
22S2 Main liana stem reaches host stem after 130 cm, OR liana does not have a host plant

22S21 Either without any adventitious roots, OR with small adventitious roots not reaching the soil, OR with well developed and woody adventitious roots reaching the soil but growing from the main stem at less than 130 cm. Measure main stem at 130 cm from the original rooting point (attach main tag here). Measure and tag every accessible branch (with diameter greater than the diameter cutoff) at 5–20 cm from the branching point.

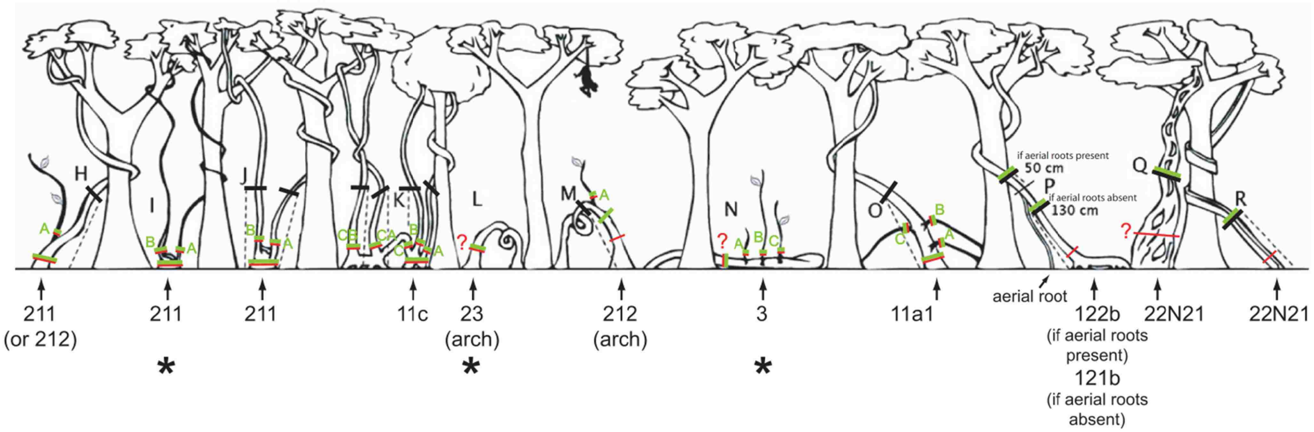
22S22 With well developed and woody adventitious roots reaching the soil and growing from the main stem above 130 cm. Measure main stem at 50 cm after the last aerial adventitious root (attach main tag here). Measure and tag every accessible branch (with diameter greater than the diameter cutoff) at 5–20 cm from the branching point.

23 Liana with no branches (e.g., young liana with unbranched main stem from which leaves come out directly; or ground-to-ground lianas with no stem/leaf sprouts). Measure main stem at 130 cm from the original rooting point or, if this is not possible, at an arbitrary representative non-deformed point along the main stem where the tag is clearly visible.

3 Rooted liana whose presumable original rooting point cannot be clearly defined, and/or the location of its PDM is dificult/impossible to assign following the criteria above. Lianas that are “neither climbing nor free-standing” and that are usually creeping (e.g., a live fallen branch that has randomly rooted and leafed successfully) tend to fall in this category. Measure main stem at a non–deformed point near a rooting point, or at an arbitrary area representative of the main stem or the main branch. Measure and tag every accessible branch (with diameter greater than the diameter cutoff) at 5–20 cm from the branching point.



The code "M-S" means "Main stem that ascends ["SUBE", in Spanish] to the canopy for the last time". This "-S" code is also used for branches.



* = Cases that are excluded from the sample according to G/S protocol, but not according to G/R protocol.

Appendix 1 Figure. Graphical comparison between the Gerwing/Schnitzer protocol (Gerwing et al. 2006, Schnitzer et al. 2008) and the Gerwing/Romero protocol used in the present study. See text for more information. Original figures were modified with permission fromthe publisher .

APPENDIX 2

Abundance (as # individuals) and frequency (as # quadrats) of all liana taxa (families, genera, and species–level taxa [species and morphospecies]) censused in thirty 20×20 m quadrats (1.2 ha) established in the ridge (N = 17 quadrats) and the valley (N = 13 quadrats) topographic habitats of the Yasuní Forest Dynamics Plot.

The list is ordered alphabetically from family to species. Morphospecies are indicated with a "$" code, and their names, arbitrarily created, are within quotation marks (for practical purposes, given the high diversity of lianas present, we have decided not to enumerate the morphospecies as "sp. 1", "sp. 2", etc.). Acronyms of species-level taxa were formed by the first three letters of the genus in UPPERCASE followed (usually) by the first three letters of the species epithet (or the morphospecies name) in lowercase. All species-level taxa, even if the genus or family was unknown, were assigned a species-level name. When the genus was unknown, it was codified as "Zzz"; when the family was unknown, it was codified as "ZZZ". Lianas that were neither identified nor collected (180 lianas) were codified as "Zzz zzz".

The best collections of each species-level taxon (H. Romero-Saltos' collections) were selected as official botanical vouchers; these are deposited at the QCA herbarium at the Pontificia Universidad Católica del Ecuador and at the informal reference herbarium of the YFDP project at Yasuní Research Station. However, at QCA not all specimens were mounted because of internal herbarium regulations on specimens quality (indicated by NM). Duplicates of some species were also donated to other herbaria (see Methods). More than one voucher was sometimes selected to better represent the morphological variation of a taxon.

The species that formed part of the set of 80 most common species—which were arbitrarily defined as those with total abundance ≥5 individuals and total frequency ≥2 quadrats—are indicated with a "80MC" code. The species that formed part of the set of 31 most dominant species—those species among the 20 most abundant in the whole sampled area, or in ridge habitat only, or in valley habitat only, OR those species among the 10 most frequent in the whole area sampled, or in ridge habitat only or in valley habitat only—are indicated with a "31MD" code (see Table 2.3).

FAMILY ***Genus*** **80MC? 31MD?**	***Species-level taxon***	**Acronym**	**Vouchers (HRS #)**	**ridge abund.**	**ridge freq.**	**valley abund.**	**valley freq.**
ACANTHACEAE				**11**	**7**	**9**	**6**
Mendoncia				**11**	**7**	**9**	**6**
	Mendoncia glabra Poepp. & Endl.	MENgla	2443	3	3	1	1
80MC	*Mendoncia* cf. *glomerata* Leonard	MENglo	2593	6	5	7	5
	Mendoncia sericea Leonard	MENser	1823	2	1	1	1
AMARANTHACEAE				**1**	**1**	**1**	**1**
Chamissoa				**1**	**1**	**1**	**1**
	Chamissoa altissima (Jacq.) Kunth	CHAalt	2600	1	1	1	1
APOCYNACEAE				**23**	**11**	**11**	**7**
Forsteronia				**22**	**11**	**3**	**3**
80MC	*Forsteronia acouci* (Aubl.) A. DC.	FORaco	2282	9	6	2	2
80MC-31MD	*Forsteronia affinis* Müll. Arg.	FORaff	2632	13	7	1	1
Odontadenia				**1**	**1**	**8**	**7**
	Odontadenia funigera Woodson	ODOfun	1963	0	0	2	2
	Odontadenia puncticulosa (Rich.) Pulle	ODOpun	3661	0	0	4	4
	Odontadenia stemmadeniifolia Woodson	ODOste	1729	1	1	2	2
ARECACEAE				**6**	**4**	**1**	**1**
Desmoncus				**6**	**4**	**1**	**1**
80MC	*Desmoncus orthacanthos* Mart.	DESort	2085	6	4	1	1
ARISTOLOCHIACEAE				**4**	**4**	**1**	**1**
Aristolochia				**4**	**4**	**1**	**1**
	Aristolochia cf. *fragrantissima* Ruiz	ARIfra	2337	1	1	0	0
	Aristolochia guentheri O.C. Schmidt	ARIgue	1527	2	2	0	0
	Aristolochia lagesiana Ule	ARIlag	3122	0	0	1	1
	Aristolochia "suavecafe" $	ARIsua	3051	1	1	0	0
ASTERACEAE				**11**	**6**	**13**	**6**
Ichthyothere				**0**	**0**	**2**	**1**
	Ichthyothere scandens S.F. Blake	ICHsca	3026	0	0	2	1
Mikania				**6**	**6**	**10**	**5**
	Mikania guaco Bonpl.	MIKgua	2646	0	0	1	1
80MC	*Mikania hookeriana* DC.	MIKhoo	1730	5	5	1	1
80MC	*Mikania* cf. *leiostachya* Benth.	MIKlei	2569	1	1	6	4
	Mikania "cornuda" $	MIKcor	2467	0	0	1	1
	Mikania "like-weber" $	MIKlik	1957	0	0	1	1
Piptocarpha				**5**	**2**	**1**	**1**
80MC	*Piptocarpha lechleri* (Sch. Bip.) Baker	PIPlec	2280	5	2	1	1
BIGNONIACEAE				**77**	**15**	**85**	**13**

FAMILY ***Genus*** **80MC? 31MD?**	***Species-level taxon***	**Acronym**	**Vouchers (HRS #)**	**ridge abund.**	**ridge freq.**	**valley abund.**	**valley freq.**
Adenocalymna				**24**	**5**	**0**	**0**
80MC-31MD	*Adenocalymna impressum* (Rusby) Sandwith	ADEimp	2602	24	5	0	0
Amphilophium				**4**	**4**	**1**	**1**
	Amphilophium crucigerum (L.) L.G. Lohmann	AMPcru	2438	1	1	0	0
	Amphilophium magnoliifolium (Kunth) L.G. Lohmann	AMPmag	2907	3	3	1	1
Bignonia				**10**	**3**	**10**	**4**
80MC-31MD	*Bignonia aequinoctialis* L.	BIGaeq	3502,3710	10	3	7	2
	Bignonia hyacinthina (Standl.) L.G.Lohmann	BIGhya	3687	0	0	1	1
	Bignonia sciuripabala (Bureau & Schum.) L.G. Lohmann	BIGsci	2812	0	0	2	1
Callichlamys				**24**	**5**	**29**	**8**
80MC-31MD	*Callichlamys latifolia* (Rich.) K. Schum.	CALlat	1580, 3140	24	5	29	8
Fridericia				**7**	**5**	**16**	**5**
	Fridericia nicotianiflora (Kraenzl.) L.G. Lohmann	FRInic	2736	0	0	5	1
80MC-31MD	*Fridericia schummaniana* (Loes) L.G. Lohmann	FRIsch	2119	6	4	11	5
	Fridericia "pelischumma" $	FRIpel	2435	1	1	0	0
Mansoa				**0**	**0**	**11**	**5**
80MC-31MD	*Mansoa verrucifera* (Schltdl.) A.H. Gentry	MANver	2214, 3108	0	0	11	5
Martinella				**2**	**2**	**2**	**2**
	Martinella obovata (Kunth) Bureau & K. Schum.	MARobo	2055	2	2	2	2
Stizophyllum				**5**	**4**	**7**	**5**
	Stizophyllum inaequilaterum Bureau & K. Schum.	STIina	2831	0	0	2	2
80MC	*Stizophyllum riparium* (Kunth) Sandwith	STIrip	2959	5	4	5	3
Tanaecium				**1**	**1**	**8**	**5**
80MC	*Tanaecium affine* (A. H. Gentry) L. G. Lohmann	TANaff	3780	0	0	5	3
	Tanaecium pyramidatum (Rich.) L.G. Lohmann	TANpyr	2836	1	1	3	2
Zzz							
	Zzz "miriam" $	ZZZmir	1897^{NM}	0	0	1	1
BORAGINACEAE				**7**	**7**	**7**	**6**
Tournefortia				**7**	**7**	**7**	**6**
	Tournefortia angustiflora Ruiz & Pav.	TOUang	2954	0	0	1	1
80MC	*Tournefortia bicolor* Sw.	TOUbic	2247	3	3	2	2
80MC	*Tournefortia coriacea* Vaupel	TOUcor	2499	1	1	4	3
	Tournefortia ulei Vaupel	TOUule	2238	1	1	0	0
	Tournefortia "peluda" $	TOUpel	2796	2	2	0	0
COMBRETACEAE				**46**	**8**	**95**	**12**
Combretum				**46**	**8**	**95**	**12**
80MC-31MD	*Combretum laxum* Jacq.	COMlax	2151	46	8	95	12
CONNARACEAE				**23**	**11**	**11**	**6**
Connarus				**12**	**6**	**3**	**2**
80MC	*Connarus patrisii* (DC.) Planch.	CONpat	2895	7	4	3	2
80MC	*Connarus punctatus* Planch.	CONpun	2534	5	3	0	0
Pseudoconnarus				**1**	**1**	**0**	**0**
	Pseudoconnarus agelaeoides (G. Schellenb.) Forero	PSEage	2228	1	1	0	0
Rourea				**10**	**8**	**8**	**6**
80MC	*Rourea amazonica* (Baker) Radlk.	ROUama	3062	4	3	4	3
80MC	*Rourea camptoneura* Radlk.	ROUcam	1645	6	5	4	3
CONVOLVULACEAE				**16**	**11**	**15**	**6**
Dicranostyles				**8**	**8**	**6**	**4**
	Dicranostyles ampla Ducke	DICamp	1528	1	1	0	0

FAMILY ***Genus*** **80MC? 31MD?**	***Species-level taxon***	**Acronym**	**Vouchers (HRS #)**	**ridge abund.**	**ridge freq.**	**valley abund.**	**valley freq.**
80MC	*Dicranostyles holostyla* Ducke	DIChol	3132	7	7	5	3
	Dicranostyles laxa Ducke	DIClax	2023	0	0	1	1
Maripa				**8**	**7**	**9**	**5**
80MC	*Maripa pauciflora* D.F. Austin	MARpau	2031	2	2	3	3
80MC	*Maripa peruviana* Ooststr.	MARper	1909	5	4	6	3
	Maripa "exfasci" $	MARexf	2590	1	1	0	0
CUCURBITACEAE				**6**	**6**	**5**	**4**
Cayaponia				**3**	**3**	**1**	**1**
	Cayaponia cf. *macrocalyx* Harms	CAYmac	2891	2	2	1	1
	Cayaponia "lobulmany" $	CAYlob	2144	1	1	0	0
Gurania				**1**	**1**	**2**	**2**
	Gurania cf. *acuminata* Cogn.	GURacu	1700	1	1	0	0
	Gurania eriantha (Poepp. & Endl.) Cogn.	GURori	2551	0	0	1	1
	Gurania rhizantha (Poepp. & Endl.) C. Jeffrey	GURrhi	1526	0	0	1	1
Psiguria				**1**	**1**	**2**	**1**
	Psiguria triphylla (Miq.) C. Jeffrey	PSItri	2778	1	1	2	1
Siolmatra				**1**	**1**	**0**	**0**
	Siolmatra pentaphylla Harms	SIOpen	2806	1	1	0	0
DICHAPETALACEAE				**12**	**7**	**14**	**7**
Dichapetalum				**12**	**7**	**14**	**7**
80MC	*Dichapetalum froesii* Prance	DICfro	1639, 3234	3	2	2	1
	Dichapetalum odoratum Baill.	DICodo	1850	0	0	3	1
80MC-31MD	*Dichapetalum spruceanum* Baill.	DICspr	2978	7	3	8	5
	Dichapetalum "jacob" $	DICjac	1803	2	2	1	1
DILLENIACEAE				**24**	**9**	**18**	**9**
Davilla				**1**	**1**	**2**	**2**
	Davilla cf. *kunthii* A. St.-Hil.	DAVkun	3145	1	1	2	2
Doliocarpus				**3**	**3**	**11**	**8**
80MC-31MD	*Doliocarpus dentatus* (Aubl.) Standl.	DOLden	3147	2	2	10	7
	Doliocarpus major J.F. Gmel.	DOLmaj	2921	1	1	1	1
Neodillenia				**1**	**1**	**0**	**0**
	Neodillenia coussapoana Aymard	NEOcou	2780	1	1	0	0
Pinzona				**2**	**1**	**0**	**0**
	Pinzona coriacea Mart. & Zucc.	PINcor	3505	2	1	0	0
Tetracera				**17**	**5**	**5**	**4**
80MC	*Tetracera volubilis* L.	TETvol	2388	7	3	0	0
80MC	*Tetracera willdenowiana* Steud.	TETwil	2894	10	4	5	4
DIOSCOREACEAE				**8**	**4**	**3**	**1**
Dioscorea				**8**	**4**	**3**	**1**
80MC	*Dioscorea* "rayamarilla" $	DIOray	1819, 2174	8	4	3	1
EUPHORBIACEAE				**3**	**3**	**1**	**1**
Omphalea				**1**	**1**	**1**	**1**
	Omphalea diandra L.	OMPdia	2832	1	1	1	1
Plukenetia				**2**	**2**	**0**	**0**
	Plukenetia polyadenia Müll. Arg.	PLUpol	1994	2	2	0	0
FABACEAE				**174**	**17**	**195**	**13**
Acacia				**1**	**1**	**2**	**2**
	Acacia cf. *tenuifolia* (L.) Willd.	ACAten	2217	1	1	2	2
Bauhinia				**54**	**15**	**60**	**13**
	Bauhinia glabra Jacq.	BAUgla	2771	0	0	1	1
80MC-31MD	*Bauhinia guianensis* Aubl.	BAUgui	2823, 2849	29	10	13	6
80MC-31MD	*Bauhinia rutilans* Spruce ex Benth.	BAUrut	1896	16	7	36	9
	Bauhinia "caripeluda" $	BAUcrp	3660	0	0	1	1
	Bauhinia "cariruti" $	BAUcrr	3106	0	0	2	1

FAMILY ***Genus*** **80MC? 31MD?**	***Species-level taxon***	**Acronym**	**Vouchers (HRS #)**	**ridge abund.**	**ridge freq.**	**valley abund.**	**valley freq.**
	Bauhinia "morada" $	BAUmor	1981	0	0	1	1
80MC	*Bauhinia* "peluda" $	BAUpel	2695	6	4	6	3
	Bauhinia "suave" $	BAUsua	3565	3	1	0	0
Clitoria				**53**	**15**	**32**	**11**
80MC-31MD	*Clitoria pozuzoensis* J.F. Macbr.	CLIpoz	1513	53	15	29	11
	Clitoria "plateada" $	CLIpla	2775	0	0	3	1
Dalbergia				**0**	**0**	**1**	**1**
	Dalbergia monetaria L. f.	DALmon	1995	0	0	1	1
Dioclea				**12**	**8**	**2**	**2**
80MC-31MD	*Dioclea* cf. *ucayalina* Harms	DIOuca	3047	12	8	2	2
Machaerium				**51**	**16**	**86**	**12**
80MC-31MD	*Machaerium cuspidatum* Kuhlm. & Hoehne	MACcus	2924	50	16	85	12
	Machaerium quinatum (Aubl.) Sandwith	MACqui	3782	1	1	0	0
	Machaerium "crista" $	MACcri	3093	0	0	1	1
Piptadenia				**0**	**0**	**12**	**4**
80MC-31MD	*Piptadenia anolidurus* Barneby	PIPano	2774	0	0	11	3
	Piptadenia uaupensis Spruce ex Benth.	PIPuau	2204	0	0	1	1
Zzz							
	Zzz "peliblanco" $	ZZZpel	2167, 3364	3	1	0	0
GNETACEAE				**2**	**2**	**3**	**3**
Gnetum				**2**	**2**	**3**	**3**
80MC	*Gnetum peruvianum* sp. nov. in prep. Hyo. Won	GNEper	2325, 2359	2	2	3	3
HIPPOCRATEACEAE				**160**	**17**	**52**	**10**
Anthodon				**6**	**4**	**0**	**0**
80MC	*Anthodon decussatum* Ruiz & Pav.	ANTdec	2142	6	4	0	0
Cheiloclinium				**10**	**8**	**5**	**2**
80MC-31MD	*Cheiloclinium* cf. *cognatum* (Miers) A.C. Sm.	CHEcog	1743, 2634	10	8	5	2
Cuervea				**75**	**16**	**21**	**6**
80MC-31MD	*Cuervea kappleriana* (Miq.) A.C. Sm.	CUEkap	1623	75	16	21	6
Hylenaea				**15**	**10**	**2**	**2**
80MC-31MD	*Hylenaea* cf. *comosa* (Sw.) Miers	HYLcom	3079	15	10	2	2
Peritassa				**13**	**7**	**4**	**4**
80MC-31MD	*Peritassa pruinosa* (Seem.) A.C. Sm.	PERpru	3356	13	7	4	4
Salacia				**21**	**11**	**9**	**6**
	Salacia elliptica (Mart. ex Schult.) G. Don	SALell	1958	1	1	1	1
80MC-31MD	*Salacia multiflora* (Lam.) DC.	SALmul	2265	20	10	6	5
	Salacia cf. *opacifolia* (J.F. Macbr.) A.C. Sm.	SALopa	1923	0	0	2	1
Tontelea				**20**	**10**	**11**	**3**
	Tontelea cf. *emarginata* A.C. Sm.	TONema	1684	3	2	1	1
80MC-31MD	*Tontelea* cf. *fuliginea* Lombardi	TONful	2253, 2904, 3372	17	9	10	3
ICACINACEAE				**11**	**7**	**10**	**6**
Leretia				**11**	**7**	**10**	**6**
80MC-31MD	*Leretia cordata* Vell.	LERcor	1731	11	7	10	6
LILIACEAE				**2**	**2**	**7**	**3**
Smilax				**2**	**2**	**7**	**3**
80MC	*Smilax* "caripoepp" $	SMIcar	2846	1	1	6	3
	Smilax "fina" $	SMIfin	2850	0	0	1	1
	Smilax "lanza" $	SMIlan	2434^{NM}	1	1	0	0
LOGANIACEAE				**16**	**8**	**3**	**2**
Strychnos				**16**	**8**	**3**	**2**
	Strychnos jobertiana Baill.	STRjob	1643	1	1	1	1
80MC	*Strychnos mitscherlichii* M.R. Schomb.	STRmit	2869	5	4	1	1
80MC	*Strychnos ramentifera* Ducke	STRram	3067	7	6	1	1

FAMILY ***Genus*** **80MC? 31MD?**	***Species-level taxon***	**Acronym**	**Vouchers (HRS #)**	**ridge abund.**	**ridge freq.**	**valley abund.**	**valley freq.**
	Strychnos "aspera" $	STRasp	3060	1	1	0	0
	Strychnos "corapeli" $	STRcor	2875	1	1	0	0
	Strychnos "mate" $	STRmat	2362	1	1	0	0
MALPIGHIACEAE				**60**	**16**	**35**	**10**
Alicia				**1**	**1**	**0**	**0**
	Alicia macrodisca (Triana & Planch.) W.R. Anderson	ALImac	2486^{NM}	1	1	0	0
Dicella				**6**	**4**	**10**	**4**
80MC-31MD	*Dicella julianii* (J.F. Macbr.) W.R. Anderson	DICjul	3745	6	4	10	4
Diplopterys				**7**	**5**	**6**	**4**
	Diplopterys cabrerana (Cuatrec.) B. Gates	DIPcab	2244, 3148	3	2	0	0
80MC	*Diplopterys* cf. *lucida* (Rich.) W.R. Anderson & C.Cav. Davis	DIPluc	2995	2	1	4	2
	Diplopterys "carbon" $	DIPcar	1610^{NM}	2	2	1	1
	Diplopterys "opaca" $	DIPopa	2560^{NM}	0	0	1	1
Ectopopterys				**6**	**3**	**3**	**2**
80MC	*Ectopopterys soejartoi* W.R. Anderson	ECTsoe	3252	6	3	3	2
Heteropterys				**2**	**2**	**0**	**0**
	Heteropterys aureosericea Cuatrec.	HETaur	3076	2	2	0	0
Hiraea				**9**	**5**	**8**	**5**
	Hiraea affinis Miq.	HIRaff	2071	2	2	1	1
80MC	*Hiraea fagifolia* (DC.) A. Juss.	HIRfag	3069	2	2	5	3
80MC	*Hiraea valida* W.R. Anderson	HIRval	2599	5	2	2	1
Jubelina				**3**	**2**	**0**	**0**
	Jubelina uleana (Nied.) Cuatrec.	JUBule	2709	3	2	0	0
Mascagnia				**7**	**6**	**4**	**3**
80MC	*Mascagnia* cf. *dissimilis* C.V. Morton & Moldenke	MASdis	1948	2	2	3	2
80MC	*Mascagnia divaricata* (Kunth) Nied.	MASdiv	2355	5	4	1	1
Stigmaphyllon				**2**	**1**	**0**	**0**
	Stigmaphyllon sinuatum (DC.) A. Juss.	STIsin	2406	2	1	0	0
Tetrapterys				**17**	**5**	**2**	**2**
	Tetrapterys cf. *calophylla* A. Juss.	TETcal	2459	0	0	1	1
80MC-31MD	*Tetrapterys nitida* A. Juss.	TETnit	1960	17	5	1	1
Zzz							
	Zzz "hippo" $	ZZZhip	3105	0	0	2	1
MARCGRAVIACEAE				**2**	**2**	**7**	**4**
Marcgravia				**2**	**2**	**6**	**3**
	Marcgravia "micro" $	MARmic	2398	2	2	2	2
	Marcgravia "tetra" $	MARtet	2503	0	0	4	1
Zzz							
	Zzz "diminuta" $	ZZZdim	3102^{NM}	0	0	1	1
MENISPERMACEAE				**25**	**10**	**15**	**8**
Abuta				**4**	**2**	**4**	**2**
	Abuta cf. *pahnii* (Mart.) Krukoff & Barneby	ABUpah	2035^{NM}	1	1	0	0
80MC	*Abuta* cf. *solimoesensis* Krukoff & Barneby	ABUsol	3760	3	1	4	2
Anomospermum				**0**	**0**	**1**	**1**
	Anomospermum "miniterci" $	ANOmin	3112^{NM}	0	0	1	1
Curarea				**10**	**7**	**2**	**2**
80MC	*Curarea tecunarum* Barneby & Krukoff	CURtec	2637	10	7	2	2
Disciphania				**0**	**0**	**1**	**1**
	Disciphania "corazon" $	DIScor	2735^{NM}	0	0	1	1
Odontocarya				**1**	**1**	**2**	**1**
	Odontocarya "exbj" $	ODOexb	2310	1	1	2	1
Sciadotenia				**4**	**3**	**4**	**2**
80MC	*Sciadotenia toxifera* Krukoff & A.C. Sm.	SCItox	1788	4	3	4	2

FAMILY ***Genus*** **80MC? 31MD?**	***Species-level taxon***	**Acronym**	**Vouchers (HRS #)**	**ridge abund.**	**ridge freq.**	**valley abund.**	**valley freq.**
Telitoxicum				**6**	**4**	**1**	**1**
80MC	*Telitoxicum krukovii* Moldenke	TELkru	2785^{NM}	5	3	1	1
	Telitoxicum minutiflorum (Diels) Moldenke	TELmin	2725	1	1	0	0
PASSIFLORACEAE				**6**	**4**	**6**	**5**
Dilkea				**0**	**0**	**4**	**3**
	Dilkea "retuparvi" $	DILret	3001	0	0	4	3
Passiflora				**6**	**4**	**2**	**2**
	Passiflora cf. *ambigua* Hemsl.	PASamb	2436	2	2	0	0
80MC	*Passiflora spinosa* (Poepp. & Endl.) Mast.	PASspi	1521	4	4	2	2
PHYTOLACCACEAE				**1**	**1**	**0**	**0**
Seguieria				**1**	**1**	**0**	**0**
	Seguieria americana L.	SEGame	1753	1	1	0	0
PIPERACEAE				**0**	**0**	**1**	**1**
Piper				**0**	**0**	**1**	**1**
	Piper armatum Trel. & Yunck.	PIParm	3022, 3027	0	0	1	1
POLYGALACEAE				**11**	**6**	**0**	**0**
Moutabea				**11**	**6**	**0**	**0**
80MC-31MD	*Moutabea aculeata* (Ruiz & Pav.) Poepp. & Endl.	MOUacu	2063, 2617	11	6	0	0
POLYGONACEAE				**7**	**5**	**6**	**5**
Coccoloba				**7**	**5**	**6**	**5**
80MC	*Coccoloba excelsa* Benth.	COCexc	2765	1	1	4	4
	Coccoloba cf. *obovata* Kunth	COCobo	2336	4	3	0	0
	Coccoloba "decurrente" $	COCdec	2639, 3402	2	1	2	2
RHAMNACEAE				**1**	**1**	**10**	**4**
Gouania				**1**	**1**	**10**	**4**
	Gouania colombiana Suess.	GOUcol	3094	0	0	3	2
80MC	*Gouania lupuloides* (L.) Urb.	GOUlup	2399^{NM}	1	1	5	1
	Gouania mollis Reissek	GOUmol	2751	0	0	2	1
RUBIACEAE				**5**	**4**	**10**	**1**
Chomelia				**4**	**3**	**10**	**1**
31MD	*Chomelia* cf. *estrellana* Müll. Arg.	CHOest	2825	0	0	10	1
	Chomelia malaneoides Müll. Arg.	CHOmal	2889	4	3	0	0
Randia				**1**	**1**	**0**	**0**
	Randia altiscandens (Ducke) C.M. Taylor	RANalt	2043	1	1	0	0
SOLANACEAE				**4**	**3**	**5**	**1**
Markea				**2**	**1**	**0**	**0**
	Markea coccinea Rich.	MARcoc	2605^{NM}	2	1	0	0
Solanum				**2**	**2**	**5**	**1**
80MC	*Solanum barbeyanum* Huber	SOLbar	1517, 1591	2	2	5	1
SAPINDACEAE				**78**	**17**	**95**	**13**
Paullinia				**69**	**17**	**84**	**13**
80MC	*Paullinia* cf. *alata* G. Don	PAUala	3038, 3056	2	1	4	3
	Paullinia bidentata Radlk.	PAUbid	2606	3	3	0	0
	Paullinia cf. *bilobulata* Radlk.	PAUbil	3394	1	1	3	2
80MC-31MD	*Paullinia bracteosa* Radlk.	PAUbra	3048	17	9	12	6
80MC	*Paullinia* cf. *capreolata* (Aubl.) Radlk.	PAUcap	1596, 3289	3	3	6	4
	Paullinia cf. *clathrata* Radlk.	PAUcla	2817	0	0	1	1
80MC-31MD	*Paullinia dasystachya* Radlk.	PAUdas	1734, 1816, 1898	3	3	9	5
	Paullinia cf. *faginea* (Triana & Planch.) Radlk.	PAUfag	2853	2	2	2	2
	Paullinia fimbriata Radlk.	PAUfim	2232	2	2	2	2
	Paullinia hispida Jacq.	PAUhis	2671, 3419	1	1	1	1
80MC-31MD	*Paullinia ingifolia* Rich ex Juss.	PAUing	2101, 2416, 3325	4	4	9	5
	Paullinia cf. *meliifolia* Juss.	PAUmel	2423	2	1	0	0

FAMILY ***Genus*** **80MC? 31MD?**	***Species-level taxon***	**Acronym**	**Vouchers (HRS #)**	**ridge abund.**	**ridge freq.**	**valley abund.**	**valley freq.**
80MC-31MD	*Paullinia* cf. *microneura* Cuatrec.	PAUmic	2353, 2816	13	6	4	3
80MC	*Paullinia* cf. *obovata* (Ruiz & Pav.) Pers.	PAUobo	1570, 2140, 2699, 2703	7	4	5	4
	Paullinia cf. *paullinioides* Radlk.	PAUpau	2844	1	1	2	2
80MC	*Paullinia* cf. *reticulata* Radlk.	PAUret	1581	1	1	5	3
	Paullinia venosa Radlk.	PAUven	2564, 2648	1	1	3	3
80MC	*Paullinia* "cafe" $	PAUcaf	1873, 2547, 2915	4	4	6	4
80MC	*Paullinia* "corteza" $	PAUcor	1934, 1941, 2583	1	1	6	3
	Paullinia "granpari" $	PAUgra	2468, 2588	0	0	2	2
	Paullinia "longteeth" $	PAUlon	2990	1	1	2	2
Serjania				**4**	**2**	**5**	**4**
80MC	*Serjania pyramidata* Radlk.	SERpyr	2559	4	2	5	4
Thinouia				**5**	**4**	**6**	**1**
80MC	*Thinouia obliqua* Radlk.	THIobl	1905, 1970	5	4	6	1
STERCULIACEAE				**0**	**0**	**1**	**1**
Byttneria				**0**	**0**	**1**	**1**
	Byttneria asterotricha Mildbr.	BYTast	2762^{NM}	0	0	1	1
ULMACEAE				**3**	**2**	**0**	**0**
Celtis				**3**	**2**	**0**	**0**
	Celtis iguanaea (Jacq.) Sarg.	CELigu	2318	3	2	0	0
VERBENACEAE				**99**	**15**	**40**	**9**
Aegiphila				**2**	**1**	**10**	**7**
	Aegiphila cordata Poepp. ex Schauer	AEGcor	2504, 3276	0	0	2	1
	Aegiphila cf. *elata* Kunth	AEGela	3025^{NM}	0	0	1	1
	Aegiphila cf. *mollis* Kunth	AEGmol	2827^{NM}	0	0	3	2
80MC	*Aegiphila* "exelata" $	AEGexe	2976	2	1	4	4
Petrea				**97**	**15**	**30**	**4**
80MC-31MD	*Petrea maynensis* Huber	PETmay	1673	97	15	30	4
VITACEAE				**0**	**0**	**3**	**3**
Cissus				**0**	**0**	**3**	**3**
	Cissus biformifolia Standl.	CISbif	2474, 3153	0	0	2	2
	Cissus cf. *ulmifolia* (Baker) Planch.	CISulm	1864	0	0	1	1
ZZZ ***Zzz***	*Zzz zzz*	*ZZZzzz*		**84**	**17**	**96**	**12**

APPENDIX 3

Diversity and abundance of lianas in studies conducted in Yasuní, including this study. Means were calculated from the sampling unit data shown, or copied from what was reported in the publications. Totals per forest type are also shown. We report: forest type (if terra firme, topographic habitat in parentheses), sampled area, diameter cutoff used, number of species (# spp.) and number of individuals (# ind.). Data from Romero-Saltos, Valencia, and Macía (2001) was re-analyzed excluding the 60 unidentified lianas. The data in boxes □ are those being compared to our study (see Table 2.4). Studies are ordered chronologically.

	Site name	Forest type (if terra firme, topographic habitat is also shown)	Sampled area in ha (dimensions in m)	Diameter cutoff (cm)	# spp.	# ind.
Nabe-Nielsen (2001)						
Sampling unit values	Yasuní 1	terra firme (ridge)	0.2 (20×100)	all lianas	96	318
	Yasuní 2	terra firme (ridge)	0.2 (20×100)	all lianas	86	288
Mean values		terra firme (ridge)	0.2 (20×100), *N*=2	all lianas	91	303
		terra firme (ridge)	0.1 (20×50), *N*=4	all lianas	62	152
		terra firme (ridge)	0.1 (20×50), *N*=4	≥1.0	44	94
		terra firme (ridge)	0.1 (20×50), *N*=4	≥2.5	21	33
Total values		terra firme (ridge)	0.4 (2 × (20×100))	all	138	606
Romero-Saltos, Macía, and Valencia (2001)						
Sampling unit values	02	terra firme (ridge)	0.1 (20×50)	≥2.5	24	43
	04	terra firme (ridge)	0.1 (20×50)	≥2.5	13	21
	05	terra firme (ridge)	0.1 (20×50)	≥2.5	20	41
	06	terra firme (ridge)	0.1 (20×50)	≥2.5	22	36
	07	terra firme (ridge)	0.1 (20×50)	≥2.5	21	49
	15	terra firme (ridge)	0.1 (20×50)	≥2.5	28	57
	16	terra firme (ridge)	0.1 (20×50)	≥2.5	22	31
	17	terra firme (ridge)	0.1 (20×50)	≥2.5	15	24

	Site name	Forest type (if terra firme, topographic habitat is also shown)	Sampled area in ha (dimensions in m)	Diameter cutoff (cm)	# spp.	# ind.
	18	terra firme (ridge)	0.1 (20×50)	≥2.5	23	44
	20	terra firme (ridge)	0.1 (20×50)	≥2.5	14	21
	01	floodplain	0.1 (20×50)	≥2.5	11	24
	03	floodplain	0.1 (20×50)	≥2.5	20	54
	10	floodplain	0.1 (20×50)	≥2.5	13	20
	11	floodplain	0.1 (20×50)	≥2.5	9	21
	12	floodplain	0.1 (20×50)	≥2.5	7	7
	19	floodplain	0.1 (20×50)	≥2.5	13	24
	21	floodplain	0.1 (20×50)	≥2.5	12	47
	22	floodplain	0.1 (20×50)	≥2.5	16	30
	08	swamp	0.1 (20×50)	≥2.5	10	23
	09	swamp	0.1 (20×50)	≥2.5	10	24
	13	swamp	0.1 (20×50)	≥2.5	1	2
	14	swamp	0.1 (20×50)	≥2.5	5	7
	23	swamp	0.1 (20×50)	≥2.5	11	29
	24	swamp	0.1 (20×50)	≥2.5	1	1
	25	swamp	0.1 (20×50)	≥2.5	4	7
Mean values		terra firme (ridge)	0.1 (20×50), *N*=10	≥2.5	20	37
		floodplain	0.1 (20×50), *N*=8	≥2.5	13	28
		swamp	0.1 (20×50), *N*=7	≥2.5	6	13
		terra firme (ridge) & floodplain & swamp	0.1 (20×50), *N*=25	≥2.5	14	27
Total values		terra firme (ridge)	1.0 (10 × (20×50))	≥2.5	117	367
		flood plain	0.8 (8 × (20×50))	≥2.5	70	227
		swamp	0.7 (7 × (20×50))	≥2.5	30	93
		terra firme (ridge) & floodplain & swamp	2.5 (25 × (20×50))	≥2.5	173	687
Burnham (2002), Burnham (2004)						
Sampling unit values	Monkey PC	terra firme (ridge & valley)	0.2 4×500	≥1.0	88	302

	Site name	Forest type (if terra firme, topographic habitat is also shown)	Sampled area in ha (dimensions in m)	Diameter cutoff (cm)	# spp.	# ind.
	Monkey PD	terra firme (ridge & valley)	0.2 4×500	≥1.0	109	314
	Capiron	terra firme (ridge & valley)	0.2 5×(4×100)	≥1.0	104	344
	Aulestia Piraña	terra firme (ridge & valley)	0.2 5×(4×100)	≥1.0	100	433
	Puente TBS	terra firme (ridge & valley)	0.2 5×(4×100)	≥1.0	105	347
	Maquisapa Guacamayo	terra firme (ridge & valley)	0.2 5×(4×100)	≥1.0	86	313
	TBS Floodplain	floodplain	0.2 5×(4×100)	≥1.0	71	360
	Caiman Durmiente	floodplain	0.2 5×(4×100)	≥1.0	72	430
	Yasuni Floodplain	floodplain	0.2 5×(4×100)	≥1.0	87	292
	ECY Floodplain	floodplain	0.2 5×(4×100)	≥1.0	82	435
	Laguna Nutria	floodplain	0.2 5×(4×100)	≥1.0	89	441
	Laguna Hoatzin	floodplain	0.2 5×(4×100)	≥1.0	62	337
Mean values		terra firme (ridge & valley)	0.2 (5×(4×100)), *N*=6	≥1.0	99	342
		floodplain	0.2 (5×(4×100)), *N*=6	≥1.0	71	382
		terra firme (ridge & valley) & floodplain	0.2 (5×(4×100)), *N*=12	≥1.0	88	362
Total values		terra firme (ridge & valley)	1.2 (6 × (5×(4×100))	≥1.0	254	2053
		floodplain	1.2 (6 × (5×(4×100))	≥1.0	179	2295
		terra firme (ridge & valley) & floodplain	2.4 (12 × (5×(4×100))	≥1.0	311	4348
This study						
Sampling unit values	YFDP_R_02,02	terra firme (ridge)	0.04 (20×20)	≥1.0	24	39
	YFDP_R_02,07	terra firme (ridge)	0.04 (20×20)	≥1.0	38	92
	YFDP_R_02,17	terra firme (ridge)	0.04 (20×20)	≥1.0	25	73
	YFDP_R_07,02	terra firme (ridge)	0.04 (20×20)	≥1.0	21	43
	YFDP_R_07,07	terra firme (ridge)	0.04 (20×20)	≥1.0	20	43
	YFDP_R_07,17	terra firme (ridge)	0.04 (20×20)	≥1.0	30	72
	YFDP_R_07,22	terra firme (ridge)	0.04 (20×20)	≥1.0	33	69
	YFDP_R_12,02	terra firme (ridge)	0.04 (20×20)	≥1.0	24	61
	YFDP_R_12,17	terra firme (ridge)	0.04 (20×20)	≥1.0	26	69
	YFDP_R_12,22	terra firme (ridge)	0.04 (20×20)	≥1.0	15	34

	Site name	**Forest type** (if terra firme, topographic habitat is also shown)	**Sampled area in ha (dimensions in m)**	**Diameter cutoff (cm)**	**# spp.**	**# ind.**
	YFDP_R_17,02	terra firme (ridge)	0.04 (20×20)	≥1.0	30	56
	YFDP_R_17,12	terra firme (ridge)	0.04 (20×20)	≥1.0	31	64
	YFDP_R_17,17	terra firme (ridge)	0.04 (20×20)	≥1.0	25	58
	YFDP_R_22,02	terra firme (ridge)	0.04 (20×20)	≥1.0	31	97
	YFDP_R_22,17	terra firme (ridge)	0.04 (20×20)	≥1.0	22	43
	YFDP_R_22,22	terra firme (ridge)	0.04 (20×20)	≥1.0	22	36
	YFDP_R_27,17	terra firme (ridge)	0.04 (20×20)	≥1.0	40	80
	YFDP_V_02,12	terra firme (valley)	0.04 (20×20)	≥1.0	31	96
	YFDP_V_02,22	terra firme (valley)	0.04 (20×20)	≥1.0	12	40
	YFDP_V_07,12	terra firme (valley)	0.04 (20×20)	≥1.0	31	81
	YFDP_V_12,07	terra firme (valley)	0.04 (20×20)	≥1.0	19	44
	YFDP_V_12,12	terra firme (valley)	0.04 (20×20)	≥1.0	25	52
	YFDP_V_17,07	terra firme (valley)	0.04 (20×20)	≥1.0	34	69
	YFDP_V_17,22	terra firme (valley)	0.04 (20×20)	≥1.0	29	83
	YFDP_V_22,07	terra firme (valley)	0.04 (20×20)	≥1.0	20	61
	YFDP_V_22,12	terra firme (valley)	0.04 (20×20)	≥1.0	25	56
	YFDP_V_27,02	terra firme (valley)	0.04 (20×20)	≥1.0	41	100
	YFDP_V_27,07	terra firme (valley)	0.04 (20×20)	≥1.0	26	76
	YFDP_V_27,12	terra firme (valley)	0.04 (20×20)	≥1.0	34	68
	YFDP_V_27,22	terra firme (valley)	0.04 (20×20)	≥1.0	33	64
Mean values		terra firme (ridge)	0.04 (20×20), *N*= 17	≥1.0	27	61
		terra firme (valley)	0.04 (20×20), *N*= 13	≥1.0	28	68
Total values		terra firme (ridge & valley)	1.2 (30 × (20×20))	≥1.0	195	1919

APPENDIX 4

Leaf traits of the 43 liana species included in the functional traits analyses. The habitat association (or non-association) of species was classified (CLASS.) as: *ridge* species (R), *valley* species (V), *generalist* species (G), and *widespread with habitat association* species (W, subclassified in WR: with ridge association, and WV: with valley association) (see Methods, and Tables 3.1 and 3.2). SLA=specific leaf area, LDMC=leaf dry matter content, LT=leaf lamina thickness, L:W=length to width ratio of whole leaf (incl. petiole), LSR=individual-level leaf size range=lamina area of largest leaf observed − lamina area of smallest leaf observed in the same individual, C=carbon concentration, N=nitrogen concentration, P=phosphorus concentration, $\delta^{13}C$=relative abundance of the stable isotope carbon-13 in delta units, $\delta^{15}N$=relative abundance of the stable isotope nitrogen-15 in delta units, C:N=ratio of carbon concentration to nitrogen concentration, N:P=ratio of nitrogen concentration to phosphorus concentration. Species acronyms (in **bold**) were formed by the first three letters of the genus (in UPPERCASE) and the first three letters of the epithet. Names within quotation marks are morphospecies. Family acronyms (in parentheses) were formed by a three-letter code. Species are ordered by family.

Values reported are: mean ± 1 standard deviation, minimum and maximum values (in parentheses) and number of individuals sampled (*N,* in parentheses) (if *N*=2, no mean was calculated).

FAMILY ***Species***	**CLASS.**	**SLA (mm^2/mg)**	**LDMC (mg/g)**	**LT (mm)**	**L:W (ratio)**	**LSR (cm^2)**	**C (%)**	**N (%)**	**P (%)**	**C:N (ratio)**	**N:P (ratio)**	**δ^{13}C**	**δ^{15}N**
APOCYNACEAE (APO)													
***FOR**steronia* ***aff**inis*	R	23±6.8 (13.9–28.5) (*N*=4)	species not sampled	0.08±0.01 (0.07–0.09) (*N*=4)	2.6±0.7 (2.2–3.7) (*N*=4)	33±17 (21–53) (*N*=3)	62–72.2 (*N*=2)	3.2–3.3 (*N*=2)	0.08–0.09 (*N*=2)	19.3–21.8 (*N*=2)	35.4–43.9 (*N*=2)	-34.6 – -31.1 (*N*=2)	2.27-3.59 (*N*=2)
ARECACEAE (ARE)													
***DES**moncus* ***ort**hacanthos*	R	9.6±3.1 (6.1–15.2) (*N*=6)	409.5–452.9 (*N*=2)	0.18±0.03 (0.13–0.21) (*N*=6)	2.6±0.4 (2.2–3.4) (*N*=6)	1061±152 (970–1237) (*N*=3)	36.1–47.3 (*N*=2)	2.4–2.7 (*N*=2)	0.1–0.11 (*N*=2)	13.5–20 (*N*=2)	20.8–26.5 (*N*=2)	-33.9 – -33.3 (*N*=2)	3.15-6.55 (*N*=2)
ASTERACEAE (AST)													
***MIK**ania* ***lei**ostachya*	V	22.5±6 (17.1–34.9) (*N*=7)	175.2 (*N*=1)	0.17±0.03 (0.13–0.22) (*N*=7)	2.6±0.5 (1.8–3.2) (*N*=7)	47±23 (14–72) (*N*=5)	45.7±5.1 (41.1–51.6) (*N*=4)	2.4±0.2 (2.1–2.6) (*N*=4)	0.16±0.02 (0.15–0.18) (*N*=4)	19.1±0.6 (18.6–19.8) (*N*=4)	15.1±1.7 (13.8–17.5) (*N*=4)	-32.2±1.6 (-34.4 – -31) (*N*=4)	3.07±0.44 (2.64-3.56) (*N*=4)
BIGNONIACEAE (BIG)													
***ADE**nocalymna* ***imp**ressum*	R	14.9±4.9 (10.1–25.2) (*N*=10)	398.3±46.4 (345.9–438.6) (*N*=4)	0.14±0.03 (0.12–0.2) (*N*=10)	1.1±0.3 (0.6–1.6) (*N*=10)	144±120 (48–421) (*N*=8)	36.9–42.4 (*N*=2)	3.1–3.6 (*N*=2)	0.13–0.16 (*N*=2)	11.6–11.8 (*N*=2)	22.5–24.3 (*N*=2)	-32.5 – -30.6 (*N*=2)	0.6-1.63 (*N*=2)
***BIG**nonia* ***aeq**uinoctialis*	G	17.2±6.4 (7.7–27.9) (*N*=13)	347.3±63.7 (283.1–460.8) (*N*=7)	0.11±0.02 (0.08–0.16) (*N*=13)	1.1±0.2 (0.8–1.4) (*N*=13)	106±67 (19–229) (*N*=7)	43.1±4.7 (39.8–48.5) (*N*=3)	2.3±0.1 (2.2–2.5) (*N*=3)	0.11±0.01 (0.1–0.12) (*N*=3)	18.6±2.2 (16.2–20.6) (*N*=3)	21.2±2.3 (19–23.7) (*N*=3)	-30.6±1.4 (-32 – -29.2) (*N*=3)	1.96±0.11 (1.89-2.09) (*N*=3)
***MAN**soa* ***ver**rucifera*	V	21.4±3.7 (16.9–27.3) (*N*=7)	424 (*N*=1)	0.09±0.02 (0.08–0.12) (*N*=7)	1±0.2 (0.7–1.3) (*N*=7)	184±127 (46–348) (*N*=4)	45.6–78.9 (*N*=2)	3.9–6.4 (*N*=2)	0.12–0.16 (*N*=2)	11.6–12.4 (*N*=2)	31.9–39.2 (*N*=2)	-36.8 – -33.3 (*N*=2)	1.91-3.96 (*N*=2)
***STI**zophyllum* ***rip**arium*	G	30.4±8.9 (19.4–49.8) (*N*=12)	310±38.1 (277.2–364.6) (*N*=4)	0.08±0.02 (0.04–0.11) (*N*=12)	1.1±0.2 (0.9–1.4) (*N*=12)	177±139 (12–435) (*N*=10)	43–52.4 (*N*=2)	3.4–3.5 (*N*=2)	0.16–0.17 (*N*=2)	12.2–15.4 (*N*=2)	21–21.3 (*N*=2)	-33.3 – -33 (*N*=2)	1.17-3.67 (*N*=2)
***TAN**aecium* ***aff**ine*	V	19.1±6.1 (13.5–25.6) (*N*=3)	245.8 (*N*=1)	0.13±0.03 (0.12–0.17) (*N*=3)	1.2–1.3 (*N*=2)	48–79 (*N*=2)	50±5.9 (43.2–53.6) (*N*=3)	3.4±0.1 (3.3–3.5) (*N*=3)	0.15±0.05 (0.1–0.2) (*N*=3)	14.6±2 (12.5–16.3) (*N*=3)	25.4±8.2 (17.5–33.9) (*N*=3)	-34.1±0.7 (-34.9 – -33.6) (*N*=3)	2.52±1.8 (0.45-3.78) (*N*=3)
BORAGINACEAE (BOR)													
***TOU**rnefortia* ***bic**olor*	G	18.8±7.8 (11.6–32.7) (*N*=8)	213.9±36.4 (158–258.4) (*N*=5)	0.29±0.11 (0.16–0.45) (*N*=8)	2.3±0.5 (1.4–2.8) (*N*=8)	67±29 (36–120) (*N*=7)	41.1±1.7 (38.7–42.5) (*N*=4)	2.8±0.8 (1.6–3.3) (*N*=4)	0.14±0.08 (0.07–0.24) (*N*=4)	16±5.4 (12.2–24) (*N*=4)	24.9±15.1 (12.1–46.8) (*N*=4)	-34.1±0.8 (-34.8 – -33) (*N*=4)	1.99±1.17 (1.01-3.38) (*N*=4)
COMBRETACEAE (COM)													
***COM**bretum* ***lax**um*	WV	13.8±3.2 (9–23.7) (*N*=31)	422.6±59.6 (246.9–527.3) (*N*=15)	0.12±0.02 (0.09–0.18) (*N*=31)	3.1±0.4 (2.1–4.4) (*N*=31)	49±26 (16–117) (*N*=25)	41.6±3.8 (37.7–45.2) (*N*=3)	2±0.3 (1.7–2.2) (*N*=3)	0.1±0.01 (0.08–0.11) (*N*=3)	21.6±4.5 (18.6–26.7) (*N*=3)	21±6.4 (15.6–28.1) (*N*=3)	-31.3±1 (-32.4 – -30.7) (*N*=3)	1.91±1.62 (0.88-3.77) (*N*=3)
CONNARACEAE (CNN)													
***CON**narus* ***pat**risii*	G	9.4±1 (8–11.5) (*N*=10)	472.6±78.6 (357.7–570.5) (*N*=5)	0.15±0.02 (0.12–0.18) (*N*=10)	1.5±0.3 (0.9–2) (*N*=10)	479±291 (148–839) (*N*=4)	50.7±5.1 (46.5–56.3) (*N*=3)	1.9±0.3 (1.6–2.2) (*N*=3)	0.1±0.01 (0.08–0.1) (*N*=3)	27.2±1.9 (25.1–28.8) (*N*=3)	20.3±6.2 (16.3–27.5) (*N*=3)	-34.6±0.8 (-35.3 – -33.7) (*N*=3)	1.9±1.78 (-0.06-3.4) (*N*=3)

FAMILY ***Species***	**CLASS.**	**SLA (mm^2/mg)**	**LDMC (mg/g)**	**LT (mm)**	**L:W (ratio)**	**LSR (cm^2)**	**C (%)**	**N (%)**	**P (%)**	**C:N (ratio)**	**N:P (ratio)**	**δ^{13}C**	**δ^{15}N**
__ROU__rea __ama__zonica	G	12.2±3.7 (7.1–20) (*N*=10)	542.5±95 (442.5–665.6) (*N*=7)	0.18±0.03 (0.13–0.21) (*N*=10)	1.3±0.4 (0.8–1.8) (*N*=10)	192±150 (26–432) (*N*=7)	43.6±3.5 (40.5–47.3) (*N*=3)	1.9±0.4 (1.5–2.3) (*N*=3)	0.1±0.02 (0.07–0.12) (*N*=3)	23.1±3.9 (18.9–26.5) (*N*=3)	19.6±1 (18.8–20.8) (*N*=3)	-34.8±1.6 (-36.6 – -33.4) (*N*=3)	0.75±0.66 (0.02-1.3) (*N*=3)
__ROU__rea __camp__toneura	G	16.2±4.3 (7.5–22.8) (*N*=10)	371±95.3 (285.5–504.6) (*N*=4)	0.14±0.04 (0.1–0.25) (*N*=10)	1.3±0.2 (1–1.6) (*N*=10)	328±295 (78–654) (*N*=3)	47.3±1.5 (46.2–49) (*N*=3)	2.3±0.3 (1.9–2.5) (*N*=3)	0.09±0.03 (0.07–0.12) (*N*=3)	21±2.7 (19–24.1) (*N*=3)	27.4±10.6 (16.4–37.4) (*N*=3)	-33.3±2.4 (-34.7 – -30.5) (*N*=3)	2.11±0.8 (1.5-3.01) (*N*=3)
CONVOLVULACEAE (CNV)													
__MAR__ipa __peru__viana	G	20.6±5.1 (15.2–30.8) (*N*=16)	322.3±63.3 (205.7–412.4) (*N*=10)	0.13±0.02 (0.1–0.16) (*N*=16)	3.6±0.3 (3.2–4) (*N*=16)	75±32 (36–142) (*N*=13)	45.7–49.4 (*N*=2)	2.9–3.4 (*N*=2)	0.09–0.17 (*N*=2)	13.5–17.2 (*N*=2)	20.5–33.3 (*N*=2)	-34.1 – -33.6 (*N*=2)	1.54-2.46 (*N*=2)
DICHAPETALACEAE (DIC)													
__DIC__hapetalum __fro__esii	G	14.5±4.8 (10.3–20.1) (*N*=6)	369.6±26.5 (347.4–403.6) (*N*=4)	0.17±0.03 (0.14–0.23) (*N*=6)	2.7±0.5 (1.9–3.1) (*N*=6)	78±17 (60–100) (*N*=4)	54.1–61.5 (*N*=2)	3.4–3.6 (*N*=2)	0.09–0.1 (*N*=2)	15.7–17.1 (*N*=2)	35.8–38.8 (*N*=2)	-34.6 – -33.9 (*N*=2)	4.85-5.16 (*N*=2)
__DIC__hapetalum __spr__uceanum	G	13.5±2.7 (9.1–18.5) (*N*=17)	383±47.4 (335.2–492.6) (*N*=9)	0.16±0.03 (0.1–0.22) (*N*=17)	1.9±0.3 (1.3–2.4) (*N*=17)	279±152 (102–471) (*N*=9)	43.1–60.6 (*N*=2)	2.4–3.7 (*N*=2)	0.08–0.09 (*N*=2)	16.2–18.2 (*N*=2)	30.5–39.7 (*N*=2)	-34.6 – -34.4 (*N*=2)	3.41-4.77 (*N*=2)
DILLENIACEAE (DIL)													
__DOL__iocarpus __den__tatus	V	18.2±4.7 (11.2–25.8) (*N*=14)	287.3±59.5 (198.3–415.7) (*N*=12)	0.17±0.03 (0.13–0.25) (*N*=14)	2.6±0.3 (2.1–3.4) (*N*=14)	102±85 (10–273) (*N*=13)	45.5±10.8 (38.6–64.8) (*N*=5)	1.6±0.5 (1.3–2.5) (*N*=5)	0.11±0.03 (0.06–0.15) (*N*=5)	29.4±3.2 (25.8–32.6) (*N*=5)	16.7±7.9 (9.1–27.4) (*N*=5)	-32.9±1.7 (-34.5 – -30.5) (*N*=5)	0.57±0.9 (-0.31-1.64) (*N*=5)
__TET__racera __wil__ldenowiana	G	14.6±2.7 (10.5–20.3) (*N*=14)	391.5±69.9 (280.1–490.6) (*N*=6)	0.15±0.05 (0.11–0.31) (*N*=14)	2.9±0.3 (2.5–3.4) (*N*=14)	112±50 (51–186) (*N*=10)	45.4±4.1 (40.8–48.7) (*N*=3)	1.8±0.3 (1.5–2.1) (*N*=3)	0.1±0.01 (0.1–0.11) (*N*=3)	24.9±2.1 (22.8–27) (*N*=3)	17.8±3.8 (13.4–20.2) (*N*=3)	-33.6±1.7 (-35.4 – -32) (*N*=3)	4.19±2.86 (2.13-7.46) (*N*=3)
FABACEAE (FAB)													
__BAU__hinia __"peluda"__	G	19.5±4.2 (12.1–25.4) (*N*=14)	412.7±78.3 (326.4–559.2) (*N*=7)	0.13±0.02 (0.1–0.16) (*N*=14)	1.6±0.2 (1.3–2) (*N*=14)	56±34 (16–108) (*N*=12)	41.2–42.5 (*N*=2)	2.2–2.4 (*N*=2)	0.06–0.11 (*N*=2)	17.5–19.3 (*N*=2)	19.3–37.7 (*N*=2)	-36.4 – -35.1 (*N*=2)	1-3.86 (*N*=2)
__CLI__toria __poz__uzoensis	WR	14.8±3.4 (5.3–21.6) (*N*=38)	458±91.3 (311.9–702.1) (*N*=17)	0.13±0.02 (0.09–0.2) (*N*=38)	1.1±0.2 (0.8–2) (*N*=38)	284±192 (45–850) (*N*=25)	40.1–48.5 (*N*=2)	2.2–2.5 (*N*=2)	0.09–0.17 (*N*=2)	18.1–19.2 (*N*=2)	13–26.6 (*N*=2)	-34.3 – -33.2 (*N*=2)	0.75-1.93 (*N*=2)
__DIO__clea __uca__yalina	R	15.4±4.7 (8.1–24.9) (*N*=12)	478.9±161.8 (333.5–653.2) (*N*=3)	0.09±0.02 (0.06–0.12) (*N*=12)	1.2±0.2 (0.8–1.5) (*N*=12)	442±418 (4–1007) (*N*=6)	46.1±2.8 (41.3–49) (*N*=6)	2.9±0.8 (2–3.7) (*N*=6)	0.13±0.04 (0.07–0.16) (*N*=6)	17.2±4.9 (11.2–22.4) (*N*=6)	22.7±6.2 (13.7–31.2) (*N*=6)	-31.2±1.8 (-34.1 – -29.2) (*N*=6)	0.32±0.59 (-0.7-1.03) (*N*=6)
__MAC__haerium __cus__pidatum	WV	15.3±3.2 (10.3–23.2) (*N*=41)	435.5±59.2 (349.6–551.8) (*N*=19)	0.13±0.02 (0.09–0.17) (*N*=41)	1.2±0.4 (0.8–3.8) (*N*=41)	302±236 (0–945) (*N*=28)	45.4–68.4 (*N*=2)	2.8–3.9 (*N*=2)	0.09–0.12 (*N*=2)	16.1–17.6 (*N*=2)	23.7–42 (*N*=2)	-32.4 – -31.4 (*N*=2)	-0.31-0.05 (*N*=2)
__PIP__tadenia __ano__lidurus	V	15.4±4.4 (11.7–21.4) (*N*=4)	449.3 (*N*=1)	0.09±0.02 (0.07–0.12) (*N*=4)	1.5±0.3 (1.2–1.8) (*N*=4)	41–140 (*N*=2)	53.5–55.3 (*N*=2)	4.2–4.5 (*N*=2)	0.05–0.36 (*N*=2)	12–13.2 (*N*=2)	12.4–91.8 (*N*=2)	-37.7 – -33.2 (*N*=2)	3.32-3.76 (*N*=2)
HIPPOCRATEACEAE (HIP)													

FAMILY ***Species***	**CLASS.**	**SLA (mm^2/mg)**	**LDMC (mg/g)**	**LT (mm)**	**L:W (ratio)**	**LSR (cm^2)**	**C (%)**	**N (%)**	**P (%)**	**C:N (ratio)**	**N:P (ratio)**	**δ^{13}C**	**δ^{15}N**
***ANT**hodon* ***dec**ussatum*	R	16.2–20.4 (*N*=2)	344.6–452.9 (*N*=2)	0.07–0.14 (*N*=2)	2.7–4.5 (*N*=2)	14–43 (*N*=2)	42.2–42.9 (*N*=2)	1.5–2.3 (*N*=2)	0.06–0.09 (*N*=2)	19–27.8 (*N*=2)	24.3–25 (*N*=2)	-35 – -33.9 (*N*=2)	-0.14--0.11 (*N*=2)
***CUE**rvea* ***kap**pleriana*	WR	13.7±5.1 (9.1–38.8) (*N*=33)	365.7±55.4 (272.4–491.1) (*N*=15)	0.16±0.02 (0.14–0.2) (*N*=33)	2.4±0.3 (1.8–2.8) (*N*=33)	102±46 (27–184) (*N*=25)	36–37 (*N*=2)	2.2–2.5 (*N*=2)	0.09–0.09 (*N*=2)	14.6–16.3 (*N*=2)	24.3–28.9 (*N*=2)	-35.3 – -34.1 (*N*=2)	-1.28-3.2 (*N*=2)
***HYL**enaea* ***com**osa*	R	12.2±2.4 (8.5–18.1) (*N*=20)	416.5±25.4 (381.8–460.8) (*N*=10)	0.14±0.02 (0.1–0.18) (*N*=20)	3.1±0.5 (2.2–4.7) (*N*=20)	77±42 (5–165) (*N*=15)	43.2–65.2 (*N*=2)	2.3–2.5 (*N*=2)	0.08–0.08 (*N*=2)	17.5–28.5 (*N*=2)	28.1–32.2 (*N*=2)	-34.5 – -32.8 (*N*=2)	0.87-1.79 (*N*=2)
***PER**itassa* ***pru**inosa*	R	11.7±1.8 (9.5–16.8) (*N*=18)	444.6±40.5 (372.1–519) (*N*=9)	0.16±0.03 (0.11–0.2) (*N*=18)	2.6±0.3 (2.2–3.1) (*N*=18)	105±47 (40–210) (*N*=14)	44.1–72.5 (*N*=2)	1.5–1.6 (*N*=2)	0.06–0.09 (*N*=2)	28.6–44.3 (*N*=2)	17.9–28.1 (*N*=2)	-36.1 – -35 (*N*=2)	1.05-3.05 (*N*=2)
***SAL**acia* ***mul**tiflora*	R	8.3±1.3 (5.7–11.7) (*N*=25)	363.1±34.2 (305.1–437.9) (*N*=12)	0.3±0.04 (0.22–0.38) (*N*=25)	2.4±0.3 (1.8–3.1) (*N*=25)	211±108 (9–422) (*N*=18)	45.6–47.4 (*N*=2)	1.2–1.5 (*N*=2)	0.07–0.1 (*N*=2)	32.4–37.1 (*N*=2)	15.4–17.2 (*N*=2)	-36.4 – -35.6 (*N*=2)	0.82-3.42 (*N*=2)
ICACINACEAE (ICA)													
***LER**etia* ***cor**data*	G	18.9±3.8 (11–25.6) (*N*=21)	294.4±42.9 (229.4–364.8) (*N*=13)	0.18±0.03 (0.11–0.22) (*N*=21)	3.2±0.4 (2.4–4.1) (*N*=21)	93±54 (23–228) (*N*=17)	37–44.5 (*N*=2)	2–2.6 (*N*=2)	0.13–0.16 (*N*=2)	17.2–18.1 (*N*=2)	12.7–20.3 (*N*=2)	-34.2 – -33.1 (*N*=2)	2.67-5.47 (*N*=2)
LOGANIACEAE (LOG)													
***STR**ychnos* ***mit**scherlichii*	R	13.3±3.2 (8.3–16.6) (*N*=7)	408.2–497.8 (*N*=2)	0.13±0.02 (0.09–0.15) (*N*=7)	2.6±0.4 (2–3.1) (*N*=7)	93±26 (58–121) (*N*=5)	37.4±6.7 (29.8–41.7) (*N*=3)	1.4±0.2 (1.3–1.7) (*N*=3)	0.07±0.02 (0.05–0.08) (*N*=3)	26.8±5.4 (23.1–33) (*N*=3)	23.5±11.2 (16.5–36.4) (*N*=3)	-33.7±0.7 (-34.2 – -32.9) (*N*=3)	3.33±0.52 (3.02-3.93) (*N*=3)
***STR**rychnos* ***ram**entifera*	R	16.6±3 (10.2–22) (*N*=11)	419±37.8 (381.7–476.1) (*N*=5)	0.11±0.02 (0.08–0.14) (*N*=11)	2.7±0.5 (2.1–4.1) (*N*=11)	55±36 (0–99) (*N*=7)	57.2±15.2 (39.8–67) (*N*=3)	2.5±0.7 (1.7–3) (*N*=3)	0.07±0.01 (0.06–0.08) (*N*=3)	22.9±1.1 (21.8–24) (*N*=3)	37.4±9 (27.9–45.7) (*N*=3)	-34±0.3 (-34.2 – -33.7) (*N*=3)	2.61±1.12 (1.69-3.86) (*N*=3)
MALPIGHIACEAE (MLP)													
***ECT**opopterys* ***soe**jartoi*	G	22.5±9.5 (14.2–45.1) (*N*=9)	313±34.6 (273.1–348.2) (*N*=4)	0.17±0.03 (0.13–0.22) (*N*=9)	2.7±0.4 (2–3.1) (*N*=9)	45±19 (13–66) (*N*=8)	41.7 (*N*=1)	3.1 (*N*=1)	0.09 (*N*=1)	13.2 (*N*=1)	34.3 (*N*=1)	-33.7 (*N*=1)	4.21 (*N*=1)
***HIR**aea* ***val**ida*	G	12±2.2 (10.3–15.9) (*N*=5)	430.6–431.8 (*N*=2)	0.12±0.02 (0.1–0.15) (*N*=5)	2±0.1 (1.9–2.2) (*N*=5)	302–560 (*N*=2)	44 (*N*=1)	2.3 (*N*=1)	0.08 (*N*=1)	19.1 (*N*=1)	28 (*N*=1)	-35.1 (*N*=1)	2.66 (*N*=1)
***MAS**cagnia* ***dis**similis*	G	12.5–25.9 (*N*=2)	species not sampled	0.17–0.22 (*N*=2)	2.2–2.6 (*N*=2)	109 (*N*=1)	39.4–48 (*N*=2)	2.5–4.7 (*N*=2)	0.19–0.27 (*N*=2)	10.2–15.5 (*N*=2)	13.6–17.4 (*N*=2)	-36.3 – -30.7 (*N*=2)	3.92-6.25 (*N*=2)
***TET**rapterys* ***nit**ida*	R	27±6.7 (18.7–46.3) (*N*=18)	353.9±51.3 (297.6–464.3) (*N*=10)	0.11±0.02 (0.08–0.18) (*N*=18)	2.4±0.3 (1.8–3) (*N*=18)	19±8 (7–32) (*N*=13)	41–50.2 (*N*=2)	3.5–4.7 (*N*=2)	0.07–0.13 (*N*=2)	10.6–11.7 (*N*=2)	35.9–48.4 (*N*=2)	-36.2 – -34.8 (*N*=2)	2.03-3.33 (*N*=2)
MENISPERMACEAE (MEN)													

FAMILY ***Species***	**CLASS.**	**SLA (mm^2/mg)**	**LDMC (mg/g)**	**LT (mm)**	**L:W (ratio)**	**LSR (cm^2)**	**C (%)**	**N (%)**	**P (%)**	**C:N (ratio)**	**N:P (ratio)**	**δ^{13}C**	**δ^{15}N**
***CUR**area* ***tec**unarum*	R	12.1±2 (8.1–14.5) (*N*=7)	465.8–507.3 (*N*=2)	0.16±0.03 (0.14–0.21) (*N*=7)	2.3±0.4 (1.8–2.7) (*N*=7)	199±136 (7–297) (*N*=4)	50.6–75.8 (*N*=2)	2.6–3.1 (*N*=2)	0.06–0.1 (*N*=2)	19.5–24.1 (*N*=2)	26.8–49.5 (*N*=2)	-35.1 – -33.9 (*N*=2)	-0.71-4.35 (*N*=2)
***SCI**adotenia* ***tox**ifera*	G	17.9±4.8 (11.6–24.8) (*N*=9)	302.5±53.2 (246.5–393.7) (*N*=6)	0.14±0.03 (0.09–0.19) (*N*=9)	2.2±0.3 (1.7–2.6) (*N*=9)	44±38 (5–117) (*N*=7)	45.7–46.8 (*N*=2)	2.3–2.6 (*N*=2)	0.07–0.1 (*N*=2)	17.8–20.1 (*N*=2)	23.3–36.9 (*N*=2)	-34.2 – -33 (*N*=2)	0.54-2.4 (*N*=2)
POLYGALACEAE (PGA)													
***MOU**tabea* ***acu**leata*	R	12.3±3.8 (8.8–21.3) (*N*=11)	315.8±37 (266.7–359.4) (*N*=5)	0.27±0.05 (0.17–0.36) (*N*=11)	3.4±0.8 (2.6–5.2) (*N*=11)	152±86 (80–280) (*N*=5)	46.3–67.4 (*N*=2)	2.3–3.2 (*N*=2)	0.05–0.09 (*N*=2)	14.6–28.7 (*N*=2)	25.1–61.8 (*N*=2)	-33.4 – -32.5 (*N*=2)	4.06-4.16 (*N*=2)
SAPINDACEAE (SPI)													
***PAU**llinia* ***obo**vata*	G	14.3±4.1 (8.8–22.3) (*N*=14)	540.7±99.3 (439.8–716.7) (*N*=11)	0.12±0.04 (0.08–0.2) (*N*=14)	1.2±0.2 (0.8–1.8) (*N*=14)	117±70 (31–211) (*N*=10)	46.5±12.2 (34.2–66.3) (*N*=5)	2.4±0.6 (1.6–3.1) (*N*=5)	0.19±0.09 (0.1–0.29) (*N*=5)	19.7±4.8 (14.4–26.1) (*N*=5)	14.8±7.2 (7.2–26.7) (*N*=5)	-34±1.2 (-35.1 – -32) (*N*=5)	-0.45±1.19 (-1.97-1) (*N*=5)
***SER**jania* ***pyr**amidata*	G	16.3±3.7 (9.7–23.3) (*N*=14)	343.1±100.1 (241.1–569.7) (*N*=9)	0.14±0.02 (0.1–0.18) (*N*=14)	1.4±0.2 (1.1–1.9) (*N*=14)	108±81 (1–250) (*N*=13)	45.2±2.6 (42.7–50.6) (*N*=7)	2.5±0.7 (1.9–3.8) (*N*=7)	0.17±0.09 (0.05–0.36) (*N*=7)	19±4 (11.6–23.6) (*N*=7)	17.7±9.5 (10.6–38.4) (*N*=7)	-34.2±1.4 (-35.7 – -32.2) (*N*=7)	1.6±1.31 (-0.08-3.95) (*N*=7)
***THI**nouia* ***obl**iqua*	G	22.7±9 (10.6–45.2) (*N*=18)	347.9±70.2 (253.1–451.2) (*N*=7)	0.1±0.02 (0.06–0.17) (*N*=18)	1.2±0.2 (0.9–1.6) (*N*=18)	162±154 (43–528) (*N*=12)	43.5–51.5 (*N*=2)	3.4–4.8 (*N*=2)	0.13–0.17 (*N*=2)	10.7–12.8 (*N*=2)	27–27.6 (*N*=2)	-35.4 – -33 (*N*=2)	1.9-4.17 (*N*=2)
SOLANACEAE (SOL)													
***SOL**anum* ***bar**beyanum*	G	16.7±3.3 (13.1–20.2) (*N*=5)	186.8 (*N*=1)	0.19±0.03 (0.17–0.24) (*N*=5)	1.2 (*N*=1)	196 (*N*=1)	37.2–50.9 (*N*=2)	4–6.1 (*N*=2)	0.13–0.18 (*N*=2)	8.4–9.3 (*N*=2)	22.5–45.5 (*N*=2)	-35.6 – -35.3 (*N*=2)	1.65-3.51 (*N*=2)
VERBENACEAE (VER)													
***PET**rea* ***may**nensis*	R	13.6±3.4 (8.8–22) (*N*=33)	422.2±58.9 (354.5–563.8) (*N*=16)	0.13±0.02 (0.11–0.19) (*N*=33)	3±0.4 (2.1–3.7) (*N*=33)	115±60 (4–217) (*N*=26)	35.5±1.9 (33.3–36.8) (*N*=3)	1.7±0.3 (1.5–2) (*N*=3)	0.1±0.03 (0.07–0.13) (*N*=3)	20.7±4 (16.3–24) (*N*=3)	17.9±4.9 (12.7–22.4) (*N*=3)	-32.7±1.8 (-34.7 – -31.2) (*N*=3)	1.82±0.58 (1.31-2.45) (*N*=3)

APPENDIX 5

Traits of wood specific gravity and diameter growth rate (obtained from two censuses, census 0 and census 1, separated by approximately two years) of the 43 liana species included in the functional trait analyses. The habitat association (or non-association) of species was classified (CLASS.) as: *ridge* species (R), *valley* species (V), *generalist* species (G), and *widespread with habitat association* species (W, subclassified in WR: with ridge association, and WV: with valley association) (see Methods, and Tables 3.1 and 3.2). WSG=wood specific gravity, AGR=absolute growth rate, RGR=relative growth rate. Growth rates by diameter categories and for all lianas (all diameter categories) are shown. A growth rate of "0" means no growth from census 0 to census 1. Species acronyms (in **bold**) were formed by the first three letters of the genus (in UPPERCASE) and the first three letters of the epithet. Family acronyms (in parentheses) were formed by a three-letter code. Names within quotation marks are morphospecies. Family acronyms (in parentheses) were formed by a three-letter code. Species are ordered by family.

Values reported are: mean ± 1 standard deviation, minimum and maximum values (in parentheses) and number of individuals sampled (*N,* in parentheses) (if *N*=2, no mean was calculated).

			AGR (mm/year)					RGR (1/year)				
FAMILY ***Species***	**CLASS.**	**WSG (g/cm^3)**	**1.0–1.5 cm**	**1.5–2.5 cm**	**2.5–5.0 cm**	**≥5.0 cm**	**ALL LIANAS**	**1.0–1.5 cm**	**1.5–2.5 cm**	**2.5–5.0 cm**	**≥5.0 cm**	**ALL LIANAS**
APOCYNACEAE (APO)												
FOR_steronia_ ***aff***_inis_	R	0.33±0.05 (0.27–0.39) (N=6)	0.1 (N=1)	0–0 (N=2)	no lianas	no lianas	0.03±0.06 (0–0.1) (N=3)	0.01 (N=1)	0–0 (N=2)	no lianas	no lianas	0±0 (0–0.01) (N=3)
ARECACEAE (ARE)												
DES_moncus_ ***ort***_hacanthos_	R	0.52 (N=1)	no lianas	0 (N=1)	no lianas	no lianas	0 (N=1)	no lianas	0 (N=1)	no lianas	no lianas	0 (N=1)
ASTERACEAE (AST)												
MIK_ania_ ***lei***_ostachya_	V	species not sampled	no lianas	1.31 (N=1)	no lianas	no lianas	1.31 (N=1)	no lianas	0.06 (N=1)	no lianas	no lianas	0.06 (N=1)
BIGNONIACEAE (BIG)												
ADE_nocalymna_ ***imp***_ressum_	R	0.38±0.07 (0.19–0.43) (N=11)	0.05–0.53 (N=2)	no lianas	no lianas	no lianas	0.05–0.53 (N=2)	0–0.05 (N=2)	no lianas	no lianas	no lianas	0–0.05 (N=2)
BIG_nonia_ ***aeq***_uinoctialis_	G	0.44±0.05 (0.32–0.5) (N=9)	0.48 (N=1)	no lianas	0.35 (N=1)	no lianas	0.35–0.48 (N=2)	0.05 (N=1)	no lianas	0.01 (N=1)	no lianas	0.01–0.05 (N=2)
MAN_soa_ ***ver***_rucifera_	V	0.48 (N=1)	0.43–0.58 (N=2)	0.29 (N=1)	no lianas	no lianas	0.43±0.15 (0.29–0.58) (N=3)	0.03–0.05 (N=2)	0.02 (N=1)	no lianas	no lianas	0.04±0.02 (0.02–0.05) (N=3)
STI_zophyllum_ ***rip***_arium_	G	0.44±0.04 (0.41–0.48) (N=3)	0.14 (N=1)	0–0 (N=2)	0.19 (N=1)	no lianas	0.08±0.1 (0–0.19) (N=4)	0.01 (N=1)	0–0 (N=2)	0.01 (N=1)	no lianas	0±0.01 (0–0.01) (N=4)
TAN_aecium_ ***aff***_ine_	V	0.34–0.56 (N=2)	species not sampled	species not sampled	species not sampled	species not sampled	species not sampled	species not sampled	species not sampled	species not sampled	species not sampled	species not sampled
BORAGINACEAE (BOR)												
TOU_rnefortia_ ***bic***_olor_	G	0.41 (N=1)	0.1–0.67 (N=2)	no lianas	2.21–3.79 (N=2)	no lianas	1.69±1.66 (0.1–3.79) (N=4)	0.01–0.06 (N=2)	no lianas	0.06–0.11 (N=2)	no lianas	0.06±0.04 (0.01–0.11) (N=4)
COMBRETACEAE (COM)												
COM_bretum_ ***lax***_um_	WV	0.55±0.14 (0.37–0.73) (N=5)	0.39±0.72 (0–2.17) (N=15)	0.75±1.04 (0–3.75) (N=21)	0.89±0.85 (0–3.07) (N=14)	1.13±1.3 (0–4.8) (N=17)	0.79±1.03 (0–4.8) (N=67)	0.03±0.05 (0–0.16) (N=15)	0.03±0.04 (0–0.14) (N=21)	0.03±0.03 (0–0.1) (N=14)	0.01±0.01 (0–0.03) (N=17)	0.03±0.04 (0–0.16) (N=67)
CONNARACEAE (CNN)												
CON_narus_ ***pat***_risii_	G	0.54±0.06 (0.44–0.63) (N=8)	3.55 (N=1)	no lianas	0.13±0.11 (0–0.19) (N=3)	no lianas	0.98±1.72 (0–3.55) (N=4)	0.27 (N=1)	no lianas	0±0 (0–0.01) (N=3)	no lianas	0.07±0.13 (0–0.27) (N=4)

			AGR (mm/year)					RGR (1/year)				
FAMILY ***Species***	**CLASS.**	**WSG (g/cm^3)**	**1.0–1.5 cm**	**1.5–2.5 cm**	**2.5–5.0 cm**	**≥5.0 cm**	**ALL LIANAS**	**1.0–1.5 cm**	**1.5–2.5 cm**	**2.5–5.0 cm**	**≥5.0 cm**	**ALL LIANAS**
__ROU__rea __ama__zonica	G	species not sampled	no lianas	0.26±0.36 (0–0.77) (N=4)	no lianas	no lianas	0.26±0.36 (0–0.77) (N=4)	no lianas	0.01±0.02 (0–0.04) (N=4)	no lianas	no lianas	0.01±0.02 (0–0.04) (N=4)
__ROU__rea __cam__ptoneura	G	0.57 (N=1)	0.75 (N=1)	0.27±0.33 (0–0.74) (N=4)	no lianas	0 (N=1)	0.3±0.35 (0–0.75) (N=6)	0.06 (N=1)	0.01±0.02 (0–0.04) (N=4)	no lianas	0 (N=1)	0.02±0.02 (0–0.06) (N=6)
CONVOLVULACEAE (CNV)												
__MAR__ipa __per__uviana	G	0.46–0.54 (N=2)	0.43±0.3 (0.19–0.77) (N=3)	0–0.73 (N=2)	no lianas	no lianas	0.4±0.33 (0–0.77) (N=5)	0.03±0.02 (0.01–0.05) (N=3)	0–0.03 (N=2)	no lianas	no lianas	0.03±0.02 (0–0.05) (N=5)
DICHAPETALACEAE (DIC)												
__DIC__hapetalum __fro__esii	G	0.44–0.46 (N=2)	0 (N=1)	0–0.4 (N=2)	2.23 (N=1)	no lianas	0.66±1.07 (0–2.23) (N=4)	0 (N=1)	0–0.02 (N=2)	0.05 (N=1)	no lianas	0.02±0.02 (0–0.05) (N=4)
__DIC__hapetalum __spr__uceanum	G	0.55±0.05 (0.49–0.59) (N=3)	0–0 (N=2)	0 (N=1)	no lianas	no lianas	0±0 (0–0) (N=3)	0–0 (N=2)	0 (N=1)	no lianas	no lianas	0±0 (0–0) (N=3)
DILLENIACEAE (DIL)												
__DOL__iocarpus __den__tatus	V	0.33–0.39 (N=2)	0.24±0.3 (0–0.77) (N=8)	0–0.38 (N=2)	0.05–1.34 (N=2)	1.44 (N=1)	0.39±0.51 (0–1.44) (N=13)	0.02±0.03 (0–0.07) (N=8)	0–0.02 (N=2)	0–0.03 (N=2)	0.02 (N=1)	0.02±0.02 (0–0.07) (N=13)
__TET__racera __wil__ldenowiana	G	0.46±0.04 (0.4–0.53) (N=11)	0.34±0.67 (0–1.34) (N=4)	0.9±0.9 (0.24–1.93) (N=3)	0.84±0.86 (0–2.02) (N=6)	1.74±3.39 (0–7.77) (N=5)	0.99±1.84 (0–7.77) (N=18)	0.03±0.05 (0–0.1) (N=4)	0.04±0.05 (0.01–0.1) (N=3)	0.02±0.02 (0–0.05) (N=6)	0.03±0.06 (0–0.13) (N=5)	0.03±0.04 (0–0.13) (N=18)
FABACEAE (FAB)												
__BAU__hinia "__pel__uda"	G	0.44 (N=1)	0.67 (N=1)	1.76±2.01 (0.14–5.09) (N=5)	1.02±1.56 (0–3.55) (N=5)	no lianas	1.32±1.67 (0–5.09) (N=11)	0.06 (N=1)	0.07±0.07 (0.01–0.19) (N=5)	0.03±0.05 (0–0.11) (N=5)	no lianas	0.05±0.06 (0–0.19) (N=11)
__CLI__toria __poz__uzoensis	WR	0.57±0.06 (0.45–0.64) (N=7)	0.34±0.54 (0–1.78) (N=18)	0.26±0.4 (0–1.2) (N=23)	0.36±0.35 (0–0.82) (N=7)	no lianas	0.3±0.45 (0–1.78) (N=48)	0.03±0.04 (0–0.13) (N=18)	0.01±0.02 (0–0.06) (N=23)	0.01±0.01 (0–0.03) (N=7)	no lianas	0.02±0.03 (0–0.13) (N=48)
__DIO__clea __uca__yalina	R	0.43±0.17 (0.28–0.65) (N=4)	1.43±1.12 (0.14–2.22) (N=3)	0.24 (N=1)	no lianas	no lianas	1.13±1.09 (0.14–2.22) (N=4)	0.11±0.09 (0.01–0.17) (N=3)	0.01 (N=1)	no lianas	no lianas	0.08±0.09 (0.01–0.17) (N=4)
__MAC__haerium __cus__pidatum	WV	0.48±0.07 (0.39–0.6) (N=10)	0.39±0.52 (0–1.82) (N=20)	0.45±0.56 (0–1.93) (N=29)	0.69±1.37 (0–5.96) (N=33)	1.56±2.05 (0–7.16) (N=10)	0.64±1.16 (0–7.16) (N=92)	0.03±0.04 (0–0.15) (N=20)	0.02±0.03 (0–0.08) (N=29)	0.02±0.04 (0–0.17) (N=33)	0.02±0.03 (0–0.09) (N=10)	0.02±0.04 (0–0.17) (N=92)
__PIP__tadenia __ano__lidurus	V	0.31–0.38 (N=2)	0 (N=1)	no lianas	no lianas	no lianas	0 (N=1)	0 (N=1)	no lianas	no lianas	no lianas	0 (N=1)

			AGR (mm/year)					**RGR (1/year)**				
FAMILY ***Species***	**CLASS.**	**WSG (g/cm^3)**	**1.0–1.5 cm**	**1.5–2.5 cm**	**2.5–5.0 cm**	**≥5.0 cm**	**ALL LIANAS**	**1.0–1.5 cm**	**1.5–2.5 cm**	**2.5–5.0 cm**	**≥5.0 cm**	**ALL LIANAS**
HIPPOCRATEACEAE (HIP)												
***ANT**hodon* *__dec__ussatum*	R	0.5 (N=1)	no lianas	0.25–0.72 (N=2)	no lianas	0 (N=1)	0.32±0.37 (0–0.72) (N=3)	no lianas	0.01–0.03 (N=2)	no lianas	0 (N=1)	0.01±0.02 (0–0.03) (N=3)
***CUE**rvea* *__kap__pleriana*	WR	0.54±0.05 (0.46–0.58) (N=9)	0.22±0.26 (0–0.87) (N=22)	0.31±0.63 (0–3.08) (N=40)	0.55±1.59 (0–5.83) (N=13)	no lianas	0.32±0.81 (0–5.83) (N=75)	0.02±0.02 (0–0.06) (N=22)	0.01±0.03 (0–0.12) (N=40)	0.02±0.04 (0–0.16) (N=13)	no lianas	0.02±0.03 (0–0.16) (N=75)
***HYL**enaea* *__com__osa*	R	0.5 (N=1)	0.45±0.43 (0–0.87) (N=3)	0.24±0.27 (0–0.54) (N=5)	0–0.19 (N=2)	no lianas	0.28±0.31 (0–0.87) (N=10)	0.04±0.04 (0–0.08) (N=3)	0.01±0.01 (0–0.03) (N=5)	0–0.01 (N=2)	no lianas	0.02±0.03 (0–0.08) (N=10)
***PER**itassa* *__pru__inosa*	R	0.57 (N=1)	0.33±0.39 (0–0.72) (N=4)	0.56±0.8 (0–2.59) (N=10)	0 (N=1)	no lianas	0.46±0.69 (0–2.59) (N=15)	0.02±0.03 (0–0.05) (N=4)	0.03±0.04 (0–0.14) (N=10)	0 (N=1)	no lianas	0.03±0.04 (0–0.14) (N=15)
***SAL**acia* *__mul__tiflora*	R	0.5±0.08 (0.42–0.63) (N=6)	0.21±0.26 (0–0.71) (N=6)	0.79±0.49 (0–1.44) (N=10)	0.43 (N=1)	no lianas	0.56±0.49 (0–1.44) (N=17)	0.02±0.02 (0–0.06) (N=6)	0.04±0.03 (0–0.08) (N=10)	0.02 (N=1)	no lianas	0.03±0.03 (0–0.08) (N=17)
ICACINACEAE (ICA)												
***LER**etia* *__cor__data*	G	0.34±0.08 (0.26–0.51) (N=7)	0.48±0.61 (0–1.53) (N=6)	0.47±0.51 (0–1.2) (N=4)	0.26±0.23 (0–0.43) (N=3)	0–0.48 (N=2)	0.4±0.46 (0–1.53) (N=15)	0.04±0.05 (0–0.13) (N=6)	0.02±0.02 (0–0.05) (N=4)	0.01±0.01 (0–0.01) (N=3)	0–0.01 (N=2)	0.02±0.03 (0–0.13) (N=15)
LOGANIACEAE (LOG)												
***STR**ychnos* *__mit__scherlichii*	R	0.52 (N=1)	no lianas	0.77 (N=1)	no lianas	no lianas	0.77 (N=1)	no lianas	0.05 (N=1)	no lianas	no lianas	0.05 (N=1)
***STR**rychnos* *__ram__entifera*	R	0.65±0.07 (0.55–0.72) (N=6)	no lianas	0.08±0.14 (0–0.24) (N=3)	no lianas	no lianas	0.08±0.14 (0–0.24) (N=3)	no lianas	0±0.01 (0–0.01) (N=3)	no lianas	no lianas	0±0.01 (0–0.01) (N=3)
MALPIGHIACEAE (MLP)												
***ECT**opopterys* *__soe__jartoi*	G	0.48 (N=1)	2.02 (N=1)	0.11±0.19 (0–0.34) (N=3)	0 (N=1)	no lianas	0.47±0.88 (0–2.02) (N=5)	0.17 (N=1)	0±0.01 (0–0.01) (N=3)	0 (N=1)	no lianas	0.04±0.07 (0–0.17) (N=5)
***HIR**aea* *__val__ida*	G	0.51 (N=1)	0.16±0.22 (0–0.42) (N=3)	0 (N=1)	no lianas	no lianas	0.12±0.2 (0–0.42) (N=4)	0.01±0.02 (0–0.03) (N=3)	0 (N=1)	no lianas	no lianas	0.01±0.02 (0–0.03) (N=4)
***MAS**cagnia* *__dis__similis*	G	species not sampled	0 (N=1)	no lianas	no lianas	no lianas	0 (N=1)	0 (N=1)	no lianas	no lianas	no lianas	0 (N=1)
***TET**rapterys* *__nit__ida*	R	0.55–0.58 (N=2)	0.13±0.2 (0–0.63) (N=10)	0.4±0.69 (0–1.2) (N=3)	no lianas	no lianas	0.2±0.35 (0–1.2) (N=13)	0.01±0.02 (0–0.06) (N=10)	0.02±0.03 (0–0.05) (N=3)	no lianas	no lianas	0.01±0.02 (0–0.06) (N=13)

			AGR (mm/year)					RGR (1/year)				
FAMILY ***Species***	**CLASS.**	**WSG (g/cm^3)**	**1.0–1.5 cm**	**1.5–2.5 cm**	**2.5–5.0 cm**	**≥5.0 cm**	**ALL LIANAS**	**1.0–1.5 cm**	**1.5–2.5 cm**	**2.5–5.0 cm**	**≥5.0 cm**	**ALL LIANAS**
MENISPERMACEAE (MEN)												
***CUR**area **tec**unarum*	R	0.44–0.47 (N=2)	0.14–0.2 (N=2)	1.59±0.31 (1.33–1.93) (N=3)	0–6.8 (N=2)	no lianas	1.7±2.37 (0–6.8) (N=7)	0.01–0.02 (N=2)	0.08±0.02 (0.06–0.11) (N=3)	0–0.21 (N=2)	no lianas	0.07±0.07 (0–0.21) (N=7)
***SCI**adotenia **tox**ifera*	G	0.55 (N=1)	no lianas	0.06±0.12 (0–0.24) (N=4)	1.55 (N=1)	0 (N=1)	0.3±0.62 (0–1.55) (N=6)	no lianas	0±0.01 (0–0.01) (N=4)	0.05 (N=1)	0 (N=1)	0.01±0.02 (0–0.05) (N=6)
POLYGALACEAE (PGA)												
***MOU**tabea **acu**leata*	R	0.5±0.05 (0.41–0.57) (N=6)	0.74±0.41 (0.43–1.2) (N=3)	no lianas	0.48 (N=1)	2.4 (N=1)	1.02±0.83 (0.43–2.4) (N=5)	0.06±0.04 (0.04–0.11) (N=3)	no lianas	0.01 (N=1)	0.03 (N=1)	0.05±0.04 (0.01–0.11) (N=5)
SAPINDACEAE (SPI)												
***PAU**llinia **obo**vata*	G	0.48 (N=1)	0.34±0.32 (0.05–0.82) (N=6)	no lianas	no lianas	no lianas	0.34±0.32 (0.05–0.82) (N=6)	0.03±0.03 (0–0.07) (N=6)	no lianas	no lianas	no lianas	0.03±0.03 (0–0.07) (N=6)
***SER**jania **pyr**amidata*	G	0.47±0.1 (0.27–0.62) (N=9)	0.17±0.19 (0–0.34) (N=4)	0.19 (N=1)	0 (N=1)	no lianas	0.14±0.17 (0–0.34) (N=6)	0.01±0.02 (0–0.03) (N=4)	0.01 (N=1)	0 (N=1)	no lianas	0.01±0.01 (0–0.03) (N=6)
***THI**nouia **obl**iqua*	G	0.62±0.1 (0.49–0.71) (N=4)	0.19±0.19 (0–0.53) (N=7)	0.4±0.29 (0.05–0.96) (N=8)	0 (N=1)	no lianas	0.29±0.27 (0–0.96) (N=16)	0.02±0.01 (0–0.04) (N=7)	0.02±0.02 (0–0.05) (N=8)	0 (N=1)	no lianas	0.02±0.02 (0–0.05) (N=16)
SOLANACEAE (SOL)												
***SOL**anum **bar**beyanum*	G	species not sampled	0.77–2.12 (N=2)	no lianas	1.53 (N=1)	no lianas	1.48±0.67 (0.77–2.12) (N=3)	0.06–0.16 (N=2)	no lianas	0.06 (N=1)	no lianas	0.09±0.06 (0.06–0.16) (N=3)
VERBENACEAE (VER)												
***PET**rea **may**nensis*	R	0.45±0.05 (0.39–0.54) (N=6)	0.26±0.38 (0–1.97) (N=41)	0.21±0.22 (0–1) (N=42)	0.46±0.43 (0–1.19) (N=12)	no lianas	0.26±0.33 (0–1.97) (N=95)	0.02±0.03 (0–0.15) (N=41)	0.01±0.01 (0–0.05) (N=42)	0.01±0.01 (0–0.04) (N=12)	no lianas	0.02±0.02 (0–0.15) (N=95)

APPENDIX 6

Pearson (*r*) correlation matrix of all traits measured in the 43 species whose traits were analyzed in the YFDP. *P*=2-tailed probability not corrected for multiple comparisons. *N*=number of species. Traits measured were (see units in this Chapter's Figures or in Appendices 3.1 and 3.2): SLA=specific leaf area, LDMC=leaf dry matter content, LT=leaf lamina thickness, L:W=length to width ratio of whole leaf (incl. petiole), LSR=individual-level leaf size range, C=carbon concentration, N=nitrogen concentration, P=phosphorus concentration, C:N=ratio of carbon concentration to nitrogen concentration, N:P=ratio of nitrogen concentration to phosphorus concentration, δ^{13}C=relative abundance of the stable isotope carbon-13 in delta units, δ^{15}N=relative abundance of the stable isotope nitrogen-15 in delta units, WSG=wood specific gravity, and AGR=absolute growth rate. Because *P* was not corrected for multiple comparisons (e.g., via a Bonferroni correction), we considered that correlations existed only if $P \leq 0.001$ (in **red bold**).

		SLA	**LDMC**	**LT**	**L:W**	**LSR**	**C**	**N**	**P**	**C:N**	**N:P**	**δ^{13}C**	**δ^{15}N**	**WSG**	**AGR all lianas**
SLA	***r***	1													
	$P_{\text{2-tailed}}$	.													
	N	43													
LDMC	***r***	**−.508**	1												
	$P_{\text{2-tailed}}$	**.001**	.												
	N	41	41												
LT	***r***	−.387	−.357	1											
	$P_{\text{2-tailed}}$	.010	.022	.											
	N	43	41	43											
L:W	***r***	−.088	−.157	.289	1										
	$P_{\text{2-tailed}}$	.576	.327	.060	.										
	N	43	41	43	43										
LSR	***r***	−.430	.304	.061	−.234	1									
	$P_{\text{2-tailed}}$	.004	.053	.698	.131	.									
	N	43	41	43	43	43									
C	***r***	.019	.176	−.155	−.031	−.051	1								
	$P_{\text{2-tailed}}$	.903	.272	.321	.842	.747	.								
	N	43	41	43	43	43	43								
N	***r***	**.496**	−.253	−.229	−.380	−.052	.342	1							
	$P_{\text{2-tailed}}$	**.001**	.110	.140	.012	.741	.025	.							
	N	43	41	43	43	43	43	43							
P	***r***	.352	−.217	−.089	−.423	−.054	−.146	**.500**	1						
	$P_{\text{2-tailed}}$	.021	.173	.571	.005	.732	.350	**.001**	.						
	N	43	41	43	43	43	43	43	43						
C:N	***r***	**−.533**	.297	.258	.345	.004	.119	**−.821**	**−.550**	1					
	$P_{\text{2-tailed}}$	**<.001**	.059	.095	.024	.978	.448	**<.001**	**<.001**	.					
	N	43	41	43	43	43	43	43	43	43					
N:P	***r***	.126	.009	−.160	.043	−.104	**.580**	**.576**	−.219	−.342	1				
	$P_{\text{2-tailed}}$	.421	.954	.304	.783	.506	**<.001**	**<.001**	.158	.025	.				
	N	43	41	43	43	43	43	43	43	43	43				
δ^{13}C	***r***	.101	−.069	−.192	−.003	.030	−.140	−.134	.068	−.092	−.266	1			
	$P_{\text{2-tailed}}$	.518	.670	.218	.987	.850	.370	.391	.664	.555	.085	.			
	N	43	41	43	43	43	43	43	43	43	43	43			
δ^{15}N	***r***	.110	−.290	.221	.268	.107	.110	.275	.080	−.222	.269	−.164	1		
	$P_{\text{2-tailed}}$	.481	.066	.155	.083	.493	.483	.074	.610	.152	.081	.293	.		
	N	43	41	43	43	43	43	43	43	43	43	43	43		
WSG	***r***	−.165	.205	−.028	.025	.162	−.026	−.129	−.390	.150	.011	−.222	−.011	1	
	$P_{\text{2-tailed}}$	.316	.217	.867	.882	.325	.873	.435	.014	.362	.945	.174	.948	.	
	N	39	38	39	39	39	39	39	39	39	39	39	39	39	
AGR all lianas	***r***	−.113	−.256	.405	.023	−.082	.008	−.043	−.104	.084	−.017	.013	−.066	−.145	1
	$P_{\text{2-tailed}}$	.478	.111	.008	.885	.606	.961	.787	.513	.598	.916	.935	.679	.386	.
	N	42	40	42	42	42	42	42	42	42	42	42	42	38	42