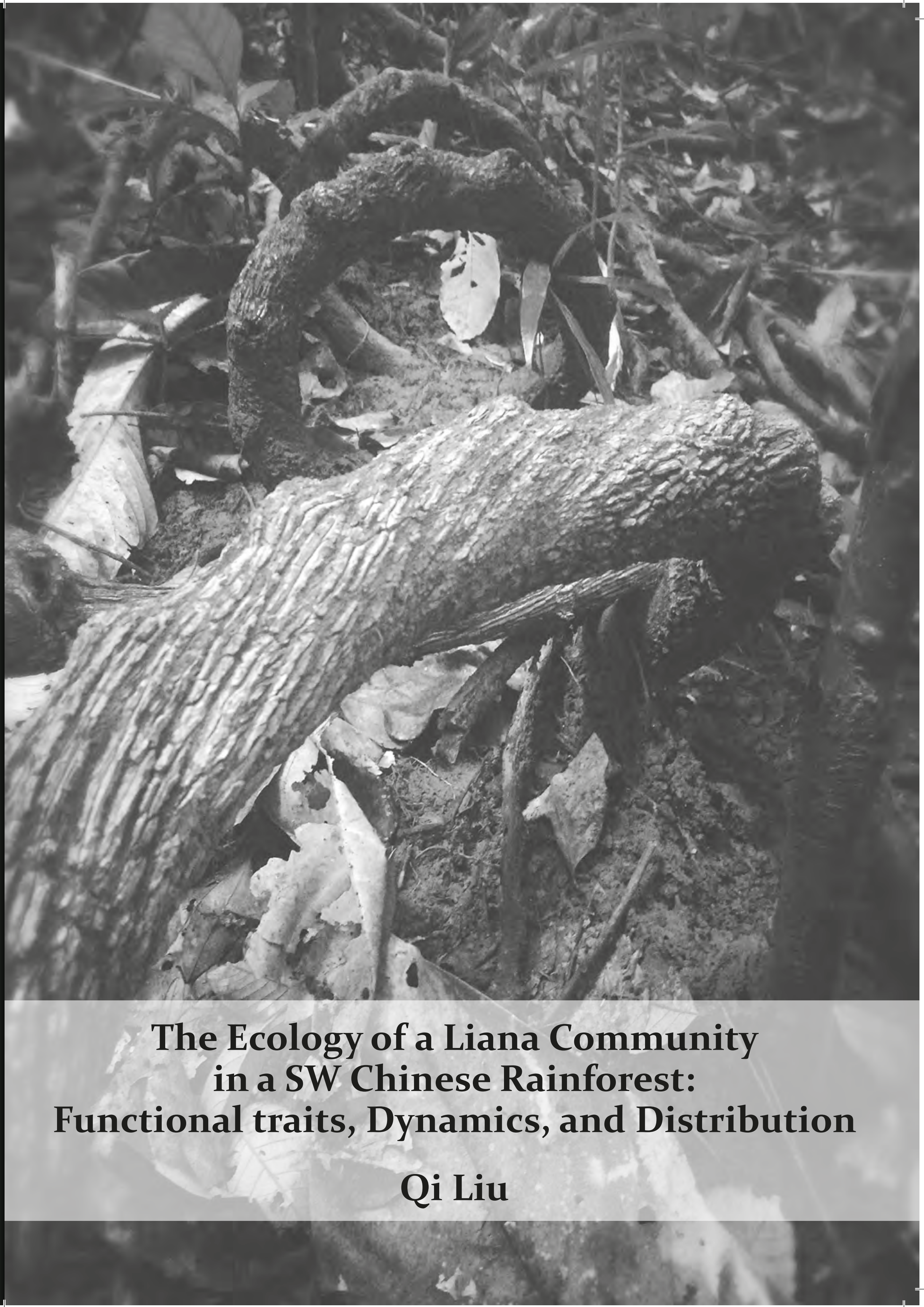
The Ecology of a Liana Community in a SW Chinese Rainforest: Functional traits, Dynamics, and Distribution

Qi Liu



The Ecology of a Liana Community in a SW Chinese Rainforest: Functional traits, Dynamics, and Distribution

Qi Liu

Invitation

You are kindly invited to
attend the public defence of
my PhD thesis entitled:

The ecology of a liana community
in a SW Chinese rainforest:
functional traits, dynamics,
and distribution

On Friday, 9 April 2021
at 16:00 in the Aula of
Wageningen University,
Gerneraal Foulkesweg 1,
Wageningen

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PROPOSITIONS

1. Lianas show a broad spectrum from conservative to acquisitive trait strategies which allows them to partition soil fertility gradients.
   (this thesis)

2. Despite the postulated role of global change drivers, local site conditions ultimately determine whether lianas will increase or decrease in tropical forests.
   (this thesis)

3. Scientific journals seem to equate novelty with novel ideas, whereas science can only advance when the validity and wider generality of those ideas are tested with novel data.

4. Scientific research needs statistical tests, although they cannot always be trusted.

5. For starting a scientific career, it is more important to select a good group that provides an enabling environment, than to select a university with a high reputation.

6. Both data and hair can occur in overwhelming numbers, but organizing them properly is what really counts.

Propositions belonging to the thesis, entitled
The ecology of a liana community in a SW Chinese rainforest: functional traits, dynamics, and distribution

Qi Liu
Wageningen, 9 April 2021

The ecology of a liana community in a SW Chinese rainforest:

functional traits, dynamics, and distribution

Qi Liu

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Qi Liu

Thesis
submitted in fulfilment of the requirements for the degree of doctor at
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Prof. Dr. A. P. J. Mol,
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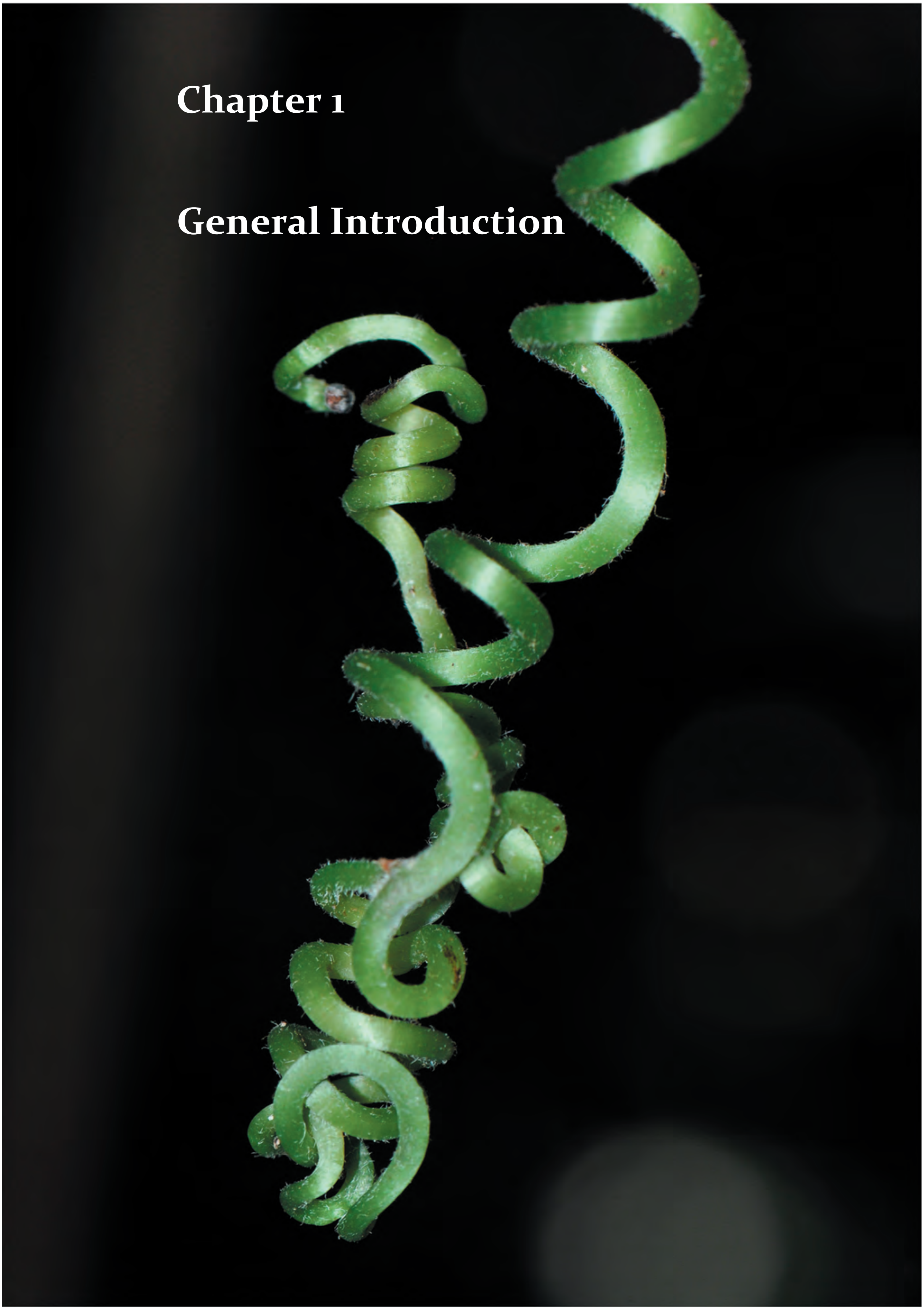
Chapter 1

General Introduction



Tropical forests provide important ecosystem services to human society by accounting for approximately one–third of Earth's terrestrial gross primary productivity and one–half of Earth's carbon stored in terrestrial vegetation (Lewis et al. 2015). Furthermore, over half of Earth's 5 to 20 million species reside in tropical forests (Groombridge et al. 2002, Scheffers et al. 2012), and more than 1 billion people directly rely on tropical forests for food, timber, medicines, and other ecosystem services (Vira et al. 2015). Tropical forests are however experiencing large compositional, structural, and dynamic changes (Lewis et al. 2004, Wright 2010, Malhi 2012, van der Sande et al. 2016). It is however unclear whether tropical forests still constitute a net carbon sink or source globally (Popkin 2017) after decades of declining sequestration capacity among old tropical forests (Brienen et al. 2015). Although the drivers of this transition are not yet fully understood, lianas (i.e., woody vines) have been proposed as a possible cause of tropical forest structural changes (Lewis et al. 2004).

1.1 Lianas and their roles in tropical forest

Lianas are a polyphyletic group (Gianoli 2004) of woody plants all sharing a common growth strategy that centers on ascending to the canopy using the architecture of other plants, but differ from other structural parasites (epiphytes and hemi–epiphytes) in that they remain rooted to the ground throughout their lives (Putz 1991). Lianas are an important life form of tropical forest because they commonly compose 25% of the rooted woody stems and 35% of the woody plant species in tropical forest (Schnitzer et al. 2012, Schnitzer 2015), and accordingly can have strong effects on trees and the entire forest ecosystem. Lianas can for example reduce tree growth, survival, reproduction, recruitment, and tree species diversity (e.g., Peña–Claros et al. 2008, Toledo–Aceves 2015, García León et al. 2018). Lianas can in principle alter competitive hierarchies and niche structure of co–occurring tree species (Schnitzer 2018, Muller–Landau and Visser 2019). At the ecosystem level, by competing more intensely with shade-tolerant, more densely wooded trees, lianas may shift tree composition toward faster-growing species, which store relatively little carbon, and reduce the carbon storage capacity of tropical forests (van der Heijden et al. 2013), reduce available soil moisture during seasonal droughts (Reid et al. 2015), and alter nutrient fluxes of tropical forests (Asner and Martin 2015, van der Heijden et al. 2015). Lianas also influence animal species diversity and community composition, such as invertebrates, arboreal mammals, and many bird species use lianas as a food source, eating liana leaves, pollen, flowers, and fruits, because lianas in general have lower structural and chemical defences, a greater nutritional profile comparison with trees (Odell et al. 2019). Lianas connect normally isolated neighboring tree crowns and thus provide important physical habitat connections for climbing animals (Chiarello et al. 2004, Adams et al. 2019). The changes in liana community that has been observed over the past decades (e.g., Phillips et al. 2002, Laurance et al. 2014, Bongers et al. 2020) will thus have strong implications for tropical forest ecosystems.

However, there are still unresolved challenges in liana ecology, with important hypotheses that have yet to be rigorously tested in multiple environments. For example, various details about the mechanisms responsible for liana distributions remain poorly understood. Lianas appear to respond differently than trees to abiotic and biotic drivers of plant abundance and distribution (e.g., Ledo and Schnitzer, 2014) because relying on trees liana don't need spend many resources in stem (Ewers et al. 2015), and lianas are supposed to have a deep root system which may give them an advantage over trees in dry seasons (Schnitzer 2005, but see Medina-Vega et al. 2020). Furthermore, it is not yet understood to what extent liana functional traits shape liana niche dimensions, nor how the functional composition and the abiotic environmental factors affect liana community demographic processes (i.e., mortality, recruitment, and growth). This PhD research aims to improve our understanding of liana community ecology by analyzing species differences in functional traits, liana dynamics, and liana distributions in a tropical seasonal rainforest in SW China. This thesis will thus improve our ecological understanding of lianas, particularly on how their populations and spatial distribution change, and how these processes relate to underlying mechanisms in terms of environmental drivers, functional traits, and strategies.

1.2 Community spatial structure along the environmental gradients

A major goal of community ecology is to explain why communities change in a systematic fashion across space (McGill et al. 2006). Community is a group of organisms occurring in a particular environment, presumably interacting with each other and with the environment, and identifiable by means of ecological survey from other groups (Tyler–Walters and Hiscock 2003). Species differences in physiological tolerances and competitive ability can lead to species replacement along environmental gradients (Slik et al. 2009). However, there are few community–wide studies on liana distributions, which has hampered our knowledge on the drivers of liana community composition (Schnitzer 2018). While exceptions exist, lianas are considered a fast–growing, light–limited growth form associated with high–light conditions, nutrient–rich soils, and disturbed habitats, including forest edges, canopy gaps, and logged forests (Putz 1984, Schnitzer et al. 2000, Schnitzer and Carson 2010). Below, the evidence for such associations with habitats and high resource levels in particular is further explained.

Light

Lianas are believed to require high–light conditions, since they tend to deploy most of their leaves in the upper forest canopy (Avalos and Mulkey 1999, Rodriguez–Ronderos et al. 2016). High liana densities were usually found in treefall gaps and forest edges (Barry et al. 2015, Schnitzer 2015, Campbell et al. 2018). In a tropical rain forest in Panama, the abundance and species richness of lianas were higher in treefall gaps than in non–gap sites of similar size (Schnitzer and Carson 2001). This could be explained by the multiple ways of liana recruitment into gaps: lianas may be pulled into the gap by the treefall event or grow laterally into the gap from the surrounding intact forest (Putz 1984). Additionally, like trees, lianas can colonize gaps from the seed bank, seed rain, and from advanced regeneration (Putz 1983, 1984, Putz and Chai 1987). Further, lianas appear to persist in gaps for many years (> 13), long after the canopy of most gaps are closed (Schnitzer et al. 2000). Therefore, gaps may appear to maintain the diversity of lianas simply because gaps increase liana abundance for a relatively long period of time (Schnitzer and Carson 2001).

Soil nutrients

Owing to increasing anthropogenic activities, such as the use of fossil fuels and agricultural burn and fertilizer, the global nutrient deposition may further increase (Dentener et al. 2006). Such increasing fertilization may advantage lianas by allowing them to satisfy their higher resource needs, which could increase their photosynthetic capacity and thus their growth and survival rates (Schnitzer and Bongers 2011, Asner and Martin 2015). In a lowland tropical rain forest in Malaysia, liana abundance was higher in forests with relatively fertile soil (DeWalt et al. 2006). The abundance of canopy lianas often increases with soil fertility (Putz 1983, Putz and Chai 1987) and lianas show higher foliar nutrient concentrations compared to trees (e.g., Cai and Bongers 2007, Zhu and Cao 2010, Asner and Martin 2012). Soil fertility therefore could be a driver of liana spatial distribution. Species differences in nutrient limitation (Denslow et al. 1987) are still poorly studied (Aerts et al. 2003), and also the relative role of different soil resources including nitrogen (N), phosphorus (P), or potassium (K), or combinations of these (e.g., Ceccon et al. 2004, Wright et al. 2011, Pasquini and Santiago 2012), have been more poorly studied for liana communities (but see DeWalt et al. 2006, Malizia et al. 2010).

Water

Rainfall amount and seasonality are strong predictors of liana density among forests (Schnitzer 2005). One mechanism proposed for this pattern is that lianas have well–developed root systems that allow them to more effectively tap water from deeper soil sources than neighbouring trees, giving lianas the chance to outgrow trees during the dry season, a hypothesis that has received some empirical support (e.g., Zhu and Cao 2009, Chen et al. 2015, but see Medina-Vega et al. 2020). Thus, amount and seasonality of annual rainfall and access to soil water in deeper layers may provide a good explanation for the spatial patterns of liana density (Manzané–Pinzón et al. 2018).

Topography

Within forests, topography may be a key factor driving resource availability, for water, soil nutrient as well as light availability. In small scale plot surveys, liana species richness has been shown to vary between floodplain and upland habitat types in the western Amazon, with higher richness on the upland sites (Burnham and Anderson 2002, 2004), and across a gradient of soil fertility and nutrient availability in northern Borneo, with higher richness on more fertile, less drought–prone sites (DeWalt et al. 2006). In a moist old growth forest in Panama, forty–four percent of all liana species showed habitat preferences, with 26 species showing significant associations with slopes and drier soils (Dalling et al. 2012). This implies that topography can be a good predictor for local variation in the abundance and composition of lianas, but the underlying mechanisms are still less clear.

1.3 Functional traits and plant strategies

Functional traits

Functional traits are morphological–physiological–phenological feature measured at the individual level that directly impact fitness, through their effects on plant growth, survival, and reproduction (Calow 1987, Keddy 1992, Violle et al. 2007) and hold the promise to explain plant species distribution patterns (McGill et al. 2006, Sterck et al. 2011, 2014). Plant traits can be closely associated for biophysical reasons (e.g., larger leaves require more robust stems for mechanical support), because of allocation trade–offs (e.g., plants can invest limiting resources either in above or belowground organs), and/or because they reflect adaptations to similar environmental conditions. Trait associations therefore reflect ecological strategies of species to successfully complete in the environment(s) that they encounter during their life (Grime 1974, Reich et al. 2003). Lianas differ from trees in critical patterns of biomass allocation and other key life–history traits (Dias et al. 2019). For example, in their climbing form, lianas rely on other vegetation as trellises to gain access to the canopy, and thus they typically invest proportionally less resources into woody stem tissue than trees (but see Selaya et al. 2007, Zhang et al. 2019, Medina-Vega et al. 2020).

Plant strategies

Plant strategies could be defined as groupings of similar or analogous phenotypic characteristics which recur widely among species or population and cause them to exhibit similarities in ecology (Grime 2006a). Plant functional traits can represent fundamental tradeoff axes that indicate life history strategies, the abiotic and biotic interactions of individuals and species, and their overall fitness or performance given the abiotic and biotic contexts (e.g., Ackerly 2003, Funk et al. 2017, Amahowe et al. 2018). Plant ecological strategies may therefore affect the success of species under different environmental conditions stronger than individual plant traits do (Grime 2006b, Westoby and Wright 2006). There is a global spectrum of plant strategies, ranging from 'slow' species with conservative traits (e.g., small leaf area and stomates) that increase resource conservation and plant survival, to 'fast' species with acquisitive trait values (e.g., large leaf area and stomates) that increase light capture and growth (e.g., Poorter and Bongers 2006, Sterck et al. 2006, Reich 2014, Díaz et al. 2016) (Figure 1.1). This continuum is also known as the leaf economics spectrum (LES) (Wright et al., 2004). At the stem level, a similar trait continuum, which is known as the wood economics spectrum (WES) (Chave et al. 2009, Sterck and Schieving 2011). The WES leads to a trade–off between growth and survival potential mainly determined by the wood density and its association with the mechanical and hydraulic properties of the stem, such as vessel size (Chave et al. 2009, Kattge et al. 2011, 2020) (Figure 1.1).

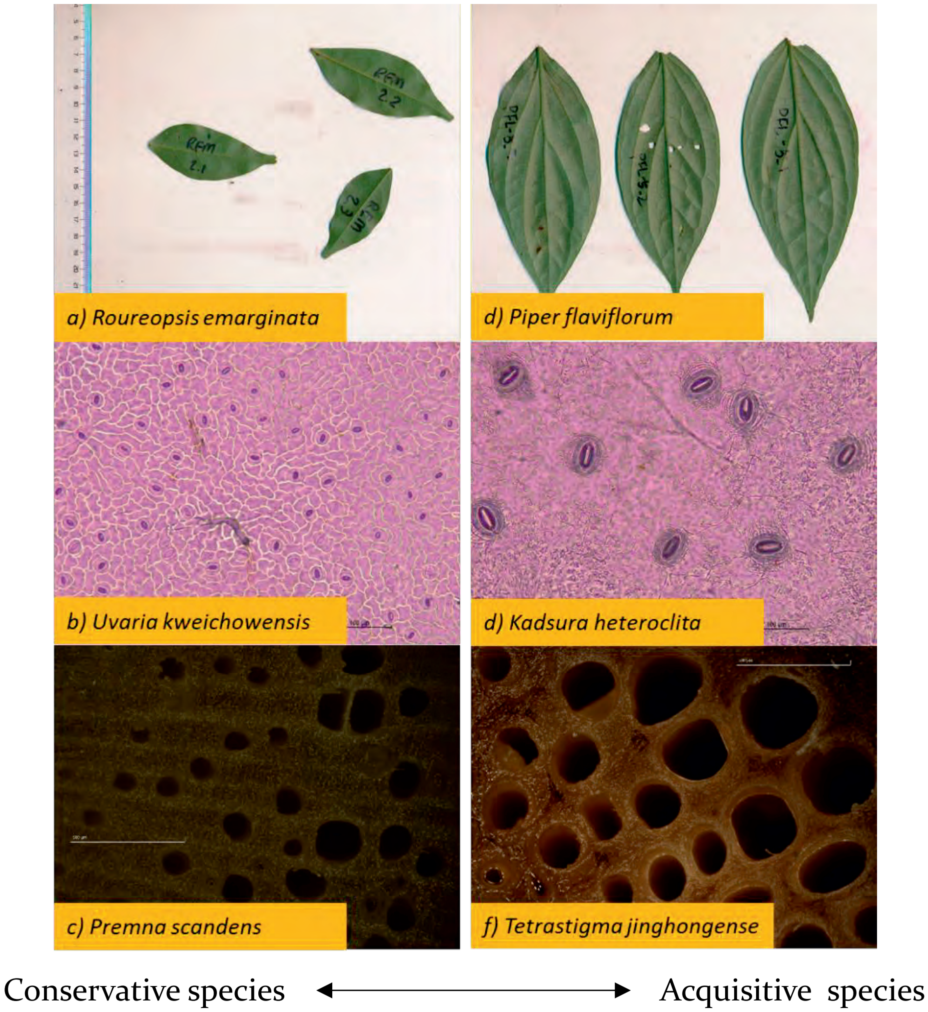


Figure 1.1 Examples of six conservative and acquisitive rainforest liana species in Xishuangbanna that reflects the extremes of the plant economics spectrum. The left pannel represents conservative species, with small leaf area (a), smaller stomata (b) and narrower vessels (c). The right panel represents acquisitive speices, which has relatively larger leaf area (d), larger stomata (e)and widder vessels (f). The figures in each row have same scales.

Species niche dimensions

Although trait–based ecology has the promise to turn community ecology into a more predictive science (McGill et al. 2006), it has been challenging to determine what traits best predict organisms' multidimensional niche space (Chase and Leibold 2003). The species niche is defined as the n–dimensional hypervolume of environmental and biotic conditions under which a species can grow and reproduce (Hutchinson 1957) and reflects therefore multiple niche dimensions. Niche theory predicts that species differ in their distribution when they are functionally different and specialized for different resource niches (Hutchinson 1957, Kitajima and Poorter 2008). Trait–based approaches have been used to infer niche differentiation and predict species distributions (Sterck et al 2014). Increasing evidence shows the existence of a trait-based trade–off that requires species to either rapidly acquire resources and grow fast under high resource conditions (often referred to as 'acquisitive' or 'fast' species), or to conserve resources and survive under low resource conditions ('conservative' or 'slow' species; Grime 1974, Díaz et al. 2004, Rich 20014). Such trade–offs are found within biomes across the globe (Reich et al. 1997), and for species that partition gradients in light (Veneklaas and Poorter 1998, Poorter and Bongers 2006), water (Markesteijn and Poorter 2009, Sterck et al. 2011), or nutrient availability (Grime et al. 1997). The use of traits for predicting such differential distributions of species across environments remains nevertheless limited, since the same trait combination may be suitable for different environments, and different trait combinations may be suitable for the same environment (Marks and Lechowicz 2006). Previous studies quantified niche dimensions of species, but in most cases only for trees (Sterck et al. 2011, 2014), whereas those ideas have little been tested for lianas (but see van der Sande et al. 2019).

1.4 Dynamics processes

Liana dynamics reports

Since Phillips et al (2002) first documented the increase of liana abundance and biomass in tropics forests, dozens of studies using a variety of metrics have supported the pattern of increasing liana abundance, biomass, or productivity. These studies were mostly carried out in the Neotropics (Figure 1.2) and proposed several putative mechanisms to explain this pattern (e.g., Schnitzer 2005, Wright and Calderón 2006, Chave et al. 2008, Ewango 2010, Schnitzer et al. 2020). However, regarding to liana increase, some pieces of evidence document different patterns in recently studies, such as liana decline in Cameroon (Thomas et al. 2015), Congo (Bongers et al. 2020) or unchanged abundance in the USA (Londré and Schnitzer, 2006) (Figure 1.1). Perhaps the patterns are erratic because local drivers (i.e., disturbance) may override more global drivers (Bongers et al. 2020). The lack of consensus about large–scale patterns in liana change and its possible drivers urges for additional studies on lianas dynamics covering a wider geographic range (Gerolamo et al. 2018), and as can be observed in Figure 1.2 studies on Asian liana communities are particularly scarce.

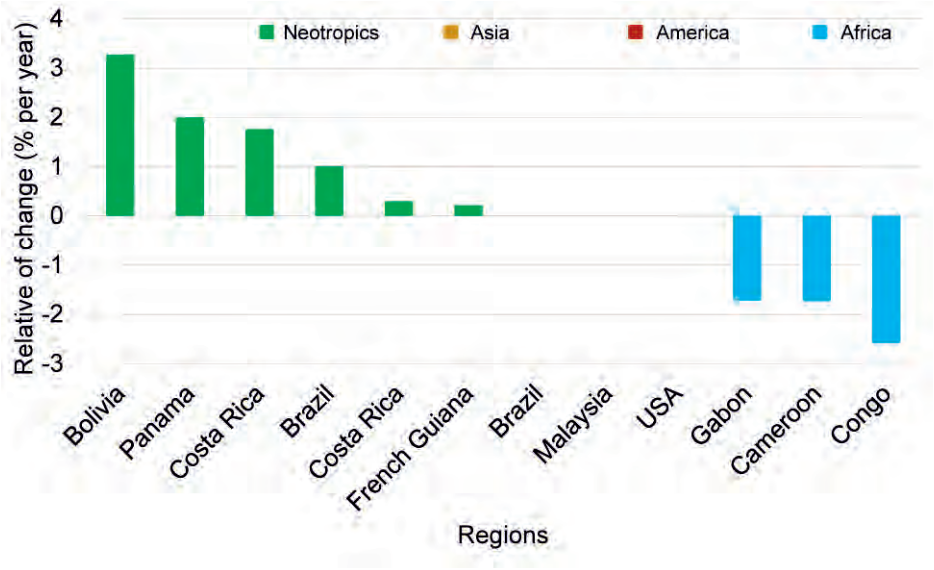


Figure 1.2 Studies examining the changes in liana abundance or dominance through time from countries around the globe.

Sources (from left to right): Phillips et al. 2002, Schnitzer et al. 2012, Yorke et al. 2013, Laurance et al. 2014, Enquist and Enquist 2011, Chave et al. 2008, Gerolamo et al. 2018, Wright et al. 2015; Londré and Schnitzer 2006, Caballé and Martin 2001, Thomas et al. 2015, Bongers et al 2020.

Hypotheses explaining global liana increasing.

As lianas are inherently fast growing, acquisitive species (Schnitzer et al. 2004), they may increase strongly in growth and abundance due to an increase in resource availability such as an increase in atmospheric CO_2 concentrations (e.g., Granados and Korner 2002, Mohan et al. 2006), fire–derived nutrient deposition (Hietz et al. 2011, Schnitzer 2015), increase in sunshine that comes along with reduced cloud cover (Graham et al. 2003), or increased forest disturbance and tree turnover rates (Laurance et al. 2001, Phillips et al. 2002). As lianas are thought to be more drought tolerant because they may tap water from deeper soil layers, they may also increase in abundance because of decreasing rainfall and increasing seasonality (Schnitzer 2005, Swaine and Grace 2007, DeWalt et al. 2010).

Changes in liana abundance or basal area are the result of underlying demographic processes (i.e., vital rates), including recruitment, growth, and survival. These demographic processes may be driven by abiotic and biotic factors. Topography and soil may cause spatial variation in liana dynamics because liana density was generally higher in more fertile soils and increased in the valleys with higher water availability (Gerolamo et al. 2018). Plant functional traits are thought to determine plant growth, survival, and reproduction (Ackerly 2003) as described above. Competition for limiting resources by lianas and trees affect liana dynamics. For example, plot tree basal area was associated with increased growth but decreased recruitment of trees in tropical moist forests (van der Sande et al., 2017, Rozendaal et al. 2020). Yet, few studies have assessed the complete chain of cascading effects– from functional traits to performance to species niches and distribution to forest dynamics, and to my knowledge on study has done so far for lianas.

1.5 Aims, research questions, hypotheses, and thesis outline

This PhD research aims to improve our understanding of liana community ecology by understanding how biotic and abiotic environmental conditions influence liana functional traits, and how conditions and trait together shape the local dynamics and distributions of liana species. To this end, I studied a liana community in a tropical rainforest in Xishuangbanna, SW China. I mapped, identified, and monitored approximately 20,000 liana individuals in a 20–ha plot from 2013–2019, used available environmental data on topography, soil nutrients and light gaps, measured liana functional traits. This dissertation consists of five chapters: the general introduction (chapter 1), three research chapters (chapter 2–4, Figure 1.3) and the general discussion (synthesis, chapter 5). Here I briefly explain the questions addressed per research chapter. In all cases, my work refers to the liana community in the same 20–ha forest plot mentioned above.

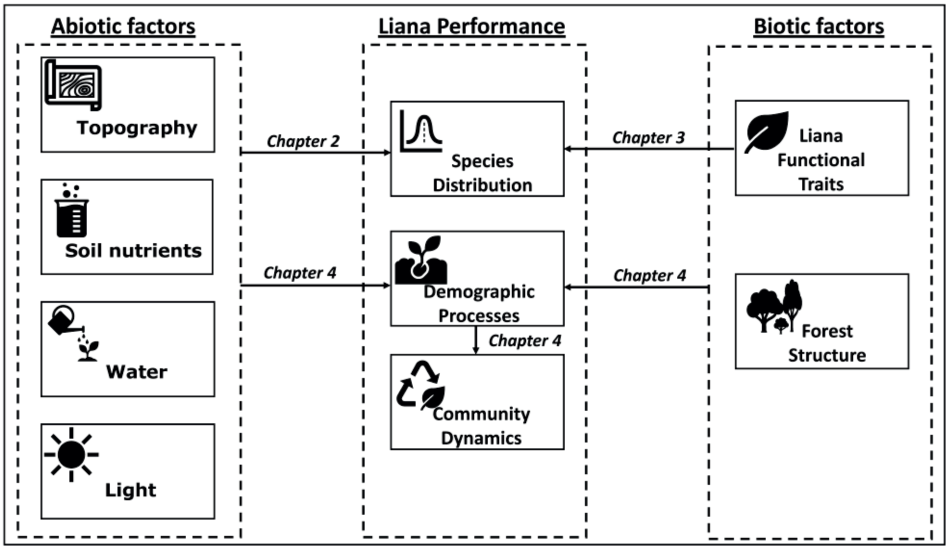


Figure 1.3 Conceptual model showing the relationships between the three research chapters, with respect to the aspects they address for the effects of abiotic (left column) and biotic (right column) factors on liana performance (central column) in terms of species distribution, demographic processes, and community dynamics. Arrows represent relationships between the research components and chapter numbers indicate the relationships studied for each of the chapters.

In ***Chapter 2***, the general question is how abiotic environmental factors structure liana communities. I evaluate the distribution patterns of the 50 most abundant liana species in the 20–ha forest plot. For each species, the distribution is quantified as the liana abundance in 500 small (20 m x 20 m) subplots. I analyze the relationship between liana species distributions and the availability of key resources for liana growth:

topography (which modifies resource availability), canopy gaps (which reflects light conditions), and soil nutrients (Figure 1.3). I hypothesize that canopy gaps are a stronger driver of abundance of individual liana species than soil fertility because most lianas need gaps to establish. For soil nutrients, I expect that liana distributions will be most strongly driven by P, followed by N and K. Given the assumed acquisitive nature of lianas, I expect that most liana species specialize for high soil nutrients to support the inherently fast growth rate that comes along with the liana growth form (Schnitzer et al 2014).

In ***Chapter 3***, two major questions are addressed: 1) how do plant trait associations and possible trait trade–offs lead to different liana strategies; and 2) how do these traits shape species' light, water and soil nutrient niche dimensions of coexisting lianas. I analyze for 29 abundant co–occurring liana species in a 20–ha forest plot 18 functional traits related to light, water and nutrients use, and quantify species niches using species distribution data (see chapter 1, Figure 1.3). In line with the plant economics spectrum, I expect liana species to show a trait spectrum, ranging from trait values that increase resource acquisition and use to trait values that increase resource conservation (Reich 2014, Díaz et al. 2016). I also predict that liana species with more acquisitive trait values generally occupy higher light, water, and nutrient resource niches.

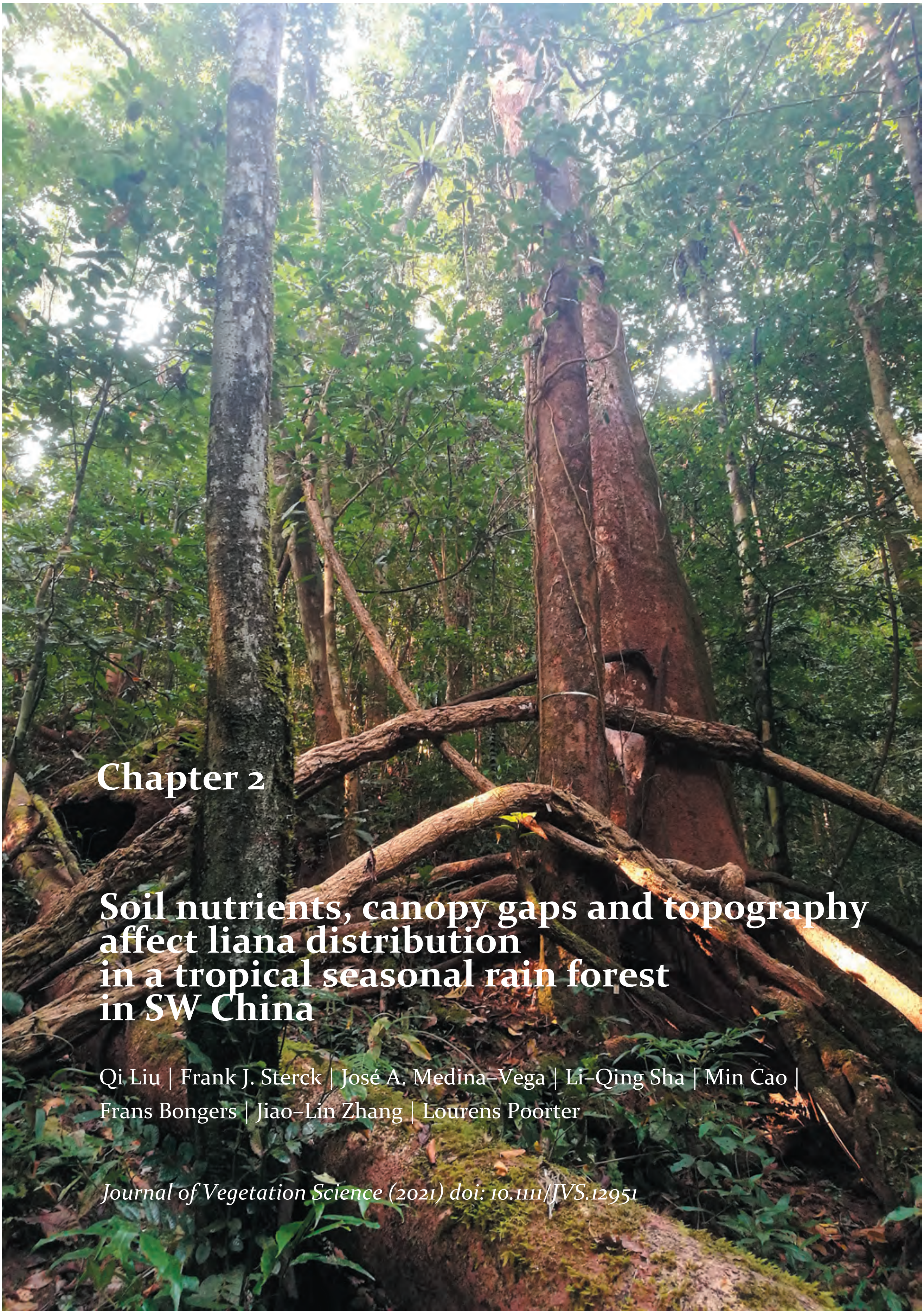
Chapter 4 addresses the question how functional traits and environmental conditions affect demographic processes of the liana community and may cause a decrease or increase in liana abundance and basal area. I therefore first evaluate the net changes in liana density and basal area in the 20–ha plot over a 5–year period (2013–2019). I then relate these changes to the vital rates (recruitment, growth, and mortality) that characterize the demography. Finally, I evaluate how the observed liana changes were driven by abiotic environmental variables (light, water, and nutrients), forest structure, and functional composition (Figure 1.3). I expect that lianas in Xishuangbanna will benefit from global change such as increasing atmospheric CO_2 concentrations, and therefore will increase in abundance and basal area from 2014 to 2019. I also predict that faster growth and recruitment rate can be explained by better light conditions and resource availability (water and nutrients) and that species with more acquisitive trait values (e.g., high specific leaf area, wide vessels, low wood density) will not only have a faster growth and recruitment rates but also higher mortality rates.

Finally, ***Chapter 5*** provides the synthesis of this thesis. I summarize and integrate, the main findings of this thesis and discuss how it advances our understanding of liana ecology, provide research recommendations, and discuss the future of lianas in a changing world.

1.6 Study area

The study was conducted in a seasonal tropical rainforest in Xishuangbanna, Southwest China (101° 34′ E, 21° 36′ N). The climate is shaped by warm–wet air masses from the Indian Ocean and continental air masses from the sub–tropical regions in summer and winter, which results in an alternation of dry and rainy seasons with a typical monsoon climate. The mean annual temperature is 21 °C and precipitation is 1, 532 mm/yr. More than 80% of precipitation occurs from May to October (rainy season) (Lan et al., 2009). The main soil type is laterite (Cao et al. 2006). A 20–ha permanent plot was established in 2007 in Xishuangbanna to monitor the spatial and temporal dynamics of the forest based on a standardized protocol (Condit 1998). The topography of the plot is heterogeneous with an elevational range from 709 m to 869 m a.s.l. The plot is trisected by three perennial streams that join in the Southwest of the plot (Lan et al. 2009). The vegetation in the area is a tropical seasonal rainforest with a canopy height of up to 60 m (Zhu 2006). All free–standing trees with ≥ 1 cm diameter at breast height (DBH), were tagged and identified to species level, and tree species in this plot are dominated by *Parashorea chinensis* (Dipterocarpaceae), *Pittosporopsis kerrii* (Icacinaceae) and *Garcinia cowa* (Clusiaceae).

From 2013–2015, all rooted lianas ≥ 1 cm diameter were tagged, mapped, measured to the individual level in 500 20 m × 20 m quadrats in the 20–ha plot. We spatially mapped the rooting point of each liana. The rooting point was defined as the last substantial rooting point before the stem ascends. If the stems were connected below the soil surface, then we considered them to be independent stems. We included all liana species with woody or fibrous perennial stems (e.g., Desmoncus, Gnetum, Smilax, Dioscorea), but excluded epiphytes, hemi–epiphytes, and climbing bamboos (Gerwing et al. 2006, Schnitzer et al. 2008). We identified all lianas to species level in the field using a combination of leaves, bark, and trunk characteristics. The most abundant lianas were *Parameria laevigata* (Apocynaceae), *Byttneria aspera* (Malvaceae) and *Fissistigma polyanthum* (Annonaceae).



Chapter 2

Soil nutrients, canopy gaps and topography affect liana distribution in a tropical seasonal rain forest in SW China

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Frans Bongers | Jiao–Lin Zhang | Lourens Poorter

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ABSTRACT

Lianas are a conspicuous element of tropical forests but have largely been ignored in species–level vegetation surveys. As a result, there is a limited understanding of how environmental factors structure liana communities. We evaluated the distribution of the 50 most abundant liana species, comprising >18,000 individuals, in a 20–ha forest dynamics plot in Xishuangbanna National Nature Reserve, SW China. Ordination analysis and generalized linear mixed models were used to evaluate how species distribution and abundance are associated with soil pH, soil phosphorous (P), soil nitrogen (N), and soil potassium (K), canopy gaps and topography. We calculated the average weighted distribution as a proxy for the optimum resource condition for each species.

The first two axes of a canonical correspondence analysis explained 65% of the variation in liana species composition, with pH and P being the strongest drivers and highly correlated with each other. We modelled the responses of liana species to soil nutrients, and found a negative, unimodal, or positive response of liana abundance with increasing soil nutrient concentrations. Forty–six of the 50 species occurred under significantly higher or lower soil nutrient conditions than expected at random. Lianas mainly separated along the P gradient, whereas for N and K most liana species tended to occupy locations with high nutrient

concentrations.

Although lianas are thought to be notoriously light–demanding, soil conditions were stronger drivers of liana species distribution than gaps. Species differences in distributions were mainly driven by soil gradients in pH and P, which highlights the importance of soil nutrient status for liana niche partitioning in wet tropical forests on highly weathered soils. Most liana species had high resource requirements for N, K, and light, which come along with their fast growth and acquisitive resource use strategy. Hence, belowground resource availability plays an important role in shaping the assembly of liana communities.

2.1 INTRODUCTION

To understand patterns in the spatial structure of plant communities it is necessary to examine species distributions along environmental gradients (McGill et al. 2006). Differences in physiological tolerances and competitive ability can lead to species replacement along these environmental gradients. In classical continuum theory, species are supposed to have symmetric, unimodal response curves, which have often been quantified with species distribution models (Araujo and Guisan 2006, Guisan and Thuiller 2005).

Lianas (i.e., woody climbers) are one of the key life forms in tropical forests. Lianas comprise up to 35% of the woody plant species and 25% of the rooted woody stems, thereby contributing substantially to the forest leaf area and biomass (Schnitzer et al. 2012, Schnitzer 2015). Lianas play a major role in tropical forest dynamics by competing with trees for both aboveground and belowground resources (Schnitzer and Bongers 2002), resulting in reduced tree growth, survival, fecundity, and recruitment (Schnitzer et al. 2000, Peña–Claros et al. 2008). These negative liana impacts may substantially alter tropical forest structure, composition, and carbon storage (Schnitzer and Bongers 2011, van der Heijden et al. 2015, Estrada–Villegas and Schnitzer 2018). Most studies have evaluated lianas as a single functional group, potentially concealing important interspecific differences in liana responses which are key to understand community dynamics. Several studies have reported that liana species had habitat preferences, such as low hill areas (Ibarra–Manríquez and Martínez–Ramos 2002, Addo–Fordjour et al. 2014, Addo–Fordjour and Rahmad 2015), and liana composition and abundance are most strongly correlated with features of the physical environment (Malizia et al. 2010). Studies that relate liana distribution to soil nutrients are scarce, and are restricted to seedlings (Manzané–Pinzón et al. 2018) or to relatively small plots (e.g., 1 ha forest, in Chettri et al., 2010). Adult lianas may show stronger relationships with soil nutrients because filtering has occurred over longer periods of time, and they have greater competitive effects on canopy tree performance (Tobin et al. 2012). There are few community–wide studies on liana distribution, which has hampered our knowledge on the drivers of liana community composition (Schnitzer 2018). Here we analyse to what extent environmental drivers (soil nutrients, canopy gaps and topography) affect the distribution of the liana species in a 20–ha plot in a tropical rain forest in Southwest China.

Plants require nutrients to grow, and nutrient availability should therefore determine community composition. Plant nutrient availability is determined by topography, proximity of bedrock material, soil texture and age and mineralization rates. Many liana species, in contrast to trees, can have multiple locations where they root and therefore the connection between liana individuals and the soil at a main rooting point may be less clear. In a subtropical forest in Japan, lianas tend to be distributed in the concave habitats such as valleys (Kusumoto et al. 2013), where soil moisture and nutrients accumulate, whereas poor and dry soils are often encountered on ridges (Wilcke et al. 2008). A study in Argentina found that liana diversity and abundance strongly increased with soil phosphorus (P) concentration (Malizia et al. 2010), whereas a study in Mexico found that soil fertility does not determine liana abundance (Ibarra–Manríquez and Martínez–Ramos 2002). Soil nutrients may especially be important for lianas to support their inherently fast growth rates. Nitrogen (N), P and potassium (K) are considered to be the three main macronutrients. N is required in all plant cells, proteins, and chlorophyll, and thus is a key element for plant growth. P is important for energy transfer (ATP) and DNA structure, and K increases the regulation of stomatal aperture, and disease resistance of plants (Marschner 2011). Moreover, the high growth rates of lianas match the high abundance of lianas in disturbed areas of natural forests, such as treefall gaps, where lianas can recruit rapidly and abundantly, but where they decrease over time in abundance when the gap closes (Schnitzer and Carson 2010). Lianas may not only respond positively to forest gaps because of an increase in light, but also because of an increase in nutrient availability (Veenendaal et al. 1996, Denslow et al. 1998). We thus expect that liana distribution will be associated with high concentrations of nutrients, as well as with gap.

This study aims to analyse how soil nutrient availability, gap and topography shape the distribution of the 50 most abundant liana species in a Chinese tropical seasonal rain forest. We addressed the following three questions and corresponding hypotheses:

First, to what extent do soil nutrients vary across the landscape and with topography and gap? We predict that soil nutrient concentrations are high in valleys and low on upper slopes and crests. We also expect that nutrient availability is high in tree fall gaps because of increased litter input and decomposition of fallen debris, and because there are no big trees that take up nutrients at high rates.

Second, to what extent are these environmental factors associated with the distribution of liana species? We hypothesize that canopy gaps are a stronger driver of the abundance of individual liana species than soil fertility because most lianas need gap to establish. For the soil factors, liana distribution will be most strongly driven by P, followed by N and K because P is either heavily leached or adsorbed in inaccessible fractions in old weathered and leached tropical soils (Vitousek et al. 2010). N will be the second most important factor as it is crucial for proteins and photosynthesis (Evans and Poorter 2001), and also N mineralisation rates are generally high enough to sustain vegetation N demand; K is involved in stomatal regulation and control for water loss (Marschner 2011) and most soils can generally supply sufficient K to satisfy the low requirements for plants for this element (Sparks and Huang 2015), K will therefore be the least important factor.

Third, how do liana species partition these soil resource and topography gradients? We hypothesize that most liana species specialize for high soil nutrients to support the inherently fast growth rate that comes along with the liana growth form (Schnitzer et al. 2014a). We also expect that most lianas will be associated with convex areas and relatively flat areas where irradiance and soil fertility are higher.

2.2 METHODS

2.2.1 Study site

This research was carried out in Xishuangbanna, Southwest China (101°34'2"–47"E, 21°36'42"–58"N). Xishuangbanna is located on the northern edge of the Asian tropical rain forests and is identified as a part of the Indo–Burma biodiversity hotspot (Myers et al. 2000). Mean annual precipitation is 1532 mm, of which approximately 80% occurs in the rainy season between May and October. Mean annual temperature is 21.0 °C and the soil consists of latosol (Xue et al. 2003, Lan et al. 2011). The vegetation of Xishuangbanna consists of tropical rain forest, tropical seasonal rain forest and tropical montane evergreen broad–leaved forest (Zhu et al. 2006). A 20–ha permanent plot was established in the Xishuangbanna National Nature Reserve in 2007 (Lan et al. 2011). The Xishuangbanna 20–ha plot is 400 m in width and 500 m in length at an elevation of 709 – 869 m a.s.l. (Figure 2.1) and consists of tropical seasonal rain forest. All trees ≥1 cm in diameter at breast height (DBH) were mapped and tagged with unique numbers. In total > 95,000 free–standing individuals were identified to species level, representing 468 species (Lan et al. 2011).

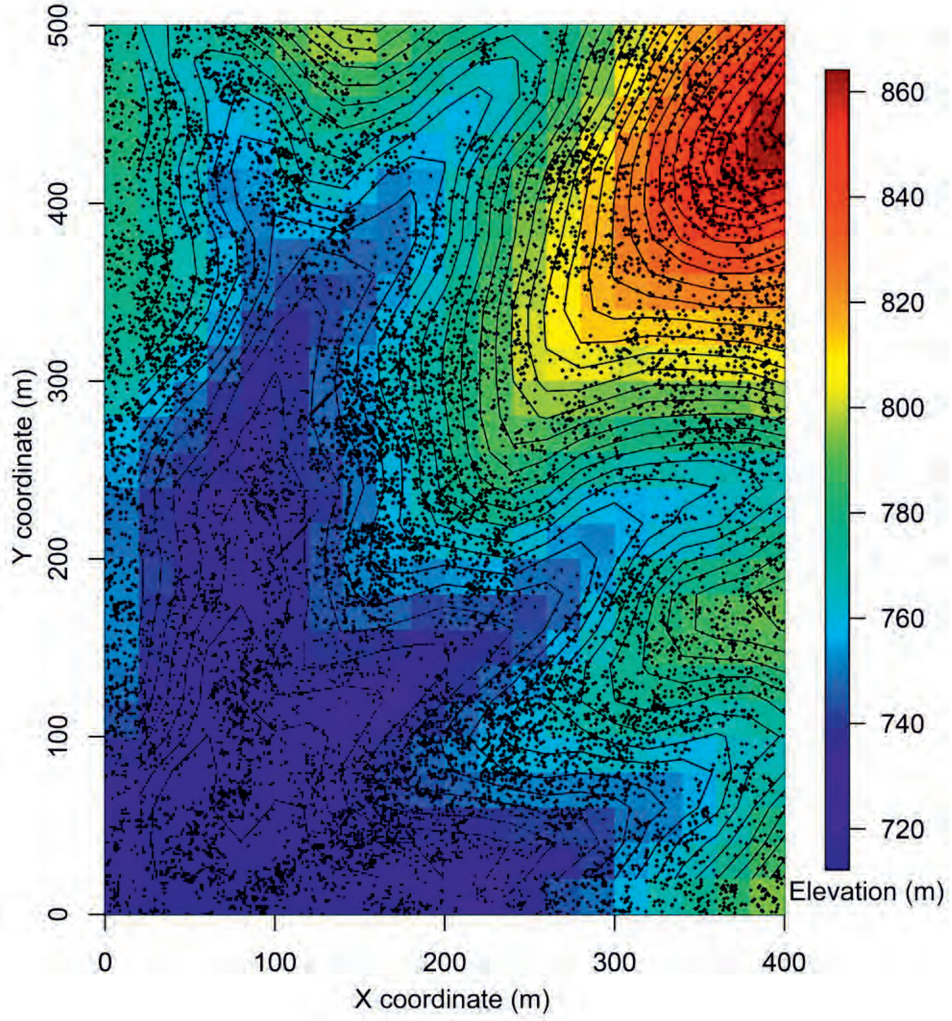

Figure 2.1 The distribution of lianas in relation to topography (elevation) in the Xishuangbanna 20–ha tropical seasonal rain forest dynamics plot. Each dot is a liana individual and colours refer to variation in elevation.

2.2.2 *Species selection*

From 2013–2015, all rooted lianas ≥ 1 cm diameter were tagged, mapped, measured to the individual level in 500 20 m × 20 m quadrats in the 20–ha plot. We spatially mapped the rooting point of each liana. The rooting point was defined as the last substantial rooting point before the stem ascends. If the stems were connected below the soil surface, then we considered them to be independent stems. We included all liana species with woody or fibrous perennial stems (e.g., Desmoncus, Gnetum, Smilax, Dioscorea), but excluded epiphytes, hemi–epiphytes, and climbing bamboos (Gerwing et al. 2006, Schnitzer et al. 2008). We identified all lianas to species level in the field using a combination of leaves, bark, and trunk characteristics. We selected for this study the 50 most abundant species that comprise 90% (18581 individuals) of all identified liana individuals (Table 2.1) (Liu et al. 2017), and determined therefore most of the liana community dynamics. For each species, we quantified the abundance by the numbers of stems per species in each of the 500 quadrats (20 m by 20 m), and related this abundance to the gap, soil pH and nutrient concentrations, and topography. One quadrat was omitted from the abundance analysis, because most of the vegetation was removed by a landslide in 2013.

Table 2.1 Distribution of optimal (average weight) soil conditions (pH; N, total nitrogen; P, total phosphorus; K, total potassium) and topography (convexity and slope) of 50 liana species. The association was tested using a randomization procedure for each species, where species with an average weight in the highest or lowest 2.5th percentile of the simulated distribution (999 times) were considered to have significantly higher (H) or lower (L) resource requirement with that parameter, and else (for those in the middle M) not significant.

Species	Code	Individuals	pH	Nitrogen	Phosphorus	Potassium	Convexity	Slope
Parameria laevigata	Pa_la	2387	L	L	L	M	H	M
Byttneria aspera	By_as	1451	M	H	H	H	H	M
Fissistigma polyanthum	Fi_po	990	L	L	L	M	H	M
Gnetum montanum	Gn_mo	849	L	L	L	M	H	M
Combretum latifolium	Co_la	776	M	M	M	H	H	M
Sargentodoxa cuneata	Sa_cu	736	L	M	L	M	H	H
Uvaria kweichowensis	Uv_kw	699	H	H	H	H	L	L
Strychnos angustiflora	St_an	695	M	M	M	M	M	H
Spatholobus uniauritus	Sp_un	693	L	M	M	H	H	M
Callerya pachyloba	Ca_pa	490	L	M	L	M	H	M
Benkara sinensis	Be_si	464	L	L	L	L	H	H
Tetrastigma cauliflorum	Te_ca	437	H	H	H	H	L	L
Uncaria macrophylla	Un_ma	433	L	M	L	M	H	M
Uncaria laevigata	Un_la	430	L	L	L	M	H	M
Paederia foetida	Pa_fo	414	L	L	L	M	H	M

Tetrastigma planicaule	Te_pl	369	L	L	L	H	H	M
Tetrastigma jinghongense	Te_ji	346	H	M	H	H	M	M
Combretum griffithii	Co_gr	345	L	M	M	H	H	M
Embelia undulata	Em_un	277	L	L	L	M	Hi	H
Premna scandens	Pr_sc	267	H	M	H	M	M	M
Millettia ichthyochtona	Mi_ic	254	M	M	H	H	M	M
Salacia sessiliflora	Sa_se	247	H	H	H	M	M	M
Dalbergia stipulacea	Da_st	241	L	L	L	L	H	M
Tetracera sarmentosa	Te_sa	238	M	L	L	M	M	H
Tetrastigma obovatum	Te_ob	214	M	M	M	M	M	M
Ventilago leiocarpa	Ve_le	213	M	M	L	L	H	M
Iodes cirrhosa	Io_ci	210	M	M	M	H	H	M
Tetrastigma xishuangbannaense	Te_xi	200	H	H	H	M	L	L
Capparis fohaiensis	Ca_fo	192	H	H	H	M	M	M
Congea tomentosa	Co_to	191	M	M	M	M	M	M
Jasminum subglandulosum	Ja_su	190	H	H	H	H	M	M
Marsdenia tinctoria	Ma_ti	188	M	H	M	M	M	H
Dalbergia rimosa	Da_ri	179	L	M	L	M	H	M
Uvaria tonkinensis	Uv_to	175	H	H	H	H	M	M
Strychnos nitida	St_ni	173	H	H	H	M	M	M
Aganope thyrsiflora	Ag_th	171	M	H	H	H	M	L
Zanthoxylum laetum	Za_la	165	H	H	H	M	M	L
Acacia vietnamensis	Ac_vi	157	M	H	H	M	M	M
Piper flaviflorum	Pi_fl	143	H	H	H	H	M	M

Ficus sagittata	Fi_sa	143	H	H	H	H	L	L
Roureopsis emarginata	Ro_em	143	L	M	L	M	H	M
Tetrastigma lenticellatum	Te_le	135	H	H	H	H	L	L
Ichnocarpus frutescens	Ic_fr	135	M	M	M	M	H	M
Marsdenia yunnanensis	Ma_yu	119	L	M	L	M	H	M
Tinomiscium petiolare	Ti_pe	117	H	M	H	M	M	M
Kadsura heteroclita	Ka_he	108	L	H	M	M	M	M
Bauhinia touranensis	Ba_to	103	M	H	M	H	M	M
Artabotrys hongkongensis	Ar_ho	102	M	M	M	M	M	M
Poikilospermum suaveolens	Po_su	94	H	M	H	M	L	L
Salacia polysperma	Sa_po	93	H	M	M	L	M	M

2.2.3 Soil nutrients

The methods to quantify soil nutrients have been described by Hu et al (2012). The soil was sampled in 2011 using a regular grid of 30 m × 30 m throughout the 20–ha plot. Each of the 252 nodes in this grid was used as a "base point". Together with each base point, two additional sampling points were located at random distances of 2 and 5 m, 2 and 15 m or 5 and 15 m along a random compass direction from the associated base point. In total 756 soil samples were taken. At each sample point, 500 g of topsoil was collected at 0–10 cm depth. Fresh soil samples were placed in plastic bags, shipped to the Biogeochemistry Laboratory at the Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, and measured for soil pH. pH is an important factor for plant distribution because it modifies nutrient availability of N, P and K by controlling the chemical forms of the different nutrients and influencing the chemical reactions they undergo. Soil pH was measured immediately after sampling in the laboratory using a potentiometer in fresh soil after water extraction (soil/water = 1/2.5 weight/volume). Subsequently, the soil was air–dried, sieved using 1 mm and 0.15 mm mesh, and stored in plastic bags for later analysis (Liu et al. 1996). Soil bulk density was measured using the soil core method, soil organic matter was measured in soil oxidised with H_2SO_4–$K_2Cr_2O_7$. The micro–Kjeldahl method was used to evaluate total N using a mixture of H_2SO_4 and K_2SO_4–$CuSO_4$–Se catalyst, and an automatic steam distilling unit was used to determine the soil N content in the solution. Micro–diffusion was used to determine the ammonium N in the soil. The soil was digested in HNO_3–$HClO_4$ solution, and the total P and K were determined using an inductively coupled plasma atomic emission spectrometer (ICP–AES/iCAP7400, Thermo Fisher Scientific, MA, USA). Extractable P was released from the soil in a solution containing 0.03 mol l^{-1} NH_4F and 0.025 mol l^{-1} HCl and estimated colorimetrically. Exchangeable K was extracted in a neutral 1 mol l^{-1} CH_3COONH_4 solution, and the total K in the extract was determined using the inductively coupled plasma atomic emission spectrometer (Hu et al. 2012).

Using these original soil data, an ordinary kriging was performed to generate a sub–quadrat grid map of 10 m × 10 m for each soil variable (Cressie 1992). The soil nutrients for each 400–m^2 quadrat were calculated as the mean of the values at each of the nine nodes of the 10 m × 10 m sub–quadrats within that quadrat by using the geoR package in the R (see Hu et al. 2012). Basing on this dataset, for each soil factor, comparisons among element concentrations were done on a volumetric basis (g cm^{-3}) rather than a mass basis (Ellert and Bettany 1995) because it indicates the plant nutrient availability per unit soil volume that can potentially be explored by plant roots. To calculate plant nutrient availability per unit soil volume, total and available, N, P and K were multiplied by the soil bulk density. A bi–variate Pearson correlation showed that most soil factors were associated (Table 2.2). To avoid the bias from measurements (such as extractable P depends on the model of extraction, see Qin et al. 2019), only total N, P and K were used in the analyses.

Table 2.2 Group differences (for gaps) and correlations between soil chemical properties across 500 400m^2 quadrats in the tropical rain forest of Xishuangbanna, China. For each variable median value for gap and non–gap are shown.

	gap	non–gap	*p*–value	pH	N	P	K	N_{am}	P_{ext}
pH	5.03	4.77	$p < 0.001$						
N	2.09	1.99	$p < 0.001$	0.49^{**}					
P	0.43	0.37	$p < 0.001$	0.84^{**}	0.64^{**}				
K	12.67	12.19	$p = 0.207$	0.28^{**}	0.35^{**}	0.49^{**}			
N_{am}	175.83	173.99	$p = 0.077$	0.24^{**}	0.83^{**}	0.43^{**}	0.27^{**}		
P_{ext}	3.52	2.94	$p = 0.012$	0.79^{**}	0.54^{**}	0.80^{**}	0.08	0.33^{**}	
K_{ex}	169.86	165.76	$p = 0.101$	0.44^{**}	0.51^{**}	0.48^{**}	0.27^{**}	0.30^{**}	0.43^{**}

**. $p < 0.01$, *. $p < 0.05$. N, total nitrogen; P, total phosphorus; K, total potassium; N_{am}, ammonium nitrogen; P_{ext}, extractable phosphorus; K_{ex}, exchangeable potassium. Soil nutrients were square–root transformed to satisfy the assumptions of normality and Pearson correlation was used for the analyses. We used a Kruskal–Wallis to compare Gap–group differences, a binary variable for light conditions (gap versus non–gap).

2.2.4 Topographical variables

The plot was subdivided into quadrats (n = 500) of 20 m × 20 m for each of which slope, convexity and elevation was measured following Harms et al. (2001). Elevation for each subplot was calculated as the mean of the elevation at its four corners. Slope was based on the mean angular deviation from the horizontal of each of the four triangular planes formed by connecting three corners. Convexity was calculated as the difference between the mean elevation of the focal subplot and the mean elevation of the eight surrounding subplots. For the marginal quadrat, convexity was defined as the elevation of the centre point of the quadrat minus the average elevation of its four corners. Concave sites have a negative value while convex sites have a positive value.

2.2.5 Gaps

To evaluate the role of gap in liana distribution, we inferred for each quadrat, light conditions based on forest structure. The quadrat was defined as a "gap" when the canopy cover in the year 2014 was less than 50% (Liu et al. 2014)

2.2.6 Data analyses

To evaluate how environmental variables shaped liana species distribution, we used a Canonical Correspondence Analysis (CCA) (Cajo 1986) to extract gradients of variation in liana species distribution (i.e., the abundance of each liana species in each 20 m x 20 m quadrat) explainable by environmental variables. We assessed which environmental variables best–explained liana community composition using forward selection implemented in the R package "vegan" (Oksanen et al. 2010), where only the most important (higher R^2) and significant variables ($p < 0.05$) were included one at a time, providing a relative order of variable importance based on the explained variation. Significance was based on a Monte Carlo permutation procedure using 999 random draws. Parallel to the CCA, we performed a Detrended Correspondence Analysis (DCA) which included all environmental variables and the ordination axes of DCA to give high confidence in the robustness of the observed patterns by using the function envfit (Oksanen et al. 2010).

We used generalized linear mixed–effects models (GLMMs) to assess the association of liana abundance with environmental factors and the shape of the response curve (i.e., positive, unimodal, or negative). We modelled liana abundance as a function of soil nutrients (soil pH, N, P, K), topography (convexity and slope) and gap (no gap = 0, gap = 1). We standardized the continuous predictors by subtracting the mean and dividing by the standard deviation. This standardization is recommended to reach model convergence and to improve computational accuracy (Hox et al. 2010, Neter et al. 1989). We included the quadratic form of the (standardized) continuous predictors to model unimodal responses of lianas to environmental gradients. We added species as random intercept and the continuous predictors (linear and quadratic forms) as random slopes. The random structure of the model allowed us to identify a species–level response of liana abundance to resource availability (soil nutrients and topography) by shifting the community–level coefficients, determined by the fixed effects, by a fixed amount for each species. We included quadrat as a random intercept to account for spatial autocorrelation within quadrats.

For the analysis, we derived a set of alternative sub–models from the most complex model which included the linear and quadratic form of pH, N, P, K, convexity, slope and the categorical predictor gap, by systematically removing (1) the quadratic and (2) linear form of the continuous predictors and (3) gap. We considered models with $\Delta AIC \leq 2$ to have a substantial level of empirical support from the data (Burnham and Anderson 2002, Carroll and Ruppert 1981). When two models had similar ΔAIC values, we selected the simplest one.

We checked for multicollinearity by using the variance inflation factor (VIF) implemented in the package ‘performance’ (Lüdecke et al. 2020), and a threshold value of 3 (Zuur et al. 2010) (Appendix S2.1). We checked for overdispersion and zero inflation in the data following Zuur et al. (2009). Due to observed overdispersion in the data, we used a negative binomial distribution type 1, where variance increases linearly with the mean and not quadratically as the standard negative binomial parameterization (Hardin et al. 2007) as it provided the better fit. Zero inflation was not detected. We tested for spatial autocorrelation by using the Moran–I test implemented in the package ‘ape’ (Paradis and Schliep 2019) via the package ‘DHARMa’ (Hartig 2020) on the conditional (on the fitted random effects) – scaled – residuals simulated from the best fitted (GLMM) model. Spatial autocorrelation was not detected (Appendix S2.2). We constructed the GLMM’s using the glmmTMB package (Brooks et al. 2017) and a sample script is provided in supporting information (Appendix S2.3).

To evaluate whether liana species have their optimum under significantly higher or lower resource concentrations than average found in the plot, we calculated for each species and each of the six environmental variables (pH, N, P, K, convexity and slope) the observed optima (weighted mean) and compared it to a random distribution. For each species, the observed optimum was calculated as: $\frac{1}{N}\sum n_i X_i$, where N is the total number of lianas in all quadrats, n_i is the liana abundance in quadrat i, and X_i is the value of the parameter in quadrat i. Then, “artificial species” were generated by assigning the same number of quadrats (and individuals) randomly to values of that environmental factor, and a “random” weighted mean was calculated. This procedure was repeated 999 times to create a distribution of random means, and test whether the observed optima were significantly higher or lower than the random weighted mean. Associations with a parameter were considered to be significant if the observed optima fell within the lowest or highest 2.5% of the simulated distribution (Paoli et al. 2006).

Statistical analyses were performed using Rstudio (Version 1.1.383) packed with R 3.6.1 (R Core Team 2019) including the package "vegan". Pearson correlation, Kendall's τ correlations and Wilcoxon–Mann–Whitney U test were performed using SPSS version 23 for Windows (SPSS Incorporated Chicago, IL).

2.3 RESULTS

2.3.1 Soil nutrients across the landscape

Across the 500 forest quadrats, total K varied 3–folds (range 7.7–20.3 g cm^{-3}, average 12.3), total P varied 3–folds (range 0.2–0.6 g cm^{-3}, average 0.4), total N varied 1–fold (from 1.8–2.4 g cm^{-3}, average 2.0) and pH varied 1.5–folds (from 4.1–6.3, average 4.9) (Appendix S2.4). Of these 500 forest quadrats, 31 were defined as gaps.

Soil nutrient concentrations were positively related to each other and pH (Table 2.2). Total and available nutrient availability were strongly correlated for N (Pearson's $r = 0.83$, $p < 0.01$) and P ($r = 0.80$, $p < 0.01$) but weakly correlated for K ($r = 0.27$, $p < 0.01$) in 500 quadrats. Kruskal–Wallis test showed that soil nutrient concentrations in gaps are significantly higher than that in non–gaps (except K). Soil nutrient concentrations varied spatially and decreased with elevation, slope, and convexity (Figure

2.2).

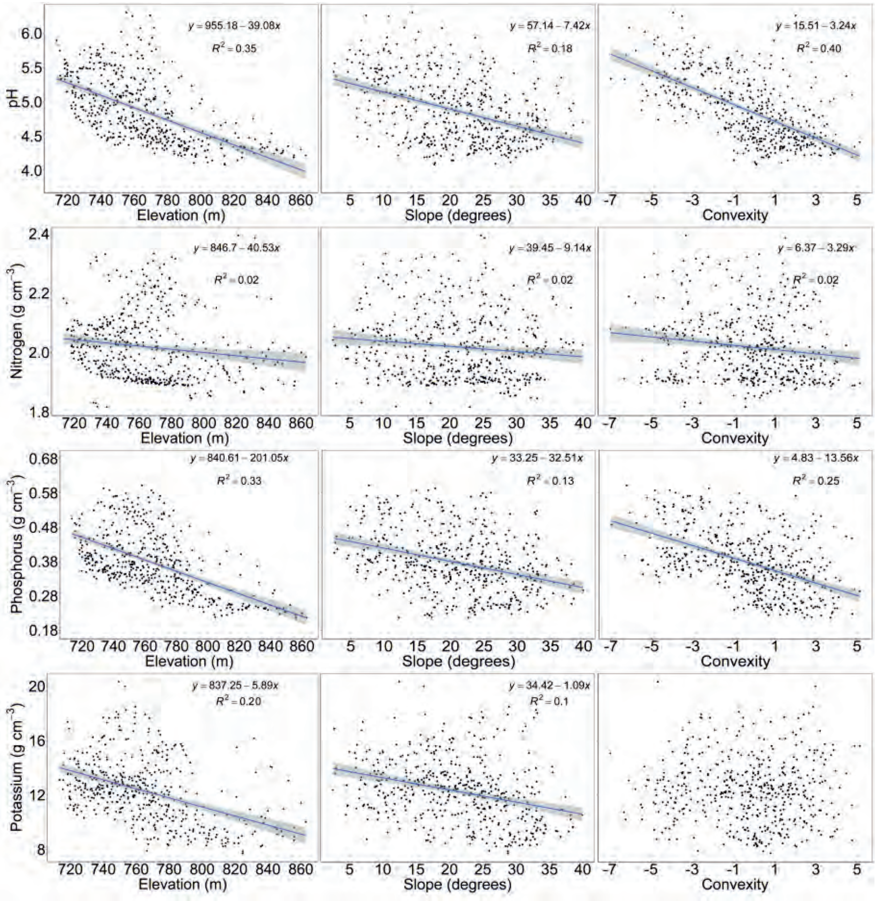

Figure 2.2 Relationships between soil conditions (pH, nitrogen, phosphorus, potassium) and topography (elevation, slope and convexity). Each dot represents the soil pH or nutrients value in each quadrat. Linear regression models were fitted, see the equation and r^2 as shown in the sub–panels, regression line only for those which are significant at 5% level ($p < 0.05$).

2.3.2 Response of liana composition to environmental factors

The differences in species composition among 20 m × 20 m quadrats were significantly related to differences in the mean levels of environmental factors in quadrats. The CCA showed that the first axis explained 44% of the variation in species composition and the second axis explained 21% from all used explanatory variables (Figure 2.3). Forward selection showed that all environmental variables were significantly related to these two CCA axes, with pH, P and convexity having the strongest effects on species composition on the first axis, and gap and K on the second axis (Appendix S2.5). We found similar results for the main axis of variation when assessing liana community composition with the DCA by using envfit function, which soil pH and P showed strong relationships with first two ordination axes (Appendix S2.6, S2.7).

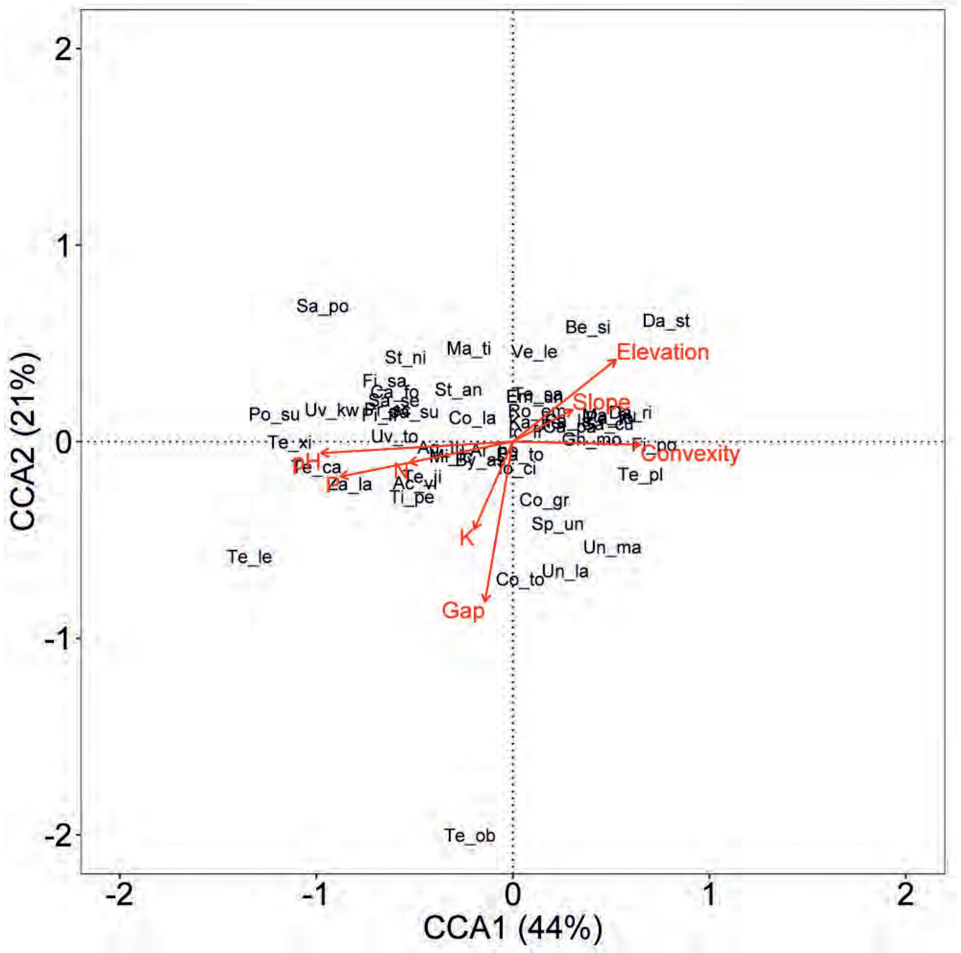

Figure 2.3 Canonical Correspondence analysis (CCA) ordination plots showing the distribution of 50 dominate liana species and associations with environmental factors in the Xishuangbanna 20–ha tropical seasonal rain forest dynamics plot. CCA1 and CCA2 were presented and the arrow represented explanatory variables used in the analysis. For species names and codes see Table 2.1.

Generalized linear mixed–effects models (GLMMs) were performed to assess the shape of the response curve of liana abundance to environmental variables. The abundance of lianas was significantly associated with soil nutrients, topography, and gap (Figure 2.4, Appendix S2.8, S2.9). At the community level, we observed a positive increase in liana abundance with a unit increase in K and convexity, and a unimodal response with a unit increase in P and slope. For pH and N, we did not observe a consistent effect across species due to a high interspecific variation. Liana abundance in gaps was higher than in non–gaps (Appendix S2.8).

We observed different responses to resource availability across liana species (Figure 2.4, Appendix S2.10). Forty–four percent of the species had a higher abundance with increasing K. Similarly, 62% of the species had an increase in abundance with increases in convexity. Eighty–four percent and sixty–two percent showed a unimodal response to changes in P and slope, respectively. For pH, 42% of the species showed a positive association with pH while 34% a negative. The response to N went in different directions for different species (positive: unimodal: negative = 38%: 38%: 24%).

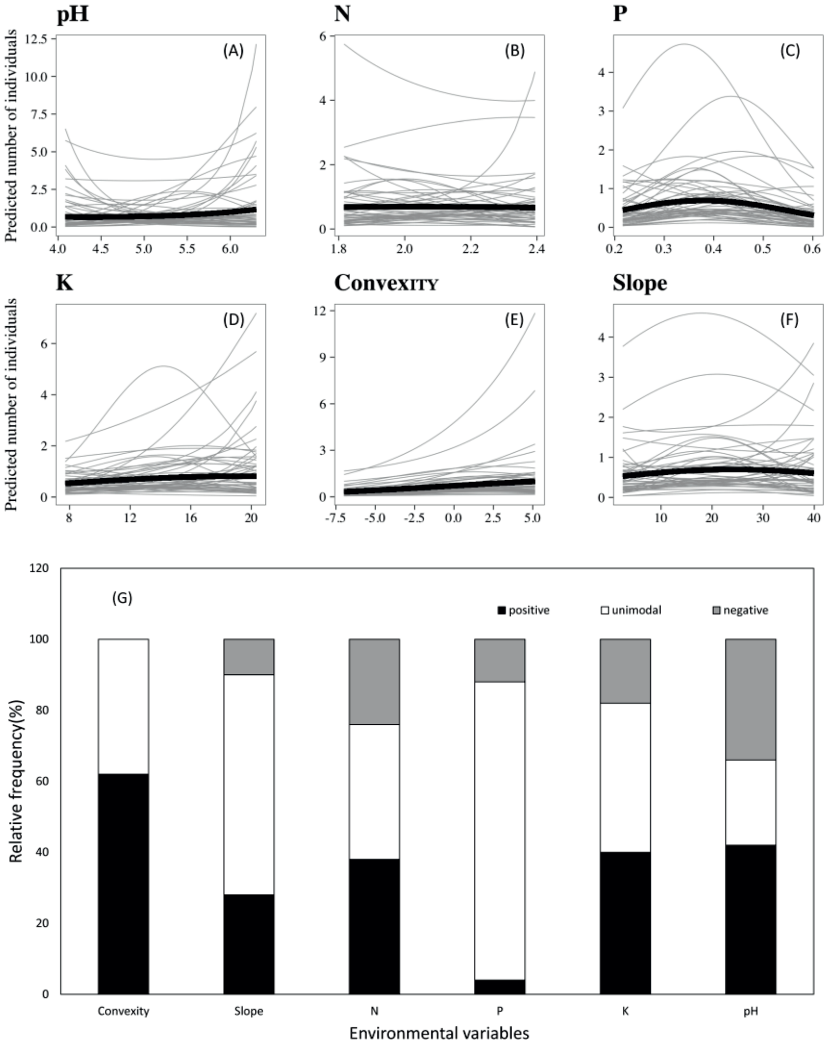

Figure 2.4 Effects of soil nutrients (pH, N, P, K, Panel A, B, C, and D, respectively) and topography (convexity and slope, Panel E and F respectively) at the community and species–level abundance of lianas. The dark black line represents the community–level predictions and the light gray lines represent the (n=50) species–level predictions from the best fitted model. For community level estimates and species–

specific estimates see Appendix S2.4. Panel G indicates the percentage of species and the species–specific response (positive, unimodal, or negative) to the considered variables.

2.3.3 Preference of lianas to resource niches

Forty–six out of the 50 species tested occurred for one or more soil nutrients under significantly higher or lower resource conditions than expected at random (Table 2.1). Nine species (such as *Byttneria aspera*, *Uvaria kweichowensis*, and *Tetrastigma cauliflorum*) were specialized for nutrient–rich conditions (i.e., for both N, P and K), whereas two species (*Benkara sinensis* and *Dalbergia stipulacea*) were specialized for nutrient–poor conditions. Liana species partitioned soil resources since some species mainly occurred at low soil nutrient concentrations while others dominated at average or high nutrient concentrations (Figure 2.5). For N and K, more species specialized for nutrient–rich conditions than for nutrient–poor conditions (for N 36% higher versus 20% lower and for K 34% higher versus 8% lower), but this was not the case for P (40% higher versus 34% lower). In addition, 44% of the species preferred areas with a higher convexity while 10% of the species preferred distributing in a steep place (i.e., high slope).

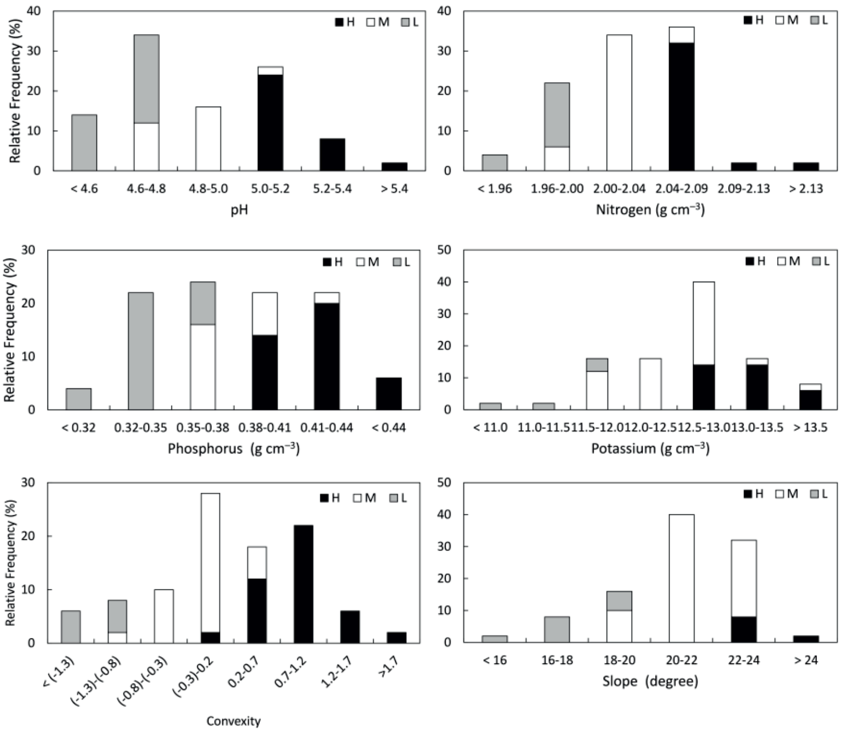

Figure 2.5 Frequency distribution of optimum (average weight) soil nutrient conditions (pH, nitrogen, phosphorus, potassium) and topographic conditions (convexity and slope) of 50 liana species. The figure summarizes the results for the randomization procedures for each species (Table 2.1), where in species with average weight in the highest or lowest 2.5th percentile of the simulated distribution (999 times) were considered to have significantly higher (H, black), middle (M, white) or lower (L, grey) resources requirements.

2.4 DISCUSSION

We asked how light and soil nutrient availability shaped the abundance and distribution of tropical liana species and found that liana abundance was mostly driven by soil pH and P, which were two strongly correlated soil factors, and that liana species partitioned soil nutrient gradients with more species tending to occur at higher N and K concentrations, but not for P.

2.4.1 Soil nutrient concentrations vary across the landscape, and with topography and gaps

We hypothesized that soil nutrient concentrations decrease with elevation because nutrient fertility is high in deep clayey soils in the valley bottom and low in the shallow sandy soils of the upper slope and crest. We indeed found that soil nutrients significantly decreased with elevation (Figure 2.2), in line with the hypothesis. Moreover, we observed that soil nutrient concentrations decreased with slope (Figure 2.2). Steep slopes may cause stronger erosion and loss of nutrients from a shallow topsoil layer, as the nutrient–rich topsoil may be washed down the slope and accumulated downslope (Brubaker, Jones, Lewis, and Frank, 1993). Alternatively, transport of soluble elements through movement of soil water, or accumulation of deeper organic soil horizons may lead to higher nutrient concentrations in downslope locations (Foster et al. 1985). Our results indicate that topography is an important driver of spatial variation in soil fertility and imply that acquisitive species such as lianas with high litter production and nutrient–rich litter are mainly expected downslope.

We hypothesized that soil nutrients would be high in tree–fall gaps because of increased litter input and decomposition rates. We found a modest increase of N and P in tree–fall gaps (Table 2.2). Higher nutrient pools in surface soils of tree–fall gaps may result from decomposition and mineralization of the large mass of fresh litter from the fallen trees (Denslow et al. 1998). Alternatively, high soil fertility leads to fast growth and more dynamic forests, and hence higher gap formation rate (Schnitzer et al. 2014b).

2.4.2 Environmental factors drive liana species distribution

We hypothesized that soil resources and gaps would be strong drivers of liana abundance because most lianas need gap to establish and lianas tend to have fast growth and inherently high resource requirements (Schnitzer et al. 2014a). Our results indicated that soil pH and P were the strongest drivers of liana distribution (Figure 2.3, Appendix S2.5), which is partially in line with our hypothesis.

We hypothesized that liana distribution would be strongly driven by pH, because pH modifies soil nutrient availability (major elements and trace elements) directly or indirectly through H^+concentration. We indeed found that pH contributed most to liana distribution (Figure 2.3). The Xishuangbanna forest plot occurs on latosol with pH values of 4.5–5.5, with mean soil pH being 4.9 (Appendix S2.4), which is slightly acid and quite similar to other tropical sites (e.g., La Planada in Colombia, mean pH = 4.7, and Yasuni in Ecuador, mean pH = 4.6), but slightly lower than Barro Colorado Island in Panama (pH = mean 5.7) (John et al. 2007). This moderately acid soil will cause changes in the availability of nutrients. Aluminium is most soluble at low pH and high aluminium inhibits root growth and may interfere with many physiological processes including the uptake and transport of calcium and other essential nutrients, cell division, cell wall formation, and enzyme activity (Rout et al 2001). Studies in tropical forest in La Planada and Yasuni indicate that soil pH indirectly exerts a strong influence on species distributions by influencing the availability of several plant nutrients (John et al. 2007), which is supported by the correlation between pH and soil nutrient concentrations in our study site (Table 2.2). Based on this, a possible explanation is that soil pH has a significant effect on major elements. For instance, P quickly binds with iron and aluminium in the soil and becomes unavailable to plants, especially when soil pH is below 5.0 (Price 2006). Thus, within the range of observed pH values in our study plot, limitations by N, P and K may influence the liana species growth and their distribution. Yet, liana species tended to partition the soil pH gradient with some species dominating low soil pH plots and others dominating high soil pH plots, which was in contradiction with the hypotheses that lianas, irrespective of species, would tend to distribute in high resource sites in general.

We hypothesized that soil P would be the most important soil nutrient for liana distributions because of a limiting P availability in old weathered and leached tropical soils (Vitousek et al. 2010). This hypothesis was confirmed (Figure 2.3). Yet, 84% of the liana species showed a unimodal response, 12% a negative response and only 4% a positive response to soil P (Figures 2.4). Thus, similar to our results for pH, which is strongly associated with P, liana species did not dominate in high P sites but rather partitioned the P gradient in this study forest, since some species occur in low P sites, others in intermediate, and others at high P sites (Figure 2.5). Previous studies on nutrients and plant growth have argued that P is more limiting than N in mature lowland tropical forests (e.g., Condit et al. 2013). P is thought to be more limiting because it is derived primarily from rock weathering, where ecosystems begin with a certain amount of P which is reduced over time because of weathering, plant uptake, and leaching, and where even very small losses cannot readily be replenished (Walker and Syers 1976, Brady and Weil 2002). Based on this, we expected and found that P should have a stronger effect on liana distribution than other nutrients. In a study on the extremely old and P poor Brazilian shield, liana biomass was therefore positively correlated with P and fertility (Laurance et al. 2001). Remarkably, however in our site, liana species partitioned the whole soil P gradient and did not show a general tendency for high P concentrations (Figure 2.5).

We hypothesized that gaps would have a strong effect on liana abundance because most lianas need gap to establish. We found that gaps did affect species distribution along the second CCA axis (Figure 2.3) and liana abundance in gaps was indeed higher than in non–gaps (Appendix S2.8). Other studies also found lianas respond favourably to canopy disturbance (Putz 1984, Schnitzer et al. 2000, Malizia and Grau 2008, Dalling et al. 2012). A variety of mechanisms may contribute to this pattern, including a high density of trellises in gaps (Putz 1984), lateral proliferation of lianas into gaps from an adjacent forest (Penalosa 1984), proliferation within gaps of lianas that survive treefalls (Putz 1984, Schnitzer et al. 2000), and a competitive advantage of lianas over trees in disturbed environments (Schnitzer 2005).

However, gaps had a rather weak effect compared to soil nutrients and accounted only for 9% of the variation in DCA analysis (Appendix S2.6). Several reasons may explain the relative weak gap responses we observed. First, the quadrats were defined as a gap when the canopy cover was less than 50%, which is a relatively coarse scale compared to the continuous scale used to estimate soil nutrient concentrations. Therefore only 31 gaps were included. As this definition is based on 20 m × 20 m quadrat, we cannot include smaller gaps in our study. Second, we measured all the liana individuals with a stem diameter > 1 cm. These relatively large and old lianas have in general already attained a position in the canopy, and their growth therefore does not need gaps anymore. In contrast, younger gaps are more likely to increase the abundance of smaller liana seedlings (Dewalt et al. 2000). We thus probably underestimate the role of gaps compared to the role of soil nutrients.

2.4.3 Liana species partition P but tend for higher N and K

We hypothesized that most liana species require high resources to support their inherently fast growth rate (Schnitzer et al. 2014a) and we found that liana optima of most species were located at higher soil resource availability for K and N (Figure 2.5), which indicates that those species specialize for high resources. Probably lianas need higher leaf N concentration to support higher Rubisco concentrations for their higher photosynthetic rates (Ca et al. 2009) and higher leaf K to regulate their gas exchange more tightly (Benlloch–González et al. 2008). Species however partitioned more equally the P and pH gradients with low and high resource specialists, which underscores again that P is a major gradient that drives the liana community structure (Table 2.1, Figure 2.3, 2.5). At the same time, liana preferred higher convexity and lower slope where have more light availability and soil moisture and nutrients accumulated (Figure 2.5). Overall, our results suggest that liana species within the community cover a gradient from more conservative to more acquisitive species along the major soil gradient (pH and P), and thus rejecting the idea that all lianas behave as acquisitive species.

2.5 CONCLUSIONS

We evaluated how environmental factors (soil nutrient availability, canopy gaps and topography) shape the liana species distribution. We found soil pH and P were strongly correlated and were drivers of liana species distributions, suggesting that lianas are particularly partitioned along gradients in pH and P. Yet most liana species prefer soils that were fertile for N and K, which comes along with their fast growth and acquisitive strategy of resource use. Overall, these results highlight that belowground resource availability plays an important role in shaping liana community assembly, partially independently of the known effects of higher light conditions.

2.6 ACKNOWLEDGEMENTS

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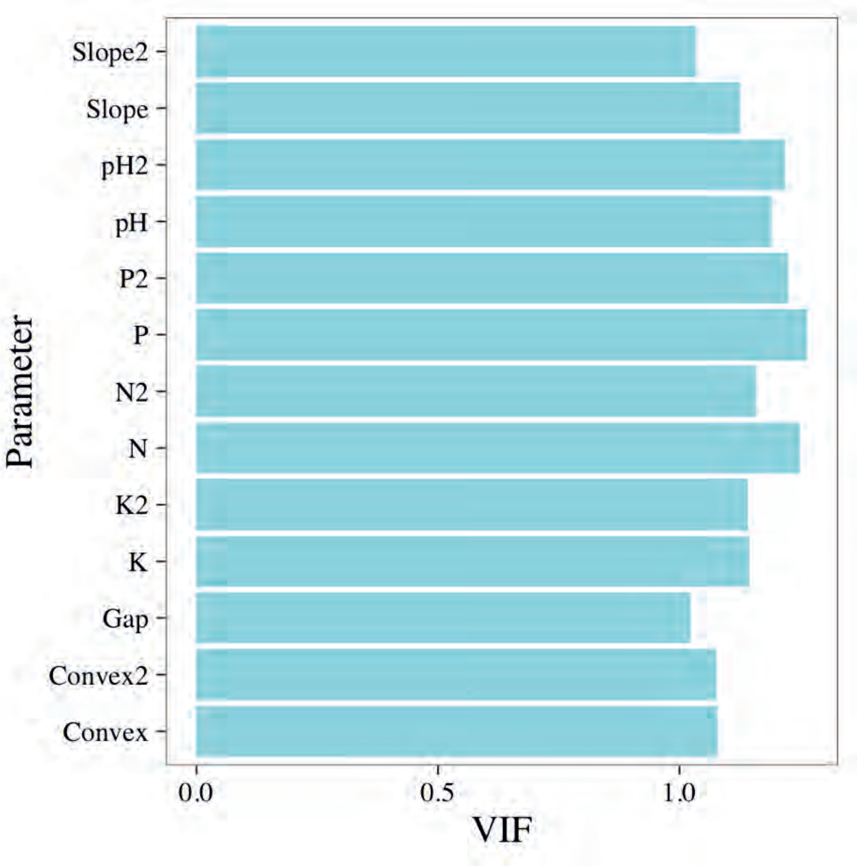
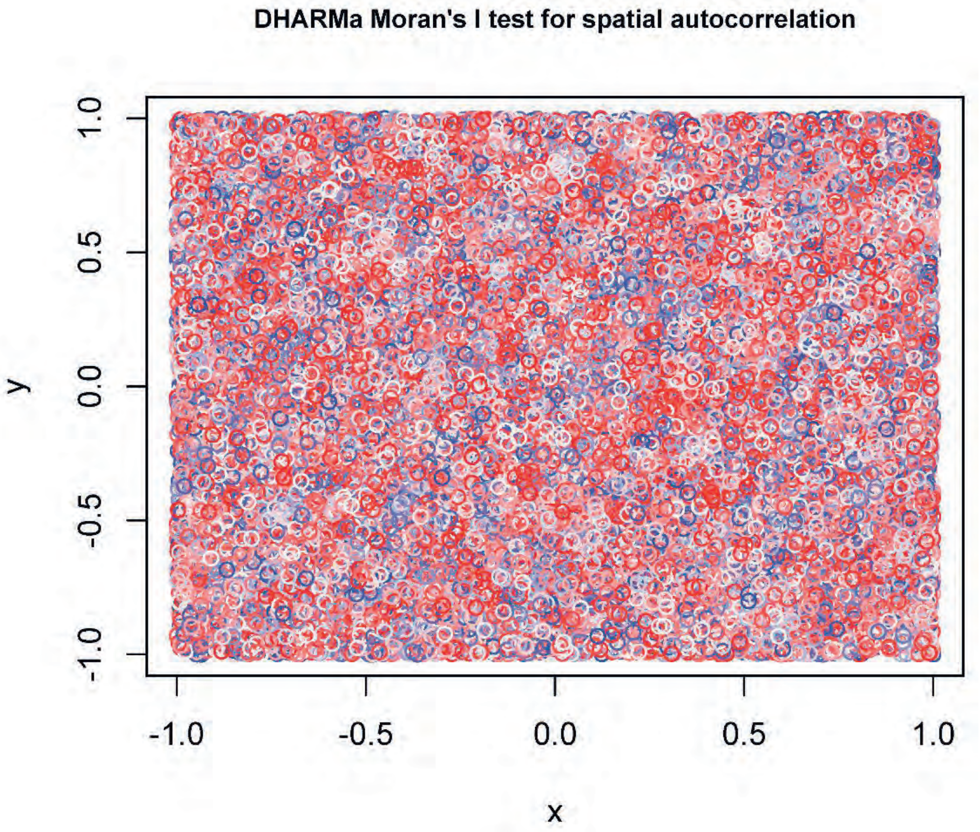
2.7 SUPPORTING INFORMATION

Appendix S2.1 Variance Inflation Factors (VIF) for the covariates included in the model that explained liana abundance in a 20–ha permanent plot in Xishuangbanna, Southwest China. VIF values were estimated using the package performance (Lüdecke *et al*. 2019) in R (R Core Team 2019). All covariates showed a VIF below 3, indicating no presence of multicollinearity (Zuur, 2009).



Appendix S2.2 Conditional –scaled– residuals from the (GLMM) model that best–fitted the abundance of lianas (>1cm stem diameter) as a function of soil nutrients, topography, and gap in a 20–ha permanent plot in Xishuangbanna, Southwest China. No spatial autocorrelation was detected (Moran's I test for spatial autocorrelation; P–value = 0.88, Ha = Spatial autocorrelation) and indicated by the homogeneity of the residuals.



Appendix S2.3 Sample code for the model that best–fitted liana abundance in a 20–ha permanent plot in Xishuangbanna, Southwest China.

```
### Load the glmmTMB library
library(glmmTMB)

### Model code
model <– glmmTMB(Abundance ~ 1 +
                    ## Fixed terms
                    pH    + I(pH ^ 2) +
                    N      + I(N ^ 2) +
                    P      + I(P ^ 2) +
                    K      + I(K ^ 2) +
                    Convex + I(Convex ^ 2) +
                    Slope    + I(Slope    ^ 2) +
                    Gap +
                    ## Random terms
                    (1 | SP) +
                    (0 + pH | SP) + (0 + I(pH ^ 2) | SP) +
                    (0 + N    | SP) + (0 + I(N    ^ 2) | SP) +
                    (0 + P    | SP) + (0 + I(P    ^ 2) | SP) +
                    (0 + K    | SP) + (0 + I(K    ^ 2) | SP) +
                    (0 + Convex | SP) + (0 + I(Convex ^ 2) | SP) +
                    (0 + Slope    | SP) + (0 + I(Slope    ^ 2) | SP) +
                    (1 | group),
                 ## Load data
                 data = dat,
                 ## Define family
                 family = "nbinom1")
```

Appendix S2.4 Physical–chemical properties of the Xishuangbanna 20–ha forest dynamics plot.

Soil variables	Minimum	Maximum	Mean	Std. Deviation
Total N (g cm^{-3})	1.82	2.39	2.02	0.11
Total P (g cm^{-3})	0.22	0.6	0.38	0.09
Total K (g cm^{-3})	7.73	20.32	12.29	2.32
Ammonium N (mg kg^{-1})	149.59	204.41	175.28	9.14
Extractable P (mg kg^{-1})	0.91	13.67	3.93	2.45
Exchangeable K (mg kg^{-1})	118.12	277.17	164.35	21.77
pH	4.08	6.3	4.87	0.47

Appendix S2.5 The output of the forward selection from a set of 8 environmental variables for the canonical correlation analysis (CCA) and output scores. The top table shows the forward selection processing, R^2 and adjusted R^2 were given based on model output. The bottom table shows the first two axes and the scores for pH, total N, total P, total K, gap, elevation, slope, and convexity.

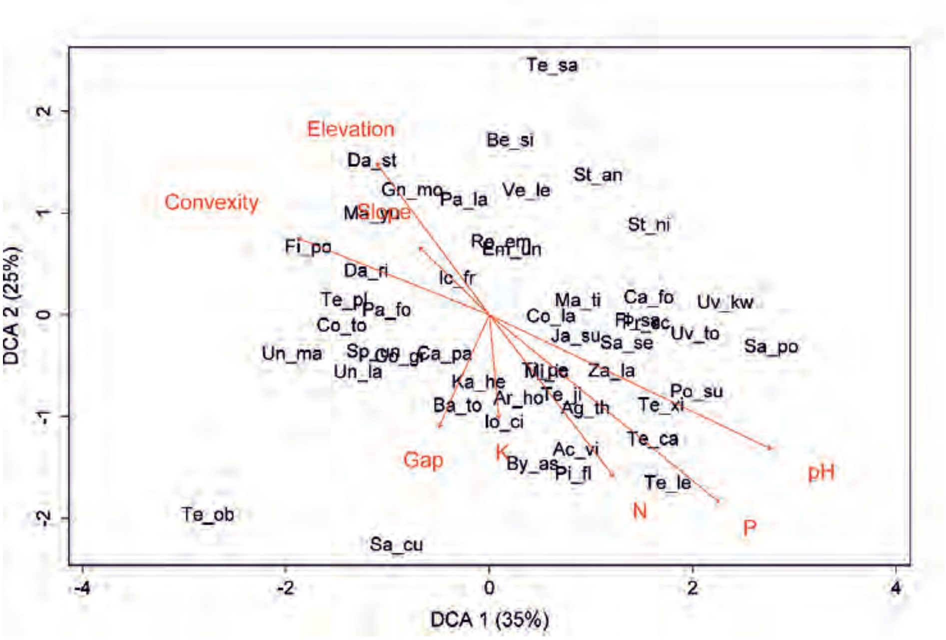
Model	R^2	Adjusted.R^2
~ 1		
~ pH	0.050	0.049
~ pH + gap	0.071	0.068
~ pH + gap + elevation	0.088	0.082
~ pH + gap + elevation + N	0.097	0.090
~ pH + gap + elevation + N + K	0.104	0.095
~ pH + gap + elevation + N + K + slope	0.111	0.100
~ pH + gap + elevation + N + K + slope + P	0.115	0.102
~ pH + gap + elevation + N + K + slope + P + convexity	0.119	0.104

Variable	CCA1	CCA2
pH	−0.975	−0.059
P	−0.877	−0.177
Convexity	0.650	−0.016
Gap	−0.142	−0.815
Elevation	0.526	0.418
N	−0.526	−0.106
K	−0.196	−0.445
Slope	0.303	0.162

Appendix S2.6 The relative relationship of environmental variables to first two ordination axes of detrended correspondence analysis (DCA) by using the function envfit (Oksanen et al. 2007).

Variable	DCA1	DCA2	R2	Pr (> r)
pH	0.903	−0.430	0.56	0.001
N	0.609	−0.793	0.24	0.001
P	0.775	−0.631	0.50	0.001
K	0.093	−0.996	0.06	0.001
Elevation	−0.597	0.802	0.20	0.001
Convexity	−0.929	0.371	0.24	0.001
Slope	−0.720	0.694	0.05	0.001
Gap	−0.410	−0.912	0.09	0.001

Appendix S2.7 Detrended correspondence analysis (DCA) ordination plots showing the distribution of 50 dominate liana species and associations with environmental factors in the Xishuangbanna 20–ha tropical seasonal rain forest dynamics plot. DCA1 and DCA2 were cosine values of the angle between each soil factor arrow and the two sort axes, indicating the correlation between the environmental factor and the sort axis.



Appendix S2.8 Community level coefficients for the abundance of lianas (>1cm stem diameter) as a function of soil nutrients, topography, and gap in a 20–ha permanent plot in Xishuangbanna, Southwest China.

Parameter	Est.	Std. Error	Z–value	P–value
Intercept	−0.54	0.12	−4.57	0.000
pH	0.10	0.09	1.11	0.267
pH^2	−0.02	0.03	−0.61	0.543
N	0.04	0.05	0.76	0.450
N^2	−0.02	0.02	−1.03	0.304
P	0.03	0.07	0.41	0.679
P^2	−0.20	0.04	−5.55	0.000
K	0.12	0.04	2.71	0.007
K^2	−0.02	0.02	−0.81	0.419
Convexity	0.22	0.03	6.51	0.000
$Convexity^2$	−0.04	0.02	−1.92	0.055
Slope	0.03	0.03	1.04	0.297
$Slope^2$	−0.06	0.03	−1.91	0.056
Gap:1	0.28	0.09	3.16	0.002

Notes: Est. indicates the community level coefficient as is in the natural log–scale. Std. Error is the standard error of the estimate. Z–value is the test statistic. P–value is the significance level. The reference level for gap is non–gap = 0. Random effects are in **Appendix S2.9**.

Appendix S2.9 Group level coefficients (random effects) for the abundance of lianas (>1 cm stem diameter) as a function of soil nutrients, topography, and gap in a 20–ha permanent plot in Xishuangbanna, Southwest China.

Parameter	σ
Sp: Intercept	0.76
Sp: pH	0.53
Sp: pH^2	0.14
Sp: N	0.21
Sp: N^2	0.08
Sp: P	0.32
Sp: P^2	0.16
Sp: K	0.22
Sp: K^2	0.08
Sp: Convexity	0.12
Sp: $Convexity^2$	0.07
Sp: Slope	0.13
Sp: $Slope^2$	0.15
Quadrat	0.38

Notes: σ indicates the group–level standard deviation. Coefficients with the prefix Sp indicate the interspecific variation in standard deviations for each of the community level coefficients (**Appendix S2.8**). Parameter intercepts and estimates are shown. Quadrat indicates the variation in standard deviations across quadrats.

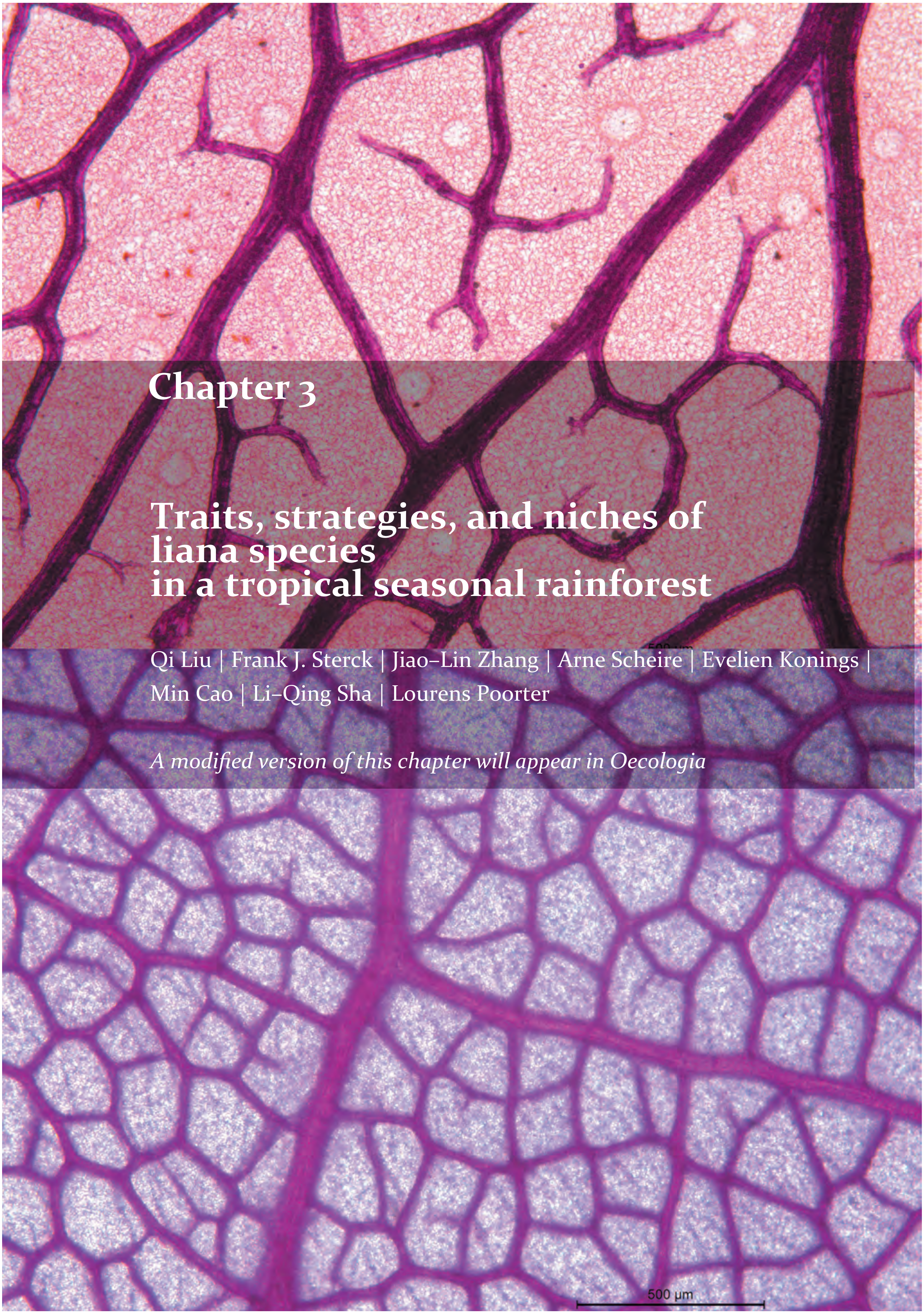
Appendix S2.10 Species level estimates for the soil nutrients and topography for the 50 abundant liana species in a 20–ha permanent plot in Xishuangbanna, Southwest China.

Species	Intercept	pH	pH^2	N	N^2	P	P^2	K	K^2	Convexity	$Convexity^2$	Slope	$Slope^2$
Acacia vietnamensis	−0.89	−0.15	−0.01	0.09	−0.07	0.30	−0.09	−0.13	−0.01	0.15	−0.12	0.00	−0.25
Aganope thyrsiflora	−0.09	−0.07	−0.04	0.06	−0.01	0.46	−0.17	−0.09	0.07	0.02	0.06	−0.23	0.02
Artabotrys hongkongensis	−0.56	0.28	−0.02	0.22	−0.03	0.01	−0.02	0.11	0.09	0.03	−0.06	−0.02	−0.04
Bauhinia touranensis	1.66	−0.10	0.03	0.05	0.01	0.26	−0.02	0.06	0.02	0.07	0.07	−0.03	−0.01
Benkara sinensis	−0.66	−0.23	0.00	0.28	0.02	−0.05	−0.12	0.27	0.06	−0.03	−0.06	0.06	0.05
Byttneria aspera	0.07	0.16	−0.15	0.02	0.04	0.38	0.12	−0.29	0.00	−0.03	0.03	0.07	0.12
Callerya pachyloba	0.55	−0.27	0.10	−0.26	−0.06	0.15	−0.06	0.12	−0.04	−0.03	0.03	−0.05	−0.14
Capparis fohaiensis	1.11	−0.12	0.07	−0.12	0.05	0.21	0.06	0.02	−0.02	−0.01	0.05	−0.01	0.05
Combretum griffithii	0.50	−0.33	0.11	0.17	0.01	−0.23	0.16	0.10	0.02	0.09	−0.02	0.00	−0.02
Combretum latifolium	−0.40	−0.33	−0.02	0.23	−0.12	−0.01	−0.03	0.05	0.03	0.00	−0.02	0.08	0.04
Congea tomentosa	−0.77	−0.92	0.10	0.07	0.01	−0.21	−0.03	0.19	0.03	0.05	−0.04	−0.01	0.02
Dalbergia rimosa	−0.68	−0.61	0.15	−0.22	0.05	−0.56	0.19	−0.07	−0.02	−0.07	0.02	−0.14	0.00
Dalbergia stipulacea	0.38	−0.09	−0.09	−0.20	0.02	−0.14	−0.12	0.01	−0.03	−0.07	−0.04	0.19	0.06
Embelia undulata	0.65	−0.98	0.12	−0.03	0.03	−0.31	0.01	0.05	0.08	−0.03	−0.03	−0.17	−0.11
Ficus sagittata	−0.35	0.23	−0.04	0.04	−0.01	0.19	0.03	0.02	−0.01	−0.11	0.05	0.01	0.20
Fissistigma polyanthum	0.72	−0.48	0.01	−0.35	0.04	−0.08	0.16	−0.02	−0.01	−0.08	0.03	−0.10	0.07
Gnetum montanum	−0.37	−0.10	0.17	−0.02	0.08	−0.05	0.07	0.03	0.09	0.03	0.02	0.04	0.04
Ichnocarpus frutescens	−0.28	−0.16	0.04	0.25	−0.02	−0.14	0.02	0.08	−0.07	0.11	−0.03	0.01	0.02
Iodes cirrhosa	−0.31	0.24	0.05	0.02	−0.02	−0.13	0.29	0.04	0.06	−0.03	−0.07	−0.04	0.14
Jasminum subglandulosum	−0.50	−0.43	0.11	0.18	0.02	0.16	0.00	0.06	−0.01	−0.09	−0.04	−0.05	−0.02

Kadsura heteroclita	0.26	0.30	0.07	−0.21	0.06	0.15	−0.11	0.17	0.04	−0.01	0.04	0.11	−0.01
Marsdenia yunnanensis	−0.29	0.14	−0.04	0.18	−0.01	−0.01	0.15	−0.26	−0.01	−0.05	0.06	0.16	0.19
Marsdenia tinctoria	−0.61	−0.43	0.08	−0.03	−0.02	−0.27	0.08	0.15	−0.08	−0.01	−0.07	0.00	0.03
Millettia ichthyochtona	0.25	−0.03	−0.17	0.01	−0.03	−0.51	0.16	−0.22	0.02	0.10	0.05	0.20	0.20
Paederia foetida	−0.46	0.26	−0.01	0.19	0.04	0.38	−0.06	0.08	0.02	0.00	0.02	0.18	−0.03
Parameria laevigata	0.24	−0.34	0.11	−0.03	0.07	−0.35	0.16	−0.05	0.04	0.13	0.03	−0.05	−0.07
Piper flaviflorum	2.05	−0.15	0.07	−0.13	0.04	−0.21	−0.02	0.16	−0.15	0.20	0.05	−0.08	0.00
Poikilospermum suaveolens	0.27	0.26	−0.16	−0.09	−0.04	0.40	−0.03	−0.28	0.01	−0.06	0.03	−0.06	0.05
Premna scandens	−1.08	0.65	−0.02	−0.14	−0.03	0.32	0.01	−0.20	0.09	−0.11	0.00	−0.06	0.02
Roureopsis emarginata	−0.21	−0.20	0.02	0.05	0.03	−0.02	−0.08	−0.19	−0.06	0.01	0.02	0.06	0.16
Salacia polysperma	1.13	0.32	−0.14	−0.15	0.02	−0.13	0.05	−0.06	0.00	−0.09	−0.01	0.13	0.13
Salacia sessiliflora	0.39	−0.90	0.10	0.09	0.14	0.17	−0.01	−0.29	0.03	−0.03	−0.05	0.05	−0.30
Sargentodoxa cuneata	−0.64	0.24	−0.14	0.36	−0.09	0.30	0.07	−0.39	0.04	0.09	0.06	−0.07	0.30
Spatholobus uniauritus	−1.63	0.55	0.07	−0.11	0.07	0.06	−0.06	−0.39	0.01	−0.04	0.02	0.14	−0.08
Strychnos angustiflora	0.28	0.35	−0.09	0.08	0.06	0.14	0.03	−0.09	0.01	−0.05	0.00	0.04	0.11
Strychnos nitida	0.95	−0.22	0.28	−0.11	−0.04	−0.15	−0.18	0.47	−0.02	0.04	0.01	−0.09	−0.16
Tetracera sarmentosa	0.36	1.02	−0.11	0.18	−0.08	0.10	−0.15	0.29	−0.05	−0.07	0.03	0.01	−0.03
Tetrastigma cauliflorum	0.72	0.76	−0.28	0.02	−0.02	0.04	−0.07	0.09	−0.04	0.02	−0.11	0.10	0.04
Tetrastigma jinghongense	−1.12	0.99	0.02	0.30	0.02	0.08	−0.21	0.20	0.01	−0.03	0.00	−0.08	0.06
Tetrastigma lenticellatum	−1.13	0.56	−0.10	0.04	−0.10	−0.03	−0.15	0.17	0.09	−0.02	−0.04	0.01	−0.23
Tetrastigma obovatum	−0.39	0.13	0.10	0.12	−0.04	0.36	−0.09	−0.10	−0.03	−0.05	−0.01	0.15	−0.01
Tetrastigma planicaule	−0.23	−1.11	−0.12	−0.26	0.03	0.08	−0.03	0.32	0.07	0.19	0.05	−0.15	−0.11
Tetrastigma xishuangbannaense	−0.48	0.12	−0.14	−0.34	−0.02	−0.44	−0.18	−0.06	−0.08	−0.11	0.01	0.07	0.14
Tinomiscium petiolare	−0.48	0.66	0.07	−0.24	0.07	−0.02	0.22	−0.18	−0.02	−0.03	−0.01	−0.09	−0.10

Uncaria laevigata	0.98	0.51	−0.06	−0.07	−0.09	0.24	0.09	0.01	−0.06	−0.13	−0.03	−0.11	−0.03
Uncaria macrophylla	0.93	−0.19	−0.06	−0.20	−0.20	−0.04	−0.31	0.09	−0.16	0.21	0.02	−0.06	−0.19
Uvaria kweichowensis	0.55	−0.81	−0.05	0.14	−0.03	−0.48	−0.21	0.24	−0.06	0.07	−0.06	−0.07	−0.33
Uvaria tonkinensis	−0.52	0.22	−0.02	−0.01	0.06	−0.04	0.06	0.00	0.02	−0.04	−0.01	−0.13	0.01
Ventilago leiocarpa	−0.32	0.29	−0.01	0.13	0.04	−0.49	0.23	−0.23	0.03	0.17	−0.04	0.08	0.11
Zanthoxylum laetum	−0.12	0.60	−0.01	−0.18	0.06	0.19	−0.06	0.06	−0.07	−0.04	0.06	0.01	−0.18

Notes: Intercept is the intercept for each species. Parameter intercepts and estimates are shown.



Chapter 3

Traits, strategies, and niches of liana species in a tropical seasonal rainforest

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A modified version of this chapter will appear in Oecologia

Abstract

Plant functional traits and strategies hold the promise to explain species distributions. However, few studies have linked multiple traits to the multiple niche dimensions that potentially drive species distributions. We analysed for 29 liana species in a Chinese tropical seasonal rainforest how: 1) trait associations and trade–offs lead to different plant strategies; and 2) how these traits shape species' niche dimensions. For each species, 18 functional traits related to light, water, or nutrient use were measured and species niche dimensions were quantified using species distributions in a 20–ha plot.

We found a tissue toughness spectrum ranging from soft to hard tissues where species also vary from acquisitive to conservative water use, and a resource acquisition spectrum ranging from low to high light and nutrient acquisition and use. Intriguingly, each spectrum partly reflects the conservative–acquisitive paradigm, but at the same time, they are uncoupled. Resource niche dimensions were better predicted by individual traits than by plant strategy spectra, which suggests that trait components that underlie multivariate strategy axes, rather than the plant strategies themselves determine species distribution. Different traits were important for different niche dimensions.

Plant functional traits and strategies can indeed explain species distributions, but not in a simple and straight forward way as we had hoped for. Although the identification of global plant strategies has significantly advanced the field, this research shows that global, multivariate generalizations are difficult to translate to local conditions, as different components of these strategies are important under different local conditions.

3.1 Introduction

Plant functional traits are defined as morphological, physiological or phenological features that determine plant growth, survival, and reproduction (Ackerly 2003), and hold the promise to explain plant species distribution patterns (McGill et al. 2006). Plant traits can be closely associated for biophysical reasons (e.g., larger leaves require more robust stems for mechanical support), because of allocation trade–offs (e.g., plants can invest limiting resources either in above or belowground organs), and/or because they reflect adaptations to similar environmental conditions. Trait associations therefore reflect ecological strategies of species to successfully complete their lifecycle in a specific environment (Grime 1974, Reich et al. 2003). Although many studies have evaluated trait spectra on broad spatial scales (e.g., Wright et al. 2004) and within local communities (e.g., Fortunel et al. 2012), few studies have evaluated how traits affect plant performance in the field (Poorter and Bongers 2006, Kunstler et al. 2016), and even fewer studies have explicitly linked multiple traits to multiple dimensions of the plant niche (Sterck et al. 2011). Here we evaluate how leaf, stem, and root traits are associated with 29 liana species, and how this shapes their light, water, and nutrient niche dimensions in a tropical seasonal rainforest.

Plant ecological strategies can explain the success of different species under different environmental conditions (Grime 2006, Westoby and Wright 2006). Because resource capture, use, and release are fundamental for plant functioning and performance, Díaz et al. (2004, 2016) proposed that, globally, plants show a trade–off between resource acquisition and conservation. For example, species with high specific leaf area and leaf nutrient concentrations can attain high photosynthetic rates and have the potential to be successful in high light environments, whereas species with higher tissue density and toughness can attain a longer life span and therefore persist in low light conditions (Wright and Westoby 2002, Poorter et al. 2006). These trait trade–offs are also known as the leaf economics spectrum (Wright et al. 2004). Similarly, species with cheap, soft stem wood and wide vessels can attain a higher hydraulic conductivity, gas exchange and growth, and can therefore achieve a competitive advantage in high resource environments (Santiago et al. 2004, van der Sande et al. 2019). By contrast, species with a high wood density, are more resistant to drought–induced cavitation, mechanical damage, and pathogen attack, and they can better survive under low resource conditions (Poorter et al. 2008, Cornwell et al. 2009). Many studies have shown that for these reasons leaf, stem, and root traits are closely coupled (e.g., Reich et al. 2003, Freschet et al. 2010). In contrast, root traits may be decoupled from leaf and stem traits, as roots have to deal with the acquisition of many different water and nutrient resources, and can obtain these resources in different ways, through mycorrhizae, nitrogen–fixing bacteria, or root exudates (Weemstra et al. 2016).

The species niche is defined as the n–dimensional hypervolume of environmental and biotic conditions under which a species can grow and reproduce (Hutchinson 1957) and therefore reflects multiple niche dimensions. When henceforth, we use the word "niche" we often refer to one of the specific dimensions of the niche. Niche theory predicts that species can differ in their distribution when they are functionally different and specialized for different conditions (Hutchinson 1957). Global plant strategies in resource capture and use (i.e., the acquisitive–conservative continuum, or the fast–slow continuum), are thought to explain species distribution and niches (Grime 1974, Díaz et al. 2004). Indeed, differential species distributions have been related to different species tolerances to shade (Sterck et al. 2006), drought (Engelbrecht et al. 2007), and nutrient stress (Baltzer and Thomas 2010). The idea is that the same conservative trait values allow plants to occupy low resource niches everywhere (Reich 2014), but this has rarely been tested, because most studies have quantified only one component of the multidimensional resource niche (either water, light or nutrients), but rarely the combination. Similarly, it is assumed that the whole trait package determines the niches, but it can be that different components of these global strategies are relevant for different dimensions of the resource niches. This study explores therefore the importance of traits and plant strategies for different dimensions (i.e., light, water, and nutrients) of the resource niche.

We focus on lianas, or woody vines, as our study system. Lianas are an important component of tropical forest systems (Gentry 1991, Appanah et al. 1993), as they comprise up to 25% of the woody stems and 35% of the species, thus contributing substantially to forest structure and ecosystem functioning (Schnitzer et al. 2012, Schnitzer 2015). Trait associations and trait–environment linkages may be different for lianas and trees; because lianas are structural parasites, they may compete more efficiently for light (Estrada–Villegas and Schnitzer 2018), and may therefore show stronger trait associations with the light niche dimension than trees. Similarly, because lianas tend to have wide vessels, they are hydraulically more efficient, and stronger water spenders (van der Sande et al. 2019) and may therefore show stronger trait associations with the (topographic) water niche dimension than trees. By having acquisitive trait values, lianas would also have an advantage on fertile soils where they can attain high photosynthetic rates and rapid growth (Pasquini et al. 2015).

Here we evaluate 18 leaf, stem, and root traits from 29 dominant liana species (Liu et al. 2017) in a tropical seasonal rainforest of Xishuangbanna, China. We first ask how liana traits are associated and which plant strategies can be recognized. We then investigate whether different traits shape different light, water, and nutrient niche dimensions of these co–occurring species. We addressed the following questions and corresponding hypotheses.

First, how are liana traits associated? In line with the plant economics spectrum, we expect liana species to show a trait spectrum, ranging from trait values that increase resource acquisition and use to trait values that increase resource conservation (Reich 2014, Díaz et al. 2016). Because lianas are structural parasites, they have to allocate fewer resources towards structural support (Zhang et al. 2019) and can invest more in leaves and roots. We expect therefore that liana stem traits are less coordinated with leaf and root traits.

Secondly, how do functional traits determine the light, water, and nutrient niche dimensions of coexisting liana species? We predict that liana species with more acquisitive trait values generally occupy higher light, water, and nutrient resource niches. Hence, species with a high capacity for water and nutrient uptake and transport (i.e., high specific root length, wide stem vessel diameter and high leaf venation density), efficient leaf display (i.e., large leaf area and high specific leaf area), high leaf nutrient concentrations and fast gas exchange (i.e., high stomatal density, length and pore index) will occupy high resource niches. In contrast, species with trait values that increase the persistence of roots, stem, and leaves (i.e., low specific root length, high wood density, high leaf thickness and dry–matter content) will occupy low resource niches. We also expect that the light niche is best predicted by traits that reflect carbon construction costs and longevity (e.g., leaf and wood density), that the water niche is best predicted by traits related to water transport (e.g., vessel diameter, leaf venation and stomata), and that the nutrient niche is best predicted by traits that reflect nutrient use (e.g., leaf nutrient concentrations and N:P ratio).

Third, which traits shape the abundance of liana species? Because the tropical forest of Xishuangbanna is relatively humid and has a tall and closed canopy (Cao et al. 2006), we expect light to be the main limiting resource for the growth and survival of liana species, and that species with conservative trait values that enhance carbon conservation and shade tolerance (i.e., high wood density and low specific leaf area) will be more abundant.

3.2 Methods

3.2.1 Study site

This study was conducted in the 20–ha Xishuangbanna Forest Dynamics Plot in the Yunnan Province, Southwest China (101°34’2”–47”E, 21°36’42”–58”N). Mean annual rainfall is 1493 mm and mean annual temperature is 21.8°C (Cao et al. 2006). The climate is shaped by warm–wet air masses from the Indian Ocean and continental air masses from the sub–tropical regions in summer and winter, which results in an alternation of dry and rainy seasons with a typical monsoon climate. The main soil type is laterite (Cao et al. 2006). The topography of the plot is heterogeneous with an elevational range from 709 m to 869 m. The plot is trisected by three perennial streams that join in the Southwest of the plot (Lan et al. 2009). The vegetation in the area is a tropical seasonal rainforest with a canopy height of up to 60 m (Zhu 2006). The forest is dominated by *Parashorea chinensis* (Dipterocarpaceae), *Pittosporopsis kerrii* (Icacinaceae) and *Garcinia cowa* (Clusiaceae).

3.2.2 Sample design

From 2013 to 2015, all rooted lianas with a diameter over 1 cm were tagged, mapped, and identified in the plot according to standard method describing by Gerwing et al. (2006) and Schnitzer et al. (2008). For species identification, plant samples were collected from October 2018 to December 2018. In total, the plot contains more than 136 liana species. For this study, we selected 29 of the most common liana species in the plot (with a density > 5 stems/ha) of which leaves and branches occurred below 8 m height so that they could be sampled. The 29 species comprised 71% of the total number of marked liana individuals. For each species, 3 to 12 individuals were randomly sampled throughout the plot

(231 individual samples in total) to avoid bias towards individuals thriving in high resource availability (Appendix S3.1). An approximately 40 cm long branch was sampled from the main stem between 3 to 8 m height, i.e., in the lower forest stratum. Only samples from healthy–looking, sun–exposed and pest–free individuals with a diameter more than 1 cm were selected. In case the branch did not have enough leaves for all analyses, additional branches were collected from the same individual to obtain additional leaves. At same time, the number of the 20 m x 20 m quadrat where the individual was rooted was recorded to link the individual in a later stage with light, soil nutrient, water, and topographic data.

3.2.3 Functional trait measurements

For each individual, morphological and anatomical leaf, stem and root traits were measured (for full names of the traits, abbreviations, units, and major eco–physiological roles, see Table 3.1). These traits were selected because they represent the key traits of the leaf, stem, and root economic spectra (Wright et al. 2004, Chave et al. 2009, Díaz et al. 2016) and are potentially important for species’ growth rates and ecological strategies (Poorter et al. 2008, Wright et al. 2010).

Table 3.1 Overview of 18 functional traits studied: groups of variables, name, abbreviations (Abb.), units, and major role in the plant.

Trait name	Units	Abb.	Major role	Source
Leaf traits				
Leaf thickness	mm	LT	increases physical leaf strength and path length for CO_2 diffusion	Niinemets 1999
Leaf area	mm^2	LA	increases light interception, carbon gain and water loss	Maharjan et al. 2011
Specific leaf area	mm^2 mg^{-1}	SLA	correlates positively with photosynthetic capacity and leaf turnover.	Pérez–Harguindeguy et al. 2013
Leaf dry matter content	mg g^{-1}	LDMC	correlates with leaf toughness.	Pérez–Harguindeguy et al. 2013
Leaf density	mg mm^{-3}	LD	dense leaves increase the resistance to CO_2 diffusion and, hence, decrease carbon gain	Niinemets 1999
Vein density	mm mm^{-2}	VD	a structural determinant of hydraulic conductance and photosynthetic rate	Pérez–Harguindeguy et al. 2013
Stomatal density	no. mm^{-2}	SD	allows for a high supply of CO_2 for assimilation; but increases transpiration	Tanaka and Shiraiwa 2009
Stomatal length	µm	SL	control the exchange of gases—most importantly water vapour and CO_2	Hetherington and Woodward 2003
Stomatal pore index (SL^2 x SD)	unitless	SPI	increases leaf hydraulic conductance, photosynthesis, and transpiration	Sack et al. 2003
Leaf Nitrogen concentration	mg g^{-1}	LNC	increases the maximum photosynthetic rate, correlated with SLA	Pérez–Harguindeguy et al. 2013

Leaf Phosphorus concentration	mg g⁻¹	LPC	contributes to photosynthesis and other metabolic processes	Pérez–Harguindeguy et al. 2013
Leaf Potassium concentration	mg g⁻¹	LKC	contributes to stomatal coordination	Lines–Kelly 2000.
Leaf Magnesium concentration	mg g⁻¹	LMgC	key component of chlorophyll and is vital for photosynthesis	Lines–Kelly 2000.
Leaf Zinc concentration	mg g⁻¹	LZnC	Zinc contributes to plant hormones responsible for stem and leaf expansion	Lines–Kelly 2000.
Leaf Nitrogen to Phosphorus ratio		N:P	indicates whether N or P is more limiting for plant growth	Pérez–Harguindeguy et al. 2013
Stem traits				
Wood density	g cm^{-3}	WD	positively correlated with strength (resistance to trunk breakage), mechanical safety, and cavitation resistances, and negatively correlated with growth rate	Van Gelder et al. 2006 Larjavaara and Muller–Landau 2010
Vessel diameter	μm	VesD	increases water transport efficiency	Tyree et al. 1994
Root traits				
Specific root length	m g⁻¹	SRL	Increases potential nutrient and water uptake rates	Weemstra et al. 2015

Trait measurements were made following protocols outlined by Pérez–Harguindeguy et al. (2013). For each individual, the branch and leaf samples were placed into a Ziplock bag with a moist paper towel to keep them hydrated. In the lab, leaves were separated from the branch, and three leaves were randomly selected. Leaf blade thickness (LT, mm) was measured at a central part of the leaf without major veins using a Syntek outside micrometer. Each leaf was scanned using a CanoScan 9000F Mark II scanner and then leaf area (LA, mm^2) was calculated using ImageJ software (v.1.52a; Wayne Rasband, National Institutes of Health, USA; http://imagej.nih.gov/ij). Leaf water–saturated fresh mass was measured after leaves have been immersed for 2 h in water. Leaves were subsequently oven dried for 48 h at 70°C for leaf dry mass.

Stomatal density was measured using the impression method. We applied clear nail varnish to a 1 cm^2 patch on the abaxial lamina immediately to the right of the mid vein (avoiding major veins). After 10 minutes, the nail polish was removed and mounted on a glass slide for making images under a microscope (Leica Microsystems Ltd., Leica DM2500, Germany). Four images were taken using 200 – 400x magnification, resulting in ca. 20 – 80 stomates per image, the scale was added at same time. Stomatal density (SD, no. mm^{-2}) of each leaf was measured by averaging the total number of stomata for each of the 4 images. Stomatal length (SL, mm) was measured for 5 randomly selected stomata on each image and was then averaged. The stomatal counts and measurements were conducted using the imaging software ImageJ (v.1.52a; Wayne Rasband, National Institutes of Health, USA; http://imagej.nih.gov/ij).

To measure the density of minor veins, for each species, several approximately 1 cm^2 diamonds were excised from the central section of sample leaves and were kept in FAA solution (Formalin: Glacial acetic acid: Ethanol (70%) = 5%: 5%: 90%) for storage. These leaf diamonds were immersed in a 5% NaOH solution and were heated in water–bath at 65°C. The solution was replaced once it had turned dark until the veins were exposed. The samples were then washed with distilled water 3 times, and the diamonds that had turned transparent were placed on glass slides and were stained with 1% safranin. For each leaf diamond, four images (with scale) were taken at 100x magnification using a microscope (Leica Microsystems Ltd., Leica DM2500, Germany). The length of the minor veins within the view field was first traced and then measured using ImageJ software (v.1.52a; Wayne Rasband, National Institutes of Health, USA; http://imagej.nih.gov/ij).

To measure leaf nutrient concentration, fresh leaf samples were cleaned with a moist tissue and then oven–dried at 70°C for at least 2 days, ground to a fine powder with a crusher, and then passed through a 60 –

mesh sieve. The powders were placed in plastic bags and sent to the Public Technology Service Centre, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences. In the laboratory, leaf nitrogen concentration (LNC, mg g^{-1}) was analysed using an Elemental Analyzer (Vario MAX CN, Elementar Analysensysteme GmbH, Germany). An inductively coupled plasma atomic–emission spectrometer (iCAP7400, Thermo Fisher Scientific U.S.A) was used to measure leaf phosphorus concentration (LPC, mg g^{-1}), leaf potassium concentration (LKC mg g^{-1}), leaf magnesium concentration (LMgC, mg g^{-1}) and leaf Zinc concentration (LZnC, mg g^{-1}).

Stem traits were determined from a 5 cm long branch segment at the base of each collected branch. First the bark and pith were excluded and then the fresh wood volume (V, cm^3) was determined using the water displacement method. This branch segment was then dried in an oven at 70°C for 72 hours and then weighted for its dry weight (DW, g).

An additional ca. 3 cm branch piece was sampled from the branch base for anatomical measurements and embedded in FAA. For each branch sample, four cross–section images were taken at 100 – 500x magnification using the microscope (Zeiss Smartzoom 5 Digital Microscope, Germany). For each original image, to avoid the threshold difference in ImageJ analysis, we first erased the vessel area with the eraser tool in Adobe Photoshop CS6, then imported to ImageJ Software (v.1.52a; Wayne Rasband, National Institutes of Health, USA; http://imagej.nih.gov/ij) where measurements were finished automatically without color. To estimate the vessel diameter (VesD, μm), the 10 widest vessel diameters from each of the 4 images were measured and averaged. We focused on the largest vessels because they are expected to contribute strongest to hydraulic conductance efficiency (Tyree et al. 1994).

In order to sample liana roots, first the target species' individuals were identified, following the main stem to find the root location, after which the roots were dug up from 0 – 20 cm soil depth. Most of the soil was removed by slightly shaking the roots. The root sample was then placed into a marked Ziplock bag with moist paper towels to keep the sample hydrated. The root system was then removed from the bag, the roots carefully cleaned and placed in a shallow tray of water. The fine roots were then fully spread out by using scissors and sellotape. Since plant roots are often divided by root (ramification) order, the third branch order of fine roots (starting at the root tip) was cut for measurements, as this part of the roots are responsible for nutrient uptake (Fitter 1982). The root length was measured by using a scanner (CanoScan 9000F Mark II) and was further analysed with the WinRHIZO (Regent Instruments Inc., Quebec, Canada) root analysis program. The roots were then oven–dried at 70 °C for 72 h and weighed for their dry mass.

3.2.4 Functional trait calculations

Specific leaf area (SLA, mm^2 mg^{-1}) was calculated as the leaf area per unit leaf dry mass. Petioles were not included in the SLA calculation as they can be very large for rainforest species, and because petioles are more related to leaf positioning than biomass efficiency for leaf display. For compound leaves, SLA was based on all available leaflets, but the rachis was not included in the SLA calculation because rachis was much heavier than the sum of the leaflet. The leaf dry matter content (LDMC, mg g^{-1}) was calculated as the leaf dry mass divided by the leaf water–saturated fresh mass. Leaf density (LD, g cm^{-3}) is the leaf dry mass per unit leaf volume, and it was calculated as 1/(SLA × LT). The minor vein density (VD, mm mm^{-2}) was calculated as the total length of minor veins per unit area. Stomatal pore index (SPI, unitless) was calculated as SD × SL^2. Wood density (WD, g cm^{-3}) was calculated as branch wood dry mass over branch fresh wood volume without bark. Specific root length (SRL, m g^{-1}) was calculated as the root length per unit root dry mass.

3.2.5 Soil nutrient niches

To quantify soil nutrient availability across the plot, soils were sampled in a systematic way to create soil nutrient maps. The soil was sampled in 2011 using a regular 30 m × 30 m grid throughout the 20–ha plot. Each of the

252 nodes in this grid was used as a “base point”. Together with each base point, two additional sampling points were added, located at random distances of 2 and 5 m, 2 and 15 m or 5 and 15 m along a random compass bearing away from the correlated base point. Hence, in total 756 soil samples were taken. At each sample point, 500 g of topsoil at 0 – 10 cm depth was collected, as the topsoil layer is most nutrient rich, and plants obtain most soil nutrients from the topsoil. Fresh soil samples were placed in plastic bags, shipped to the Public Technology Service Centre, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences and analysed for soil nutrients (nitrogen, phosphorus, and potassium). Using this original soil data, an ordinary kriging was performed to generate a sub–quadrat grid map of 10 m × 10 m for each soil variable (Cressie 1992). The soil nutrients for each 20 m × 20 m quadrat in which lianas were inventoried, were then calculated as the mean of the values at each of the nine nodes of the 10 m × 10 m sub–quadrats within that quadrat by using the geoR package in the R (see Hu et al. 2012).

3.2.6 Water availability

Spatial topographic information was used to quantify the water availability. To describe the topography, the plot was subdivided into five hundred 20 m × 20 m quadrats. For each quadrat, the elevation and slope were measured following Harms et al. (2001): the elevation was calculated as the mean of the elevation at the four quadrat corners and the slope was based on the mean angular deviation from the horizontal of each of the four triangular planes formed by connecting three corners. We used the topographic wetness index (TWI) to describe the water niche of the species. This index is defined as $TWI=\ln(\alpha/\tan\beta)$, where α is the local upslope area draining through a certain point per unit contour length and $\tan\beta$ is the local slope in radians (Beven and Kirkby 1979). The specific catchment area is a parameter describing the tendency of the site to receive water from upslope area and local slope is a parameter describing the tendency to evacuate water (Gruber and Peckham 2009). This index is therefore a relative measure of the long–term soil moisture availability of a given site in the landscape and high TWI indicates a strong water accumulation. In ArcGis Desktop 10.6.1, we used the Flow Accumulation tool to calculate α and the slope tool to calculate β.

3.2.7 Light niche

To quantify the light niche for all liana species, we inferred the light conditions for each quadrat from the forest structure. The quadrat was defined as a "gap" when its canopy cover was less than 50% in 2014 (Liu et al. 2014). In total there were 31 gaps in the 20–ha plot. For each species, the percentage of individuals in the 20–ha plot that occurred in gaps was used to quantify the species light niches.

3.2.8 Statistical analyses

The variation in environmental factors encountered in the studied forest is visualized by relative frequencies diagrams showing our observations for all quadrats (Appendix S3.2).

For the analysis, we compiled a data set with species mean values for all measured plant traits (see Table 3.1). All statistical tests were conducted using RStudio packed with R 3.6.2 (R Core Team 2019). Eight traits (LA, SLA, SD, SL, LKC, LMgC, LZnC, VesD) were ln–transformed to achieve normality. Because SRL data were missing for 4 species, we used the package "missMDA" to impute missing values, thus yielding a data set of 18 functional traits for 29 liana species.

To evaluate how traits were associated, we used pairwise Pearson's correlation and a principal component analysis (PCA) using species mean values as data points.

To evaluate which traits shape the species niche, for each niche variable an all–subsets regression analyses was done, with the 18 species' mean traits as explanatory variables and the species niches as the dependent variable. The Bayesian information criterion (BIC) was used to determine the variables with the most explanatory power. BIC is an estimate of a function of the posterior probability of a model being true, under a certain Bayesian setup, so that a lower BIC means that a model is deemed more accurate model.

To evaluate whether multivariate trait strategies can provide a better prediction of the species niche, we quantified the species strategy as the species regression scores on the first and second axis of the trait PCA, and did a series of multiple regressions of the 5 species niches on the two principle components. We then compared their r^2 with best models. The same analysis was done between liana relative abundance in the plot and functional traits.

Multicollinearity was avoided by excluding 4 variables (LD, LDMC, SL, N_P) with a Variance Inflation Factor > 10 (Zuur et al. 2010).

3.2.9 Phylogeny

Here we focus on cross–species associations because it reflected the current species performance; however, it would be better to see whether phylogenic progress would affect these associations. We further tested if trait associations are the result of evolutionary divergences using phylogenetically independent contrasts (PIC) (Felsenstein 1985, Westoby 1999). The phylogenetic tree was constructed using the package "V.PhyloMaker" (Jin and Qian 2019) in R. Phylogenetic conservatisms in all traits were then analysed using Blomberg's *K* statistic which compares the observed signal in a trait to the signal under a Brownian motion model of trait evolution on a phylogeny (Blomberg et al. 2003). *K* values closer to zero correspond to a random or convergent pattern of evolution, while *K* values greater than 1 indicate strong phylogenetic signal and conservatism of traits. We analysed phylogenetic independent contrast values (PICs) using Pearson product–moment correlations (Zanne et al. 2010). Phylogenetic analyses were performed using package APE (Paradis et al. 2004).

3.3 RESULTS

3.3.1 Trait correlations

The first two PCA axes explained 54.7% of the variation and showed two spectra of trait variation (Figure 3.1). The first PCA axis showed a range from liana species with traits referring to a more water–conservation strategy with tough tissues (on the left, i.e., high leaf density, leaf dry matter content, wood density), to liana species with a more water–spending strategy with soft tissues (high vessel diameter and stomatal length) at the right. Unexpectedly, leaf nutrient traits were not significantly associated with this axis. The second PCA axis however showed changes across liana species in leaf nutrient concentration, SRL and SLA. Furthermore, the second PCA axis reflected photosynthetic carbon gain and was mostly determined by SLA and LNC. These two traits are joined by LZnC and LKC, which are more related to metabolism (Zn) and potential gas exchange (K).

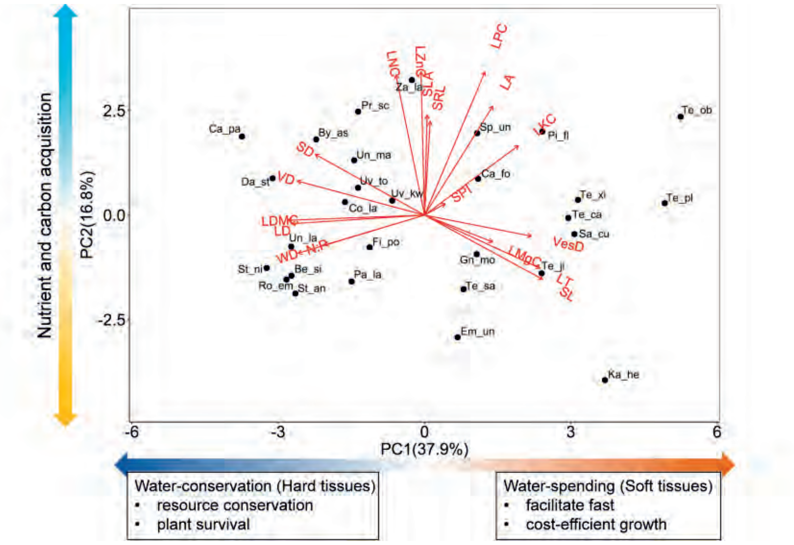

Figure 3.1 Principal component analyses (PCA) of multivariate trait associations across 29 liana species using species averages as data points. The first two PCA axes and the loadings (indicated by red arrows) of 18 traits are shown. The gradient arrows at left and bottom indicate the three spectra (tissue toughness spectrum, water use spectrum, and nutrient and carbon acquisition spectrum). Each point represents one species. For trait abbreviations see Table 3.1. For species abbreviations see Appendix S3.1. Traits were normalized as described in statistical analyses.

Functional traits were correlated amongst the 29 liana species (Table 3.2, below the diagonal). On water–conservation spectrum, LDMC, LD, VD, SD were significantly positively correlated with each other. These traits positively correlated with the stem trait wood density (WD) (Table 3.2,

Figure 3.2a), which was also in line with the water–conservation spectrum. The same trend was found in the water–acquisitive spectrum, as with increasing vessel diameter (VesD) liana species tended to have larger stomata (high SL). In the resource capture spectrum, SLA was positively associated with LNC (Figure 3.2b). Surprisingly, root trait specific root length (SRL) did not show any associations with leaf or stem traits (Table 3.2).

Of the tested relationships, most cross–species associations and phylogenetically independent contrasts (PIC) correlation analyses were incongruent (Table 3.2, above the diagonal). Regarding to water–conservation strategy with tough tissues, positive correlations between LD, LDMC and WD were retained, while the relationships with SD and VD were weak when phylogeny were considered. Furthermore, VesD did not show any relationship with SL, which was referred water–spending spectrum. The largest difference in PIC correlations was found between SLA and SPI in the resource capture spectrum. With increasing SLA, lianas tended to have higher LA and leaf nutrient concentrations, and lower LD and LDMC. Meanwhile, SPI positively correlated with LA, SLA, SL, leaf nutrient concentrations (LNC, LPC and LKC), and negatively with LD, LDMC (Table 3.2, above the diagonal). In the phylogenetic correlations, SRL showed a strong correlation with leaf traits (i.e., positively with SL, LNC and negatively with LD, LDMC) and a negative association with stem traits (WD; Table 3.2, above the diagonal).

Table 3.2 Pearson's correlation across species (below the diagonal) and correlations based on phylogenetically independent contrasts (PIC) (above the diagonal) among the 18 leaf, stem, and root traits of 29 liana species in the tropical seasonal rainforest of Xishuangbanna, China.

	LT	LA	LD	LDMC	SLA	VD	SD	SL	SPI	LNC	LPC	LKC	LMgC	LZnC	N_P	WD	VesD	SRL
LT		−0.01	**−0.40***	−0.33	−0.3	**−0.66****	−0.31	0.03	−0.21	−0.08	−0.06	0.06	**0.58****	0.22	0.02	−0.32	0.02	−0.27
LA	0.26		**−0.44***	**−0.51****	**0.46***	0.11	0.33	0.22	**0.54****	**0.50****	**0.69****	0.34	0.07	0.07	−0.27	**−0.39***	0.27	0.26
LD	**−0.71****	−0.32		**0.95****	**−0.72****	0.37	0.21	**−0.62****	**−0.55****	**−0.75****	**−0.70****	**−0.65****	−0.21	**−0.46***	−0.13	**0.60****	−0.19	**−0.41***
LDMC	**−0.67****	−0.3	**0.91****		**−0.72****	**0.42***	0.15	**−0.56****	**−0.54****	**−0.72****	**−0.76****	**−0.62****	−0.27	**−0.45***	−0.01	**0.59****	−0.21	**−0.39***
SLA	**−0.45***	0.09	−0.25	−0.2		0.17	0.01	**0.59****	**0.72****	**0.88****	**0.79****	**0.54****	−0.16	**0.42***	0.19	**−0.41***	0.06	**0.59****
VD	**−0.72****	−0.14	**0.76****	**0.84****	0.08		0.32	−0.12	0.12	−0.03	−0.01	−0.27	**−0.44***	−0.13	−0.04	0.24	−0.18	0.04
SD	**−0.50****	−0.01	**0.67****	**0.67****	−0.16	**0.67****		**−0.50****	0.18	0.06	0.17	−0.19	−0.08	−0.01	−0.12	0.17	−0.05	0
SL	**0.58****	0.14	**−0.70****	**−0.66****	0.02	**−0.68****	**−0.87****		**0.75****	**0.62****	**0.51****	**0.60****	−0.02	0.21	0.21	**−0.59****	0.11	**0.72****
SPI	0.10	0.31	−0.09	−0.03	−0.07	0.01	0.21	0.27		**0.77****	**0.73****	**0.49****	−0.08	0.24	0.15	**−0.56****	0.07	**0.81****
LNC	−0.31	0.23	0.08	0.17	**0.50****	0.16	0.19	−0.26	−0.02		**0.82****	**0.63****	−0.02	**0.51****	0.33	**−0.49****	0.1	**0.68****
LPC	0.22	**0.69****	−0.31	−0.26	0.19	−0.24	−0.05	0.09	0.12	**0.57****		**0.55****	−0.09	**0.49****	−0.24	**−0.54****	0.12	**0.48***
LKC	**0.44***	**0.39***	**−0.549****	**−0.60****	0.04	**−0.54****	−0.33	0.29	−0.13	0.07	**0.50****		0.15	0.22	0.12	−0.34	0.16	**0.59****
LMgC	0.32	0.12	−0.29	**−0.50****	−0.12	**−0.46***	−0.24	0.35	0.18	−0.33	−0.09	**0.52****		0.21	0.28	−0.09	−0.3	−0.18
LZnC	−0.28	0.15	0	−0.06	**0.40***	0.09	0.22	−0.32	−0.17	**0.41***	**0.43***	0.35	0.13		0.04	**−0.59****	−0.28	0.27
N_P	**−0.54****	**−0.57****	**0.47****	**0.49****	0.22	**0.44***	0.29	**−0.37***	−0.11	0.31	**−0.57****	**−0.46***	−0.11	−0.09		0.08	−0.1	0.31
WD	**−0.48****	**−0.58****	**0.72****	**0.75****	−0.19	**0.58****	**0.57****	**−0.63****	−0.19	0.13	**−0.40***	**−0.42***	−0.27	−0.14	**0.66****		−0.19	**−0.52****
VesD	**0.51****	0.31	**−0.57****	**−0.61****	0	**−0.59****	**−0.55****	**0.60****	0.17	−0.12	0.21	0.16	0.16	−0.15	**−0.41***	**−0.73****		0.08
SRL	−0.03	0.24	−0.08	−0.17	0.13	0.11	0.27	−0.18	0.24	0.17	0.11	0.25	0.03	0.33	−0.01	−0.18	−0.05	

Notes: Bold correlations indicate significant relationships, $p < 0.05$ (*), $p < 0.01$ (**). Traits were normalized as described in the section statistical analyses. For trait abbreviations, see Table 3.1.

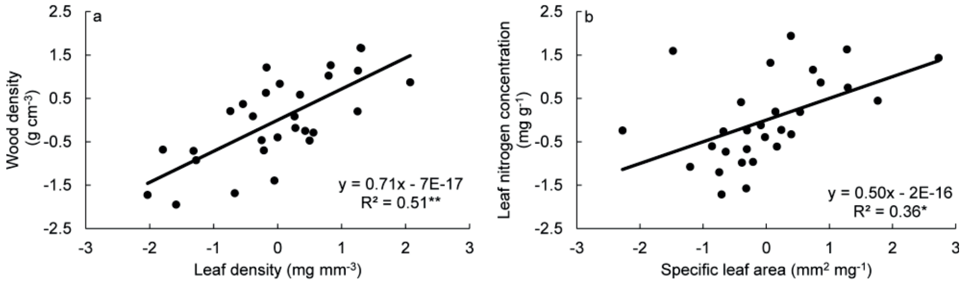

Figure 3.2 Functional trait relationships across 29 liana species in Xishuangbanna tropical seasonal rainforest that underlie respectively the first and second PCA axes. (a) wood density vs leaf density, (b) leaf nitrogen concentration vs specific leaf area. Regression lines, regression equations, R^2 and significant level (*, $p < 0.05$; **, $p < 0.01$) are shown. Each dot is a species. Traits were normalized as described in statistical analyses.

3.3.2 Functional traits as predictors of resource niches

All subsets regression analysis showed that liana resource niches were determined by different functional traits (Table 3.3, Figure 3.3). For the light niches, the best two models (i.e., with the smallest Bayesian information criterion (BIC) value) showed that species with high LPC,

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SPI, and LZnC occupied high light conditions (Figure 3.3a). Liana species occupying high water niches (TWI) had high LPC and LZnC, but narrow vessel diameter (VesD, Table 3.3). Species with an increased vessel diameter were located in soils with higher nitrogen concentration (Figure 3.3b). Higher leaf phosphorus concentration and potassium concentration species occupied niches with higher soil phosphorus and potassium levels (Table 3.3).

Table 3.3 Regression analyses between environmental variables, species relative abundance with PCA components (PCA1 and PCA2) and functional traits included in best subsets regression models. By using environmental variables and species relative abundance (71% of liana stems in the whole 20 ha plot) as dependent variables, linear regression and linear multiple regression were tested, only significant results were given in bold. The results of all subsets regression on 14 functional traits to model environmental variable of 29 liana species are shown. Traits with high Variance Inflation Factor (VIF > 10) values were removed prior to the test. Only the first two best models with the lowest Bayesian information criterion (bic) value are shown.

Variables	PC1	PC2	Model		
	r^2	r^2	r^2	Two best models	bic
Light niche (%)	0.09	**0.26**	**0.33**	1.85 + 0.60LPC	−5.02
			0.53	1.85 + 0.32LPC + 0.43LZnC + 0.27SPI + 0.29VesD	−4.98
Water niche (TWI)	0.01	< 0.01	**0.29**	1.69 + 0.03LPC − 0.03LZnC − 0.03 VesD	3.90
			0.09	1.69 − 0.02VesD	4.10
Nitrogen niche (g cm^{-3})	0.11	0.01	**0.27**	0.70 + 0.01VesD − 0.01SRL	0.74
			0.19	0.70 + 0.01VesD	0.78
Phosphorus niche (g cm^{-3})	**0.20**	< 0.01	**0.17**	0.37 − 0.02VD	1.62
			0.24	0.37 − 0.02SD + 0.01LPC	2.69
Potassium niche (g cm^{-3})	**0.22**	0.03	**0.30**	2.57 − 0.04LZnC − 0.04WD	−0.37

Relative abundance (%)	0.05	0.01	**0.34**	2.57 – 0.05LZnC – 0.03WD + 0.02LKC	1.40
			0.42	0.50 + 0.64SD – 0.26LZnC – 0.35WD – 0.29SRL	1.16
			0.26	0.49 + 0.36SD – 0.24LZnC	1.37

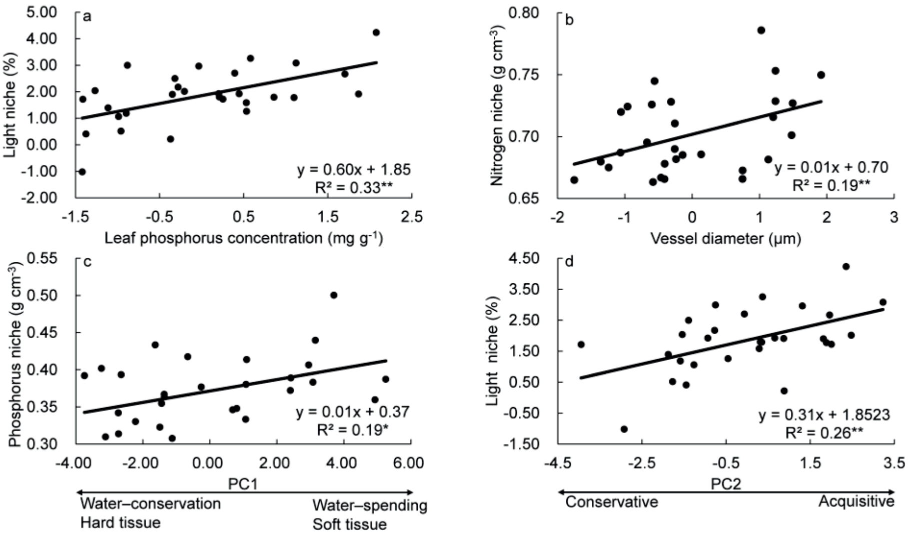

Figure 3.3 Relationships between the first two PCA axes and individual traits on a species level, across 29 liana species in Xishuangbanna tropical seasonal rainforest, related to resource niches. (a) light niche vs leaf phosphorus concentration, (b) nitrogen niche vs maximum vessel diameter, (c) phosphorus niche vs PC1, (d) light niche vs PC2. Regression lines, regression equations, R^2 and significant level (*, $p < 0.05$; **, $p < 0.01$) are shown. Each dot is a species. Resource niches and traits were normalized as described in statistical analyses.

Liana resource niches can also be predicted by multivariate trait strategies. Linear regression indicated that the functional traits located in the first component (PC1) were related to the liana species distribution along gradients in soil phosphorus ($r^2 = 0.19$, $P = 0.0186$, Figure 3.3c) and potassium ($r^2 = 0.22$, $P = 0.0104$) availability. However, the PC1 showed only a weak effect on liana distribution along the soil nitrogen gradient ($r^2 = 0.11$, $P = 0.07$). The second component (PC2) was positively related to light availability ($r^2 = 0.26$, $P = 0.0044$, Figure 3.3d). Surprisingly, neither PC1 nor PC2 showed a significant association with water niche (TWI; Table 3.3).

Liana multivariate trait strategies did not affect liana abundance (Table 3.2). Surprisingly, stomatal density was the best predictor of liana abundance, joined by LZnC, WD and SRL, with species possessing more stomates attaining a high abundance (Table 3.3, Figure 3.4), but this trend was mainly driven by species *Kadsura heteroclita*.

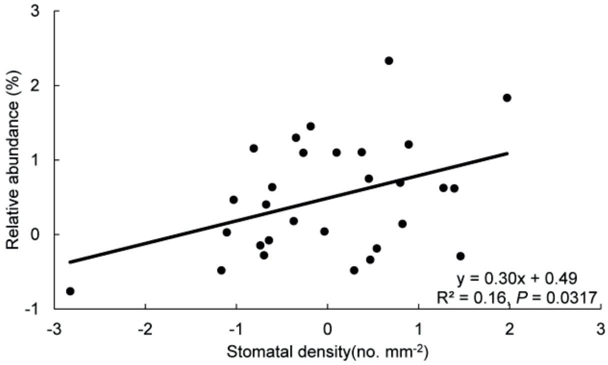

Figure 3.4 Relationship between relative abundance and stomatal density across 29 liana species in Xishuangbanna tropical seasonal rainforest. Regression lines, regression equations, and R^2 were shown. Each dot indicates a species. Variables were normalized as described in statistical analyses.

3.4 DISCUSSION

We evaluated traits from 29 co–existing liana species and asked how liana traits are associated, what plant strategies can be distinguished, and whether different traits shape different species niches. We found that lianas showed a primary spectrum in tissue toughness and water use, and a secondary spectrum in nutrient and carbon acquisition. Liana species with more acquisitive trait values occupied higher light and nutrient resource niches, but different traits were important for different niche dimensions.

3.4.1 A primary spectrum in toughness and water use, and a secondary spectrum in nutrient and carbon acquisition

We hypothesized that liana species would show a trait spectrum, ranging from trait values that increase resource acquisition and use, to traits values that increase resource conservation. Rather than one spectrum we found two spectra; the first PCA axis represents a tissue toughness and water spending spectrum, and the second PCA axis a resource acquisition spectrum (Figure 3.1). Intriguingly, each spectrum partly reflects the conservative–acquisitive paradigm, but at the same time these two spectra are also independent from each other, because they are associated with different, orthogonal PCA axes.

Spectrum in toughness and water use - The first PCA axis represents a toughness spectrum where traits are aligned along an axis from soft to hard tissues, with thick leaves to the right and high leaf – wood – and leaf venation density to the left (Figure 3.1). This trait association along the first axis underlies the growth–survival trade–off that is frequently observed across tropical liana species (Gilbert et al. 2006) and tree species (Wright et al. 2010). Species either invest in soft tissues that facilitate fast, cost–efficient growth or they invest in hard and persistent tissues that enhance resource conservation and plant survival (Poorter and Bongers 2006, Kitajima and Poorter 2010). This tissue toughness spectrum also reflects a spectrum in water spending and conservation. At the right, there is a group of traits that are important for hydraulic integration and increased water use, with wide vessels that facilitate high stem water conductivity (Tyree et al. 1994), thick leaves with a high water content that facilitates water storage (Camilleri and Ribi 1983), large stomata that facilitate stomatal conductance and gas exchange (Lambers et al. 2008), and high leaf K concentration which is used in the guard cells to fine–tune stomatal aperture and gas exchange in response to temporal variation in environmental conditions (Benlloch–González et al. 2008). At the left hand of the PCA axis, there are two hydraulic traits (leaf venation density and stomatal density) that align with tough tissues. Normally vein density is thought to be associated with high water transport capacity and high photosynthetic carbon gain (Sack et al.

2005). The fact that it does not align with the leaf photosynthetic spectrum (PCA Axis 2) meaning that vein density fulfills a different role. We measured fine, secondary veins, that are probably more important for a uniform distribution of water throughout the leaf rather than for increased water transport (Blonder et al. 2013). Moreover, veins have a dual function; they are not only important for water transport, but they also increase the structure, hardiness, and longevity of the leaf (Kitajima and Poorter 2010). The first PCA axis also shows a trade–off between the size and the number of stomata. From a developmental perspective, many small stomata are associated with leaves that make many small cells. These small cells tend to have thick cell walls and tend to be tough. Hence, the alignment of high stomatal density with high leaf density and leaf dry matter content is probably the result of developmental constraints. Moreover, a high stomatal density allows plants to regulate water loss more precisely (Lawson and Blatt 2014), thus improving water conservation.

Spectrum in nutrient and carbon acquisition - The second axis represents a nutrient and carbon acquisition spectrum, with species having a low capacity to acquire soil and light resources at the bottom to species with a high capacity to acquire and use resources at the top. High specific root length facilitates nutrient uptake (Eissenstat 1992, Eissenstat et al. 2000), large leaves and high specific leaf area facilitate light capture (Reich et al. 1998), and high nitrogen and phosphorus concentrations allow for investments in photosynthetic proteins and ATP that increase photosynthetic capacity and carbon gain (Reich et al. 2003). Although this second axis closely reflects the leaf economics spectrum (LES, Wright et al. 2004, Onoda et al. 2017), it has one important difference. It only reflects resource acquisition and use but not resource conservation, as it is not related to tough and persistent tissues such as high leaf density or wood density (Figure 3.1). Therefore, this nutrient and carbon acquisition spectrum is orthogonal to the tissue toughness spectrum. In our case, the two axes are decoupled because of the traits that underlie specific leaf area (SLA). SLA plays a pivotal role in the leaf economics spectrum, as high SLA facilitates resource capture and use, and low SLA and its underlying traits (high leaf thickness and/or high leaf density) facilitate resource conservation. A multiple regression of ln(SLA) on ln(leaf thickness) and ln(leaf density) shows that for our forest and study species, SLA is equally determined by leaf thickness (standardized regression coefficient = –1.07, $P < 0.001$) and leaf density (standardized regression coefficient = –1.06, $P < 0.001$). As leaf density (or its analogue, leaf dry matter content) has, in fact, a stronger impact on leaf toughness, leaf longevity (Kitajima and Poorter 2010, Kitajima et al. 2012) and nutrient conservation (Hodgson et al. 2011) than SLA, this explains why in our case the LES falls apart, and why we have two spectra.

Are root–stem and leaf traits coupled? - We hypothesized that liana stem traits can be decoupled from leaf and root traits, because lianas are structural parasites, investing fewer resources in structural support of the stem. We found that liana stem toughness (wood density) aligned with leaf toughness (leaf density and dry matter content) (Table 3.2, Figure 3.1), indicating a life history coordination across organs. We also found that liana stem water transport capacity (maximum vessel diameter) aligned with leaf water transpiring capacity (stomatal size) (Table 3.2, Figure 3.1), indicating a hydraulic integration across stem and leaf organs. However, Baraloto et al. (2010) found that leaf economics spectrum and stem economics spectrum were orthogonal in Neotropical trees, suggesting that trade–offs operate independently at the leaf and at the stem levels. The only root trait that we analysed (specific root length) was not significantly correlated with any of the stem and leaf traits, which is in line with the suggestion of Weemstra et al. (2016) that roots are not associated with the plant economics species spectrum, as they have to acquire many different nutrient resources, and they can acquire them in many different ways (e.g., through mycorrhizae or root exudates). Yet, specific root length did correlate with the stem and leaf traits in the phylogenetic correlation analysis, and it aligned with SLA and leaf nutrient concentrations in the PCA. Specific root length indicates how much root length can be built per unit of root mass (Ryser

2006). A high specific root length increases the root–soil interface and allows plants to forage for water (but see Westoby and Wright 2006), but especially to forage for (immobile) nutrients (Fitter 1982). Perhaps, for this reason, specific root length aligns in the PCA with leaf nutrient concentrations and SLA, but not with the water use axis. A combination of high specific root length and SLA allows species to maximize below– and aboveground resource capture, grow fast, and rapidly complete their life cycle. Such strategy is typical for fast–growing pioneer species that specialize for high resource pulses in ephemeral, early successional environments (Poorter and Markesteijn 2008).

3.4.2 Liana species with acquisitive trait values occupy higher resource niches

We hypothesized that liana species with more acquisitive trait values occupy higher light, water, and nutrient resource niche dimensions. We indeed found that different functional traits shaped different niche dimensions and multivariate trait strategies also play a role in shaping liana distribution (the first PCA axis had a significant positive effect on liana soil niches, Figure 3.3c), indicating that liana species with more acquisitive trait values (softer tissues, higher water use) were able to occupy high soil resource niches. When resource niches were predicted based on individual traits, then acquisitive trait values often increased the resource niche (i.e., vessel diameter, stomatal pore index and Zn concentrations increased different resource niches), but not always (e.g., a high specific root length decreased the soil N niche). Plant strategies are inherently multivariate and thought to better explain the species niche (Grime 2006). Yet, in our case individual traits were often better (e.g., light, water, soil N), similarly good (soil K), and only once worse (soil P) predictors of the species niche dimensions than the multivariate strategy axes. This suggests that different components of the multivariate strategy axes are important for different niche dimensions.

We hypothesised that the liana light niche would increase with traits that increase carbon gain, for example through increased light capture ability (large leaf area and high specific leaf area), high leaf N and P concentrations, and fast gas exchange (high stomatal density, length and pore index). Instead, we found that the light niche increased with a higher maximum vessel diameter, stomatal pore index, leaf P and Zn concentration (Table 3.3). This suggests that in an exposed high–light environment lianas benefit from a high–water transport capacity. Increasing vessel diameter is an anatomically cheap and efficient way to increase the water transport capacity of the stem (Schnitzer 2005, van der Sande et al. 2019) as hydraulic conductance scales with the fourth power of vessel diameter (Lambers et al. 2008). While trees can increase their water transport capacity by increasing their stem diameter, this is not an option for lianas because their climbing habit requires relatively flexible, slender stems (Hoffmann et al. 2000).

Stomatal pore index is the product of stomatal density and stomatal length. Species with high stomatal pore index occupied a higher light niche (Table 3.3), possibly because large stomates facilitate high stomatal conductance and gas exchange (Bidwell 1974) to optimally benefit from the high irradiance. At the same time, this high irradiance comes along with a high vapor pressure deficit and atmospheric drought and this may apply especially to lianas which have most of their leaves on the top of the forest canopy. Perhaps a high stomatal density allows for maximal photosynthesis (e.g. in the case of sun flecks), and possibly efficient closure of stomata to minimize transportation water loss (Lambers et al. 2008). We found leaf Zn concentration increased the light niche (Table 3.3). Zn concentration has rarely been studied in tropical rainforests, and its role in plants remains controversial (Brown et al. 1993). Zinc helps in the production of a plant hormone responsible for stem elongation and leaf expansion (Lines–Kelly 1992), with lianas may benefit a from in their climbing lifeform.

We hypothesized that the water niche would be best predicted by water transport traits (i.e., vessel diameter, stem venation and stomata), but surprisingly, neither the multivariate strategy axes, nor any of the individual traits showed a significant relationship with the water niche

(Table 3.3). Other studies do show that within the same community the topographic water niche is determined by more anatomical, morphological, and physiological traits. For example, Amazonian rainforest tree species from higher and relatively drier plateaus had lower SLA, denser wood, narrower vessels, a lower hydraulic conductivity, and stronger resistance against drought–induced cavitation than species from lower–lying wet valleys (Cosme et al. 2017, Oliveira et al. 2019). Either water is not a limiting factor in our moist and shaded forest, even in the dry season. A study in Xishuangbanna found that the strong morning fog and reduced irradiance may help to reduce water loss in the dry season (Gotsch et al. 2014). Alternatively, lianas may simply avoid drought stress by having multiple rooting sites along their long stems (Putz 1984, Caballe 1994).

We hypothesized that liana nutrient niches would increase with traits that reflect nutrient requirements and use (i.e., leaf nutrient concentrations and N:P ratio, because P is often limiting in old weathered and leached tropical soils (Vitousek et al. 2010)). However, soil N was predicted by vessel diameter (Table 3.3, Figure 3.3b), whereas soil P and K niches were positively correlated with leaf P and K concentrations (Table 3.3). In addition, soil P and K niches could also be predicted by the multivariate tissue toughness spectrum (Table 3.3, Figure 3.3c), with species bearing softer tissues occupying higher resource niches.

Species with tough and persistent tissues can retain nutrients for a longer time in their leaves and branches, and as a result have lower nutrient requirements, and can better persist under low soil resource conditions (Aerts 1996). Yet, this multivariate toughness spectrum was also associated with traits related to water use, such as vessel diameter (Figure 3.1). The multiple regression analysis showed that vessel diameter was a better predictor of species soil niches, with species with wider vessels (and hence, a high water–transporting capacity), occupying higher soil K and N niches (Table 3.3). Perhaps species with a higher water transporting capacity need higher K to better regulate stomatal aperture and reduce water loss under drought conditions (Benlloch–González et al. 2008). A higher water transport capacity is also associated with a high transpiration rate, which generates an active water flow in the soil. Especially mobile nutrients such as N are transported by and taken up through this mass flow (Fitter 1982). Species with lower specific root length occupied higher resource niches (Table 3.3), which is surprising, as high specific root length is thought to be related to acquisitive species that thrive under high resource conditions (Eissenstat and Yanai 1997). Yet variation in specific root length across species may reflect very specific species adaptations, and species with a low specific root length may increase water or nutrient uptake by producing more biomass or with mycorrhizal associations (Weemstra et al. 2020).

3.4.3 Functional traits were not associated with liana abundance

We hypothesized that in this humid, light–limited forest, conservative trait values that enhance shade tolerance (e.g., high wood density and low specific leaf area) would increase the abundance of liana species. Surprisingly, none of the traits had a significant effect on liana abundance except for stomatal density (Table 3.3, Figure 3.4). This was despite the fact that we included several traits belonging to the leaf economics spectrum and stem economics spectrum that are thought to be generally important for plant strategies and functioning (Wright et al. 2004, Chave et al. 2009). Tree studies have shown that under low light conditions, species with conservative trait values such as low SLA, high wood density and leaf dry matter content attain higher abundances at the sapling stage (Reich et al. 1997, Cornwell and Ackerly 2010) because they can retain their hardly acquired carbon for longer periods of time. Similarly, in Panama, these conservative traits are able to predict the abundance of trees, but not of lianas (van der Sande et al. 2019). Perhaps in this Panamanian study as well as in our study, no relationships between traits and liana abundance were found because relatively large lianas were studied (with a stem diameter > 1 cm) that most likely already have most of their leaves in the forest canopy, and hence, are not light limited. Stronger effects of light on lianas might be expected in the seedling stage, where more individuals are found in shaded conditions. Since traits are more strongly related to the regeneration niche than to the adult niche (Poorter 2007; van der Sande et al. 2015), the relationship between traits and abundance may also simply be absent for lianas at the adult stage. It is interesting that we found that stomatal density played an important role in shaping liana abundance. The mechanism of stomatal opening and closure is important for controlling water balance and leaf gas exchange (Düring 2015, Voelker et al. 2016). This may indicate that better water balance and leaf gas exchange control (denser but smaller stomates) would help these lianas to obtain a competitive advantage over species with large but fewer stomata in Xishuangbanna where experiences a half year dry period.

3.4.4 How functional are functional traits?

Plant functional traits and strategies can indeed explain species distribution, but not in a simple and straightforward way as we hoped for. This research shows that 1) global trait spectra can also be found in local plant communities, but part of these trait spectra can be uncoupled, 2) it is the underlying components, rather than plant strategies themselves that determine the species niche, and 3) different traits are important for different niches. Although the identification of global plant strategies has significantly advanced the field, this research shows that global, multivariate generalizations are difficult to translate to local conditions, as different components of these strategies are important under different local conditions. This brings us back to the key question about the functionality, validity, and predictability of the 'functional ecology approach'. Perhaps the field of functional ecology faces such a strong tension between generalization versus contextualization because functionality is, by definition, context dependent. This tension makes the field not only more complicated, but also more interesting and exciting.

3.5 CONCLUSIONS

We evaluated the functional trait associations and strategies among 29 lianas species, and the correlations between resource niches and functional traits. Lianas showed two orthogonal trait spectra, from tissue toughness and water conservation to tissue softness and rapid water acquisition, and a secondary spectrum in nutrient and carbon acquisition. Liana species with more acquisitive trait values occupied higher light and nutrient resource niches, but different traits were important for different niche dimensions. Surprisingly, traits were not associated with the water niche. Instead of local plant abundance, traits may better explain species distributions and their presence along gradients of resource availability.

3.6 ACKNOWLEDGEMENTS

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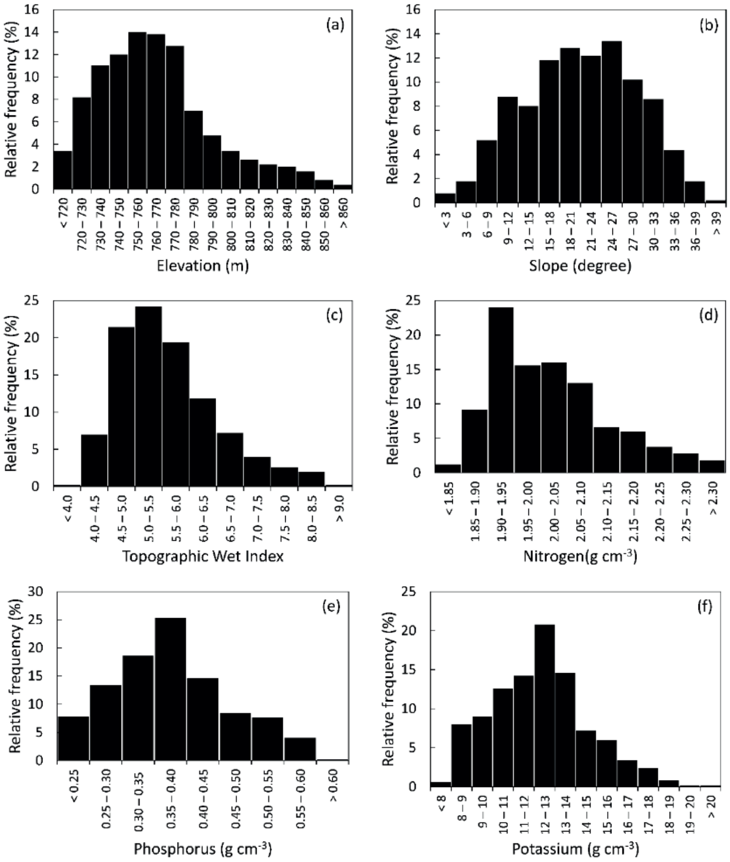
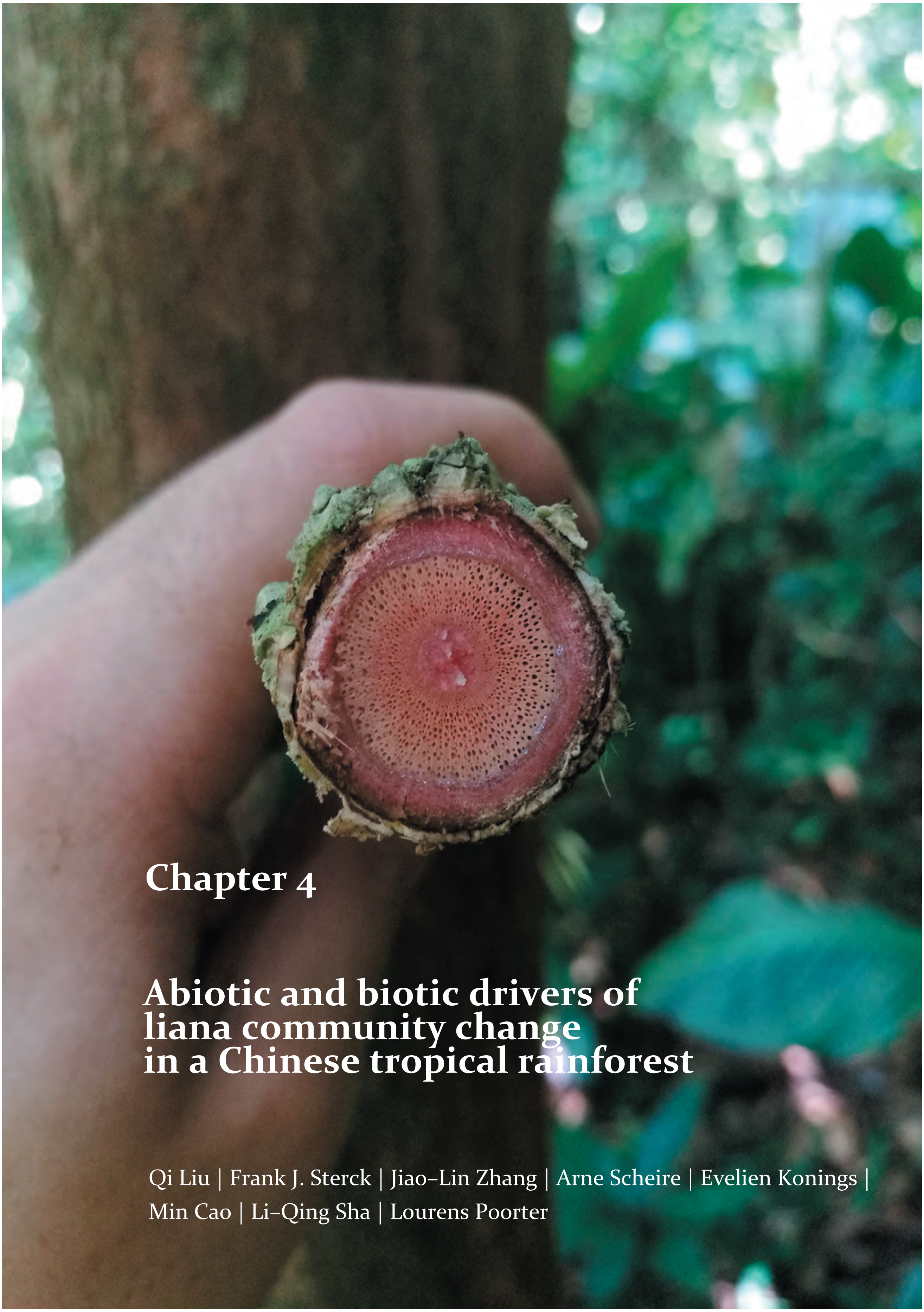
3.7 SUPPORTING INFORMATION

Appendix S3.1 Overview of the 29 dominant liana species in the Xishuangbanna 20–ha tropical seasonal rain forest dynamics plot: species, family, code, abundance and individuals sampled.

Species	Family	Code	Abundan	Sampl
Parameria laevigata	Apocynaceae	Pa_la	2386	12
Byttneria aspera	Malvaceae	By_as	1452	11
Fissistigma polyanthum	Annonaceae	Fi_po	990	10
Gnetum montanum	Gnetaceae	Gn_m	849	8
Combretum latifolium	Combretacea	Co_la	776	3
Sargentodoxa cuneata	Lardizabalace	Sa_cu	736	4
Uvaria kweichowensis	Annonaceae	Uv_k	698	5
Strychnos angustiflora	Loganiaceae	St_an	694	10
Spatholobus uniauritus	Leguminosae	Sp_un	693	6
Callerya pachyloba	Leguminosae	Ca_pa	490	6
Benkara sinensis	Rubiaceae	Be_si	464	10
Tetrastigma cauliflorum	Vitaceae	Te_ca	437	13
Uncaria macrophylla	Rubiaceae	Un_m	433	11
Uncaria laevigata	Rubiaceae	Un_la	430	9
Tetrastigma planicaule	Vitaceae	Te_pl	369	7
Tetrastigma jinghongense	Vitaceae	Te_ji	346	11
Embelia undulata	Primulaceae	Em_u	277	10
Premna scandens	Lamiaceae	Pr_sc	267	9
Dalbergia stipulacea	Leguminosae	Da_st	241	13
Tetracera sarmentosa	Dilleniaceae	Te_sa	238	7
Tetrastigma obovatum	Vitaceae	Te_ob	214	7
Tetrastigma	Vitaceae	Te_xi	200	4
Capparis fohaiensis	Capparaceae	Ca_fo	193	8
Uvaria tonkinensis	Annonaceae	Uv_to	175	3
Strychnos nitida	Loganiaceae	St_ni	173	8
Zanthoxylum laetum	Rutaceae	Za_la	165	6
Piper flaviflorum	Piperaceae	Pi_fl	143	11
Roureopsis emarginata	Connaraceae	Ro_e	143	6
Kadsura heteroclita	Schisandrace	Ka_he	108	3

Appendix S3.2 Relative frequency of 6 environmental variables in the Xishuangbanna season tropical rain forest: a) elevation, b) slope, c) topographic wet index, d) soil N concentration, e) soil P concentration, f) soil K concentration. The histograms are based on the values of 500 20 x 20 m^2 quadrats within the 20–ha forest plot. Nutrient concentrations are expressed per unit soil volume.





Chapter 4

Abiotic and biotic drivers of liana community change in a Chinese tropical rainforest

Qi Liu | Frank J. Sterck | Jiao–Lin Zhang | Arne Scheire | Evelien Konings |
Min Cao | Li–Qing Sha | Lourens Poorter

ABSTRACT

Global change is impacting forests worldwide. Most studies on tropical forest dynamics have focused on trees, whereas the role of lianas is often overlooked. Here we evaluate for a Chinese tropical rainforest whether liana abundance is increasing and assess the underlying putative mechanisms.

We monitored from 2013–2019 >20,000 lianas in a 20–ha dynamics plot, and analyzed how changes in liana communities within twenty 1–ha plots were driven by underlying vital rates (recruitment, growth, survival), abiotic factors (slope, light gaps, water, and soil phosphorus), biotic factors (tree and liana basal area), and the functional composition of liana communities based on 18 traits.

During the 5 years period, liana abundance decreased with 12.6% because of high mortality of small lianas, whereas liana basal area increased with 5.8% because of high survival and growth of large lianas. Liana communities showed a spectrum of slow to fast carbon and nutrient use, and a spectrum from slow to fast water use. Abiotic environmental factors (i.e., elevation and soil phosphorous and water) and liana functional composition influenced liana demographic processes, whereas competition by lianas and trees had little effect.

Over the 5 years period the liana community changed toward more, large, acquisitive lianas with rapid water use. This indicates that the liana community is undergoing succession, possibly driven by increased CO_2 fertilization.

4.1 INTRODUCTION

Global change is impacting forests worldwide, threatening biodiversity and ecosystem services. Understanding how forests respond to climate change is critical to make informed management decisions about forest conservation and climate change mitigation (Anderson–Teixeira et al. 2015). Most studies on tropical forest dynamics have focused on trees, whereas the role of lianas (i.e., woody vines) tends to be overlooked, probably because liana dynamics are monitored in only a few permanent sample plots (Schnitzer 2018, but see e.g., Phillips et al. 2002, Bongers et al. 2020). This is surprising because lianas are particularly abundant and diverse in tropical forests, where they comprise ca. 25% of the woody individuals and woody species (Schnitzer and Bongers 2002, Schnitzer et al. 2012), and contribute up to 40% to forest leaf area (Wright et al. 2004). Recent studies suggest that global change has led to an increase in liana abundance in several tropical forests (Laurance et al. 2014, Schnitzer et al. 2012, Yorke et al. 2013). Because lianas suppress the growth and abundance of trees (Peña–Claros et al. 2008, Visser et al. 2018) this may lead to a decline in forest ecosystem productivity and carbon storage (Lewis et al. 2004, van der Heijden et al. 2013). Here we evaluate for a Chinese tropical rainforest whether liana abundance is indeed increasing and assess the underlying putative mechanisms.

Several factors have been proposed to explain the increase in lianas in tropical forest, for instance, increased disturbance, stronger seasonal droughts, increasing atmospheric CO_2, and increasing nutrient deposition (Putz, 1984, Phillips et al. 2002, Schnitzer 2005). Many studies have shown that liana abundance and basal area are increasing in Neotropical forests (e.g., Laurance et al. 2014, Phillips et al. 2002, Schnitzer et al. 2012), whereas liana abundance was stable in the United States (Londré and Schnitzer 2006), and decreased in Africa (Bongers et al. 2020; Caballé and Martin, 2001, Thomas et al. 2015). Perhaps the patterns are erratic because local drivers (i.e., disturbance) may override more global drivers (Bongers et al. 2020). The lack of consensus about large–scale patterns in liana change and its possible drivers urges for additional studies on lianas dynamics covering a wider geographic range (Gerolamo et al. 2018). Here, we focus on liana community dynamics in a tropical seasonal rainforest in an understudied region (Asia, but see Wright et al. 2015, Roeder et al. 2019) and global biodiversity hotspot (Myers et al. 2000).

Changes in liana abundance and basal area are the result of underlying demographic processes (i.e., vital rates) such as recruitment, growth, and survival, that can inform about the drivers of change (Figure 4.1). These demographic processes may be driven by abiotic and biotic factors. Abiotic factors that reflect resource availability, such as light gaps, water availability, and soil nutrients, may all increase vital rates, whereas biotic factors such as competition for limiting resources by lianas and trees may reduce vital rates. For example, plot tree basal area was associated with increased growth but decreased recruitment of trees in a tropical moist forest (van der Sande et al. 2017). The responses of plants to global change and local conditions are shaped to a large extent by their functional traits, i.e., plant characteristics that have a direct impact on plant recruitment, growth and survival (Violle et al. 2007, Kunstler et al. 2016). There is a global spectrum of plant strategies, ranging from 'slow' species with conservative traits (e.g., a low specific leaf area, SLA) that increase resource conservation and plant survival, to 'fast' species with acquisitive trait values (e.g., high SLA) that increase light capture and growth (Poorter and Bongers 2006, Sterck et al. 2006, Reich 2014, Diaz et al. 2016). The average trait value in a plant community, should therefore be a good indicator how plants respond to global change (Soudzilovskaia et al., 2013, van der Sande et al. 2016) and drive community dynamics (Poorter et al. 2017). Few studies have explicitly linked multiple abiotic and biotic factors to liana demographic processes (but see Gerolamo et al. 2018). Gerolamo et al (2018) found that lianas were more abundant in fertile soils, in valleys because they were close to the water table, and with higher tree turnover. To our knowledge, our study is the first one that simultaneously evaluates the relative importance of abiotic environmental factors, forest structure, and community trait composition on liana community dynamics.

Here, we evaluated over a 5–year period the dynamics of all lianas in a 20–ha tropical rainforest in Xishuangbanna, SW China. We determined population change of all liana individuals and their basal area together and related these to underlying vital rates (mortality, recruitment, and growth). We addressed the following questions: (1) How is the liana community changing in terms of stem density and basal area? (2) Are these changes accompanied by changes in functional traits of the liana community? (3) Can we explain those changes from the underlying mechanism? For the first two questions we focus on overall temporal changes from 2014 till 2019. For the third question, we use the spatial variation among the twenty 1–ha plots to better understand how liana communities' changes are driven by underlying vital rates, abiotic resources (e.g., light water and nutrients), forest structure and competition (i.e., trees and lianas basal area), and the functional composition of liana communities (Figure 4.1).

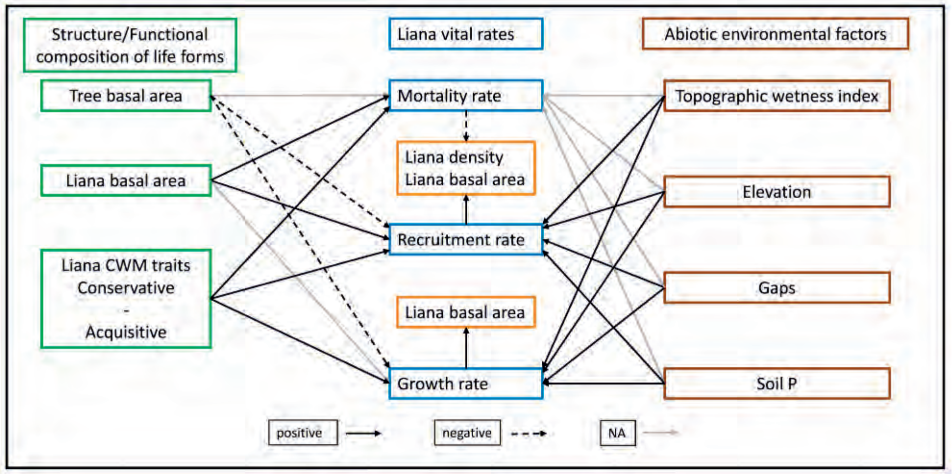


Figure 4.1 Conceptual framework showing how forest structure (i.e., tree and liana communities, green boxes), liana functional composition (i.e., leaf, stem, and root traits, green boxes), and abiotic environmental factors (i.e., topography, gaps, water, and soil nutrients, brown boxes) may affect liana vital rates (i.e., mortality, recruitment, and growth rate, blue boxes) then result in changes of the liana density and basal area (orange box). Tree basal area is based on all trees in the 20 1–ha plots in 2012, liana basal area is based on all lianas in 20 1–ha plots in first census (August 2013 to March 2014). Community–weighted mean functional traits of liana communities are based on 29 abundant liana species. Hypothesized positive effects are indicated by black solid lines and hypothesized negative effects are indicated by black dashes lines. NA indicates no significant effect (grey solid lines).

4.2 METHODS

4.2.1 Research site

This study was carried out in the 20–ha Xishuangbanna Forest Dynamics Plot (FDP) in Yunnan Province, southwest China (101°34'2"–47"E, 21°36'42"–58"N). The area is characterized by warm–wet air masses from the Indian Ocean and continental air masses from the sub–tropical regions in summer and winter respectively, which results in an alternation of dry and rainy seasons with a typical monsoon climate. Mean annual rainfall is 1 493 mm and mean annual temperature is 21.8°C (Cao et al. 2006). The main soil type is laterite (Cao et al. 2006). The topography of the plot is heterogeneous with elevation from 709 m to 869 m a.s.l and is trisected by three perennial streams that join in the southwest of the plot (Lan et al. 2009). The plot is 400 m in width and 500 m in length, which is divided into 500 20 m × 20 m quadrats. The vegetation in this area is a tropical seasonal rainforest with a canopy height of up to 60 m (Zhu 2006). The first two tree censuses were held in 2007 and 2012. The measurement, mapping and identification of the species were carried out for all the freestanding woody stems ≥ 1 cm in diameter at breast height (DBH, Condit 1998). In total > 95,000 free–standing individuals were identified to species level, which is dominated by *Parashorea chinensis* (Dipterocarpaceae), *Pittosporopsis kerrii* (Icacinaceae) and *Garcinia cowa* (Clusiaceae) (first census data; Lan et al. 2011).

4.2.2 Liana census data

From August 2013 to March 2014, all rooted lianas diameter ≥ 1 cm were tagged, mapped, measured to individual level in 500 20 m × 20 m quadrats in the 20–ha plot. We spatially mapped the rooting point of each liana. The rooting point was defined as the last substantial rooting point before the stem ascends. If the stems were connected below the soil surface, then we considered them to be independent stems. There were multiple stems in our study, but their roles seem to be functionally equivalent in the dynamics and effects on trees, and therefore they are treated separate individuals in the analysis (Schnitzer and Carson 2001). We included all liana species with woody or fibrous perennial stems (e.g., *Desmoncus, Gnetum, Smilax, Dioscorea*), but excluded epiphytes, hemi–epiphytes, and climbing bamboos (Gerwing et al. 2006, Schnitzer et al. 2008). We identified all lianas to species level in the field using a combination of leaves, bark, and trunk characteristics. For each species, we account their numbers of stems in each quadrat as the abundance data, then the abundance in each of the 500 quadrats was calculated. All liana individuals were recensused from December 2018 to March 2019. At recensus, it was checked whether individuals were alive or dead, the diameter of alive individuals was measured (same place where has marked with red paint in first census), and newly recruited individuals (diameter

≥ 1 cm) were recorded.

4.2.3 Population change, vital rates

Population change and vital rates were determined at the community level for all lianas DHB ≥ 1 cm in 20 100 m × 100 m plots in the 20–ha plot. We calculated liana individual density and basal area for the two censuses (2014 – 2019). To examine temporal changes in population density we calculated density change (DC): the ratio of the abundance in 2019 over the abundance in 2014. DC > 1 indicates a population increase, DC < 1 a population decrease, and DC = 1 indicates a constant population size. To assure a symmetric distribution around 1 of the compare increases and decreases (i.e., 0.5 and 2 have the same deviation from 1, Bongers et al. 2020), we ln–transformed DC into lnDC, and a lnDC of zero indicates a ratio of 1, and hence, no change. Annual mortality rates (MR) were calculated as $1-(N_{ST}/N_0)^{1/T}$ (Sheil et al. 1995), where N_0 and N_{ST} refer to the number of individuals recorded in the initial census and the number of surviving individuals that were present in the final census. T is the interval period in years. Annual recruitment rates (RR) were calculated as $1-(N_{ST}/N_T)^{1/T}$ (Sheil 1998), where N_T is the number of individuals recorded in the final census. This final density–based annual recruitment rate was used in this study because it has been widely employed in forest–tree census analysis and this rate denotes the proportion of stems that were not present a year before, which has the advantages that this rate is related to instantaneous recruitment only (Kohyama et al. 2018). Both mortality rate and recruitment rate can range between 0 and 1. Average growth rate (mm yr^{-1}) is calculated as $(DBH_2 - DBH_1)/T$, where DBH_1 and DBH_2 are the diameter of the individuals at the initial and final census. Average liana diameter growth values were calculated by averaging across all individuals together.

At basal area–based level, same variables were calculated, for each plot, basal area change was calculated as the ratio of the basal area at the 2019 over the basal area at the 2014, and also natural log transformed BC into lnBC. Basal area–based annual mortality rate was calculated as $(BA_D/BA_0)/T$, where BA_0 refers to the basal area of individuals recorded in the initial census and the BA_D refers to the basal area of death individuals that were present in the initial census. T is the interval period in years. Basal area–based annual recruitment rate was calculated as $(BA_R/BA_0)/T$, where BA_R is the basal area of new individuals were presented in final census period. Average basal area growth rate (mm^2 yr^{-1}) is calculated as $(BA_2 - BA_1)/T$, where BA_1 and BA_2 are the basal area of the individuals at the initial and final census.

4.2.4 Functional traits

To evaluate if liana performance is related to the functional traits of the liana community, we measured 18 functional leaf– stem– and root traits that are important for liana performance and liana response to putative drivers of liana change (i.e., disturbance, drought, and CO_2 fertilization, Table 4.1). To quantify liana community trait values, we selected 29 of the most common liana species in the plot (with a density > 5 stems/ha) that represent 71% of the liana individuals in the plot (Liu et al. 2017). For each species, on average N individuals (range 3 to 12) were randomly selected from the plot data base (231 individual samples in total) to avoid bias towards individuals thriving in high resource availability. From October 2018 to December 2018, a ca. 40 cm long branch was sampled from the main stem. For accessibility reasons, the branch was sampled between 3 to 8 m height, in the lower forest stratum. In case the branch did not have enough leaves for all analyses, additional branches were collected from the same individual to obtain additional leaves. Only samples from healthy–looking and pest–free individuals with a diameter more than 1 cm were selected. For more details about collection and measurements of these morphological and anatomy traits, see Liu et al (unpublish data).

Table 4.1 Overview of 18 functional traits studied: groups of variables, name, units, abbreviations.

Trait name	Units	Abbreviation
Leaf traits		
Leaf thickness	mm	LT
Leaf area	mm^2	LA
Specific leaf area	$mm^2\ mg^{-1}$	SLA
Leaf dry–matter content	$mg\ g^{-1}$	LDMC
Leaf density	$mg\ mm^{-3}$	LD
Vein density	$mm\ mm^{-2}$	VD
Stomatal density	$\#\ mm^{-2}$	SD
Stomatal length	Mm	SL
Stomatal pore index (SL^2 x SD)		SPI
Leaf Nitrogen concentration	$mg\ g^{-1}$	N
Leaf Phosphorus concentration	$mg\ g^{-1}$	P
Leaf Potassium concentration	$mg\ g^{-1}$	K
Leaf Magnesium concentration	$mg\ g^{-1}$	Mg
Leaf Zinc concentration	$mg\ g^{-1}$	Zn
Leaf Nitrogen to Phosphorus ratio		N:P
Stem traits		
Wood density	$g\ cm^{-3}$	WD
Vessel diameter	µm	VesDiam
Root traits		
Specific root length	$m\ g^{-1}$	SRL

4.2.5 Abiotic environmental factors

To evaluate if liana performance is related to abiotic environmental factors, we used for performance–related environmental factors that are important for responses to drought, disturbance, fertilization: elevation, gap, topography wetness index, and soil P. For each 1–ha plot, elevation, topography wetness index and soil P were calculated and measured at the quadrat level (i.e. 25 20m × 20m quadrats), and then averaged for the 1–ha plot.

Topography and soil variable were based on the protocols indicated in John et al. (2007), which was determined at quadrat level, i.e., 500 20m × 20m quadrats. For each quadrat, the elevation and slope were measured following Harms et al. (2001): the elevation was calculated as the mean of the elevation at the four quadrat corners and the slope was based on the mean angular deviation from the horizontal of each of the four triangular planes formed by connecting three corners. Preliminary analyses indicated that the 3 topographic variables (i. e., elevation, slope, convexity) showed similar associations with liana performance. To simplify our statistical model, we therefore used only elevation for the further analyses.

Soil data was previously collected by Hu et al. (2012). The soil data include soil pH, organic matter content, total nitrogen, total phosphorus, total potassium, ammonium nitrogen, extractable phosphorus, exchangeable potassium, soil bulk density. Soil sample were collected from a regular grid of 30 × 30 m in the 20–ha plot. We used 252 nodes from these grids as sampling points. Two additional sampling points were created at random combinations of 2 and 5 m, 2 and 15 m or 5 and 15 m along a random compass bearing away from each grid point. We removed the litter and humus layer from these sampling points and collected 500 g topsoil at 0 – 10 cm depth, as the topsoil layer is most nutrient rich, and plant obtain most soil nutrients from the topsoil. We collected 756 fresh soil samples and transported them the Public Technology Service Centre, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences and analysed for soil nutrients. Using original soil data, an ordinary kriging was performed to generate a sub–quadrat map of 10 m x 10 m for each soil variable (Cressie 1992). The soil nutrients for each 400–m^2 quadrat were calculated as the mean of the values at each of the nine nodes of the 10 m × 10 m sub–quadrats within that quadrat by using the geoR package in the R (see Hu et al., 2012). Element concentrations were expressed on a volume basis (g cm^{-3}) rather than a mass basis (Ellert and Bettany 1995) because it indicates the plant nutrient availability per unit soil volume that can potentially be explored by plant roots. To calculate plant nutrient availability per unit soil volume, total and available, N, P and K were multiplied by the soil bulk density. A bi–variate Pearson correlation showed that most soil factors were associated (Liu et al. 2020). Our previous studies proved that soil P was one of the most important nutrients in shaping liana distribution (Liu et al.2020). Thus, in this study, we only consider soil P.

Spatial topographic information was used to quantify the water niche. We used the topographic wetness index (TWI) to describe the water niche of the species. This index is defined as TWI=ln(α/tan β), where α is the local upslope area draining through a certain point per unit contour length and tan β is the local slope in radians (Beven and Kirkby 1979). The specific catchment area is a parameter describing the tendency of the site to receive water from upslope area and local slope is a parameter describing the tendency to drain water (Gruber and Peckham 2009). This index is therefore a relative measure of the long–term soil moisture availability of a given site in the landscape and high TWI indicates a strong water accumulation. In ArcGis Desktop 10.6.1, we used the Flow Accumulation tool to calculate α and the slope tool to calculate β.

To evaluate the role of gap disturbance in liana performance, we inferred for each quadrat, light conditions based on forest structure. The quadrat was assigned as a "gap" when the canopy cover in the year 2014 was less than 50% (Liu et al. 2014). For each plot, the percentage of gap quadrats was used to quantify the light and disturbance condition.

4.2.6 Statistical analyses

All statistical analyses were performed using RStudio and R 3.6.2 (R Core Team, 2019). To compare the liana community between the two census periods, a paired samples t–tests was carried out, using the compare_means function of the ggpubr package in R.

Forest structure was quantified for each 1–ha plot using the tree basal area in 2012 and liana basal area in 2014. Because liana and tree census are done ca. every 5 years, and the liana and tree censuses are not carried out at the same time, different reference years were used. Tree basal area (m^2 ha^{-1}) and liana basal area were calculated using all tree resp. liana individuals DBH ≥ 1 cm in each plot.

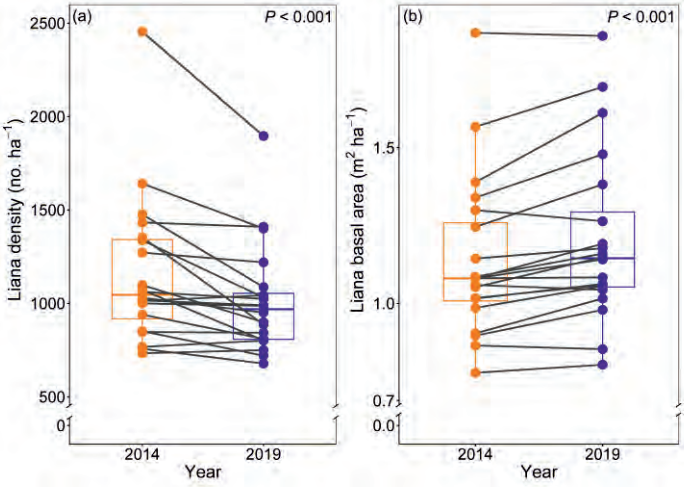
For the functional trait analysis, we compiled a data set with species mean values for all measured plant traits (see Table 4.1). Eight traits (LA, SLA, SD, SL, K, Mg, Zn, VesDiam) were ln–transformed prior to analysis, to achieve normality. Because SRL data were missing for 4 species, we used the package "missMDA" to impute missing values (3 missing values), thus yielding a data set of 18 functional traits for 29 liana species. We then calculated for each 1–ha plot the community–weighted mean (CWM) trait values for census year 2014 and 2019, based in the average value of a given trait with a plot weighted by the relative abundance of each species in 2014 and 2019. Species for which no trait were calculated were not included in the analysis (i.e., the analysis is only based on the 29 species). CWM traits were calculated for each trait in each of the k plots as $CWM_k = \sum_{i=1}^{S} a_{ik}\, t_i$, where a_{ik} is the relative abundance of specie i in plot k , t_i is the traits value of species i, and S is the number of species which have traits data. To evaluate how CWM traits are associated, a principal component analysis (PCA) was carried out. These traits data were transformed by “scale” function in R, The result is that the values in the transformed variable have the same relationship to one another as in the untransformed variable, but the transformed variable has mean 0 and standard deviation 1.

To test the impacts of forest structure, liana functional strategies and abiotic environmental factors on the estimates of density–based and basal area–based liana performance (ln density change, mortality, recruitment, and growth). To predict liana community performance, a multi–model linear regression comparison was used, by fitting all possible combinations of tree basal area in 2012, liana basal area in 2014, CWM traits of PCA components (PC1 and PC2) from 2014, abiotic environmental factors (Elevation, Gap, TWI, and soil P) as the explanatory variable. CWM trait composition in 2014 was used here because it would be better to use initial data as predictors. For the multi–model comparison, the dredge function of the MuMIn package was used (Barton 2012). Next, we selected the best–fitting models (lowest AICc < 2) for both density–based and basal area–based liana performance.

4.3 RESULTS

4.3.1 Population change

The total number of liana individuals declined 12.6% over the 5–years, from 23,155 stems in 2014 to 20,231 stems in 2019. Liana density declined significantly over time (1157.75–1011.55 individual ha^{-1}; paired t–test, $p < 0.001$, N = 20 plots), while liana basal area increased with 5.8% from 22.75 m^2 in 2014 to 24.06 m^2 in 2019 (1.14 –1.20 m^2 ha^{-1}; paired t–test, $p < 0.001$, N = 20 plots, Figure 4.2).



Fugure 4.2 Changes in liana community structure in a seasonal tropical rain forest in Xishuangbanna, SW China. Density (a) and basal area (b) per hectare are shown for two censuses (2014 and 2019). Each dot represents absolute density or basal area in a 1–ha plot (N=20). Light grey lines connect the measurements of the same plot. Significance levels (*p*) of a paired samples T–test is shown.

4.3.2 Population change and vital rate

Liana density change is mostly driven by mortality rate ($R^2 = 0.90$, $p < 0.001$) while it increases with recruitment rate ($R^2 = 0.28$, $p = 0.016$). Density change is not related to average liana diameter growth rate in the plots ($R^2 = 0.01$, $p = 0.622$) (Figure 4.3).

Similarly, liana basal area change is main driven by mortality rate ($R^2 = 0.83$, $p < 0.001$) where a high mortality leads to a smaller basal area increase or even a decline. Liana basal area change was not significantly related to recruitment rate ($R^2 = 0.00$, $p = 0.930$) or average liana basal area growth rate in the plot ($R^2 = 0.13$, $p = 0.122$) (Figure 4.3).

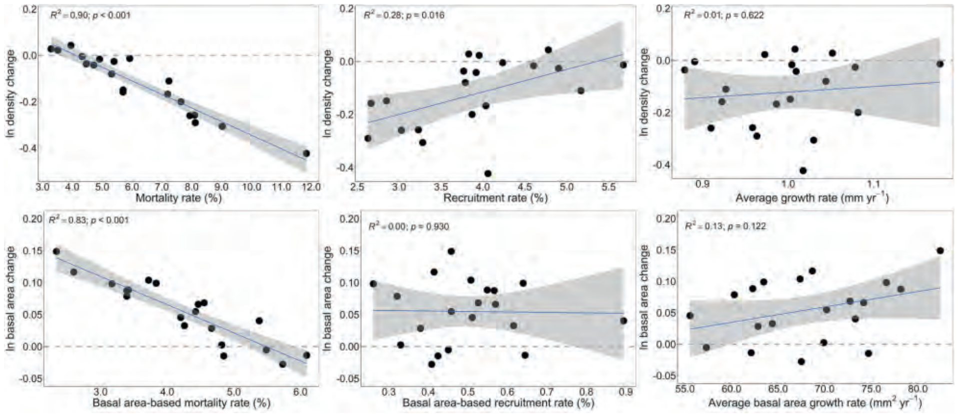


Figure 4.3 Relationships between density change (lnDC) and (a) mortality rate, (b) recruitment rate, and (c) average growth rate, and correlations between basal area change (lnBC) with basal area–based (d) mortality rate, (c) recruitment rate, (e) average basal area growth rate for all liana individuals over 5–years in Xishuangbanna seasonal tropical rain forest, China. The horizontal red line indicates zero change. Linear regressionds, coeffiecients of determination (R^2), significance level (*p*), and 95% confidence interval (grey area) are shown.

4.3.3 Liana dynamics across diameter size classes

The highest density of lianas (~35%) was concentrated in the smaller size class (10–20 mm diameter). On average, this class experienced the highest absolute reduction in density across censuses, from 428 to 349 individual ha^{-1}(i.e., –18%), followed by size classes 20–30 mm, with a reduction of 291 to 226 individual ha^{-1}(–22%) and size class 30–40 mm, with a reduction of 179 to 158 individual ha^{-1} (–12%, Figure 4.4). The larger size classes lianas (diameter ≥ 70 mm) experienced a significant increase after 5–years (Figure 4.4).

Liana basal area peaked in the intermediate diameter size classes in both censuses. Similarly, liana basal area experienced a significant decrease in small size classes (diameter < 40 mm) and significant increase in large size classes (diameter ≥ 70 mm) (Appendix S4.1).

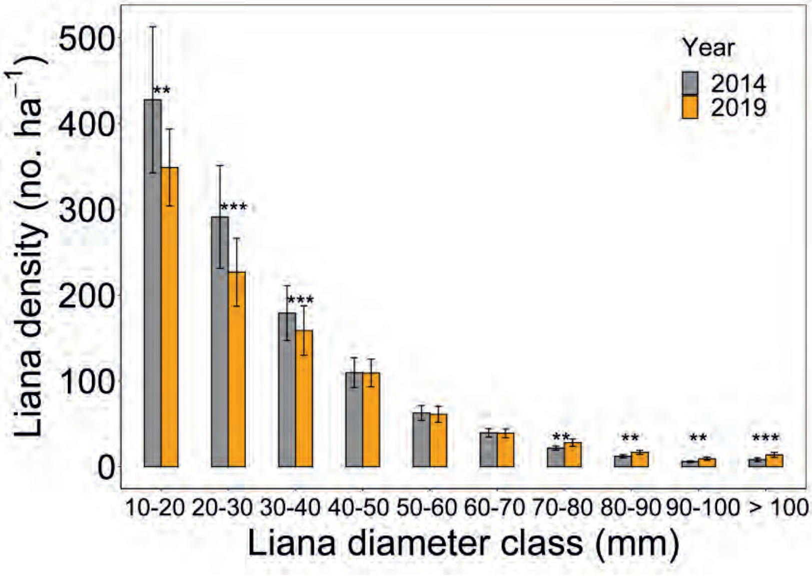


Figure 4.4 Mean (± 95% confidence interval) of liana density per diameter class in 20 1–ha plots in Xishuangbanna tropical seasonal rain forest, SW China. In white, data from the first census (2014, *n* = 23155); in grey, data for the second census (2019, *n* = 20231). Asterisk indicates significant differences between censuses of a paired samples T–test. ** indicates $p < 0.01$, *** indicates $p < 0.001$, ns indicates $p > 0.05$.

4.3.4 *CWM trait dynamics and strategies*

Liana functional composition of the 20 plots was analyzed using a principal component analysis (PCA) of 18 CWM traits. The first PCA axis (PC1) explained 48.8 % of the variation and showed a slow–fast spectrum in carbon and nutrient use. Communities at the left had 'slow' traits, with tough and persistent stem (WD) and leaf (LDMC) tissues that conserve carbon and nutrients. Communities at the right side had 'fast' traits, with wide vessels (VesDiam), high specific leaf area (SLA), specific root length (SRL) that allow to forage for light and nutrients, and high nutrient concentrations that facilitate high metabolic activity and growth. The second PCA axis (PC2) explained 25.2 % of the trait variation, which showed a trait spectrum from slow (at the bottom) to fast (at the top) water use. Communities at the top possess wide vessels (VesDiam) and large stomata (SL) and thick fluffy leaves (LT, Figure 4.5) that increase water transport and gas exchange. Over the 5 year period, liana communities showed a significant increase in the multivariate axis scores on PC1 and PC2 which indicates that over time communities have become more acquisitive in terms of carbon, nutrient, and water use (Figure 4.5; paired t–test, df=19, p < 0.001 for PC1, and p = 0.001 for PC2, appendix S4.3). Interestingly, communities that were already acquisitive in carbon and nutrient use at the start of the monitoring period (i.e., communities at the right side of PC1) showed the largest changes over time, whereas conservative communities with low PC1 scores showed little change over time. Specifically, communities with slow water use (lower right quadrant) showed especially large increases in water use (PC2), whereas communities with fast water use (upper right quadrant) showed especially large increases in carbon use (PC1).

A PCA based on basal area–weighted CWM trait values showed similar trait spectra, with PC1 explaining 40.1% of the community trait variation and PC2 explaining 20.3% (Appendix S4.2). Over the 5 year period communities also showed a significant increase in PC1 and PC2 axis scores of the basal area weighted trait values (Appendix S4.2; paired t–test, df=19, $p < 0.001$ for PC1, and $p < 0.001$ for PC2, Appendix S4.3).

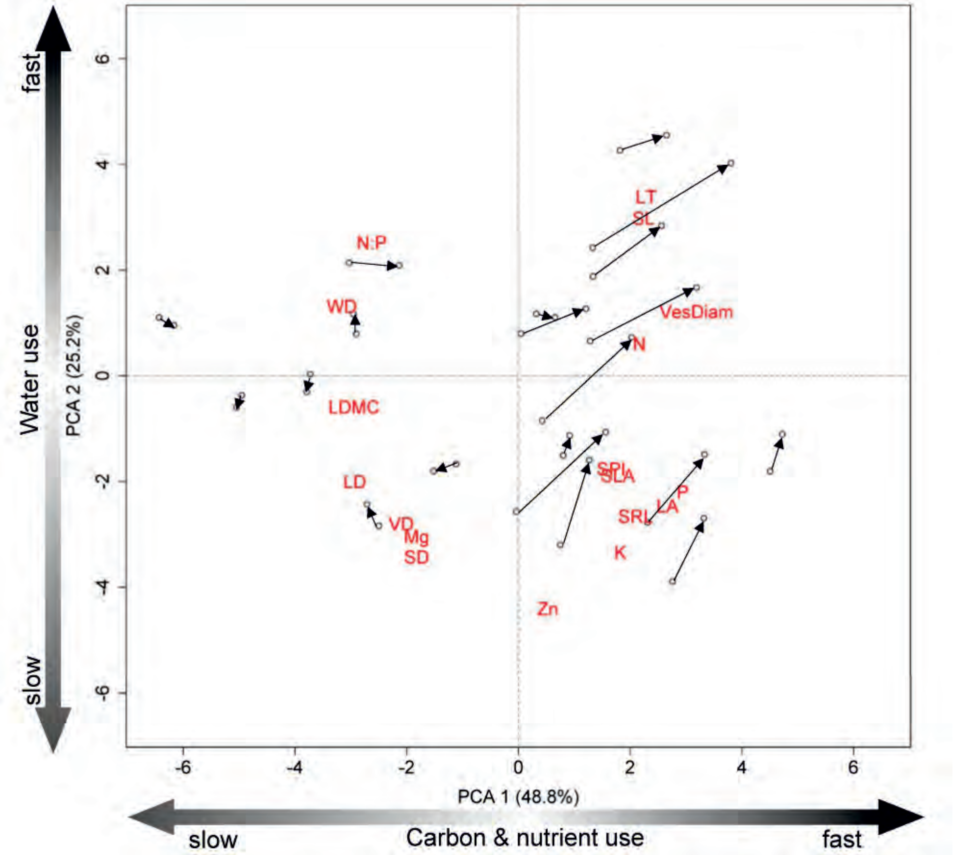


Figure 4.5 Principal component analysis (PCA) of density–based community weighted mean (CWM) traits of liana communities in 2014 and 2019 in a tropical seasonal rain forest in Xishuangbanna, SW China. The first two PCA axes are shown, reflecting variation in slow to fast carbon and nutrient use (PC1) and water use (PC2). Each dot represents the regression score of a 1–ha plot (N = 20). The arrows show for each plot the change of PCA axes loading scores over the 5–years period. Red labels represent CWM traits loadings. For trait abbreviations see Table 4.1.

4.3.5 Drivers of liana community change

We evaluated to what extent forest structure, functional trait strategies of liana communities, and abiotic environmental factors can predict liana community change, by comparing the 20 1–ha plots. Unexpectedly, competition by trees and lianas (i.e., tree basal area and liana basal area) did not affect liana performance. Instead, lianas survived better in the site with abundant lianas (low mortality rate, Figure 4.6). Liana community trait values are good predictors of liana community change. Liana communities with fast carbon and nutrient use (high values of PC1) had higher mortality rate and, therefore, a stronger decline in density. Liana communities with a faster water–use (i.e., high values of PC2) had a higher recruitment rate, a lower mortality rate, and, hence, a significant increase in liana density (Figure 4.6). Lianas located in higher elevation site have a higher recruitment rate and fast growth rate but did not show a difference in mortality rate and density change (Figure 4.6). Soil P had a significant positive effect on liana recruitment (Figure 4.6). Surprisingly, neither gaps nor water availability (TWI) had a significant effect on the performance of liana communities (Figure 4.6).

Similar but weaker relations between liana vital rates and its drivers were found when analyzing basal area change. Regarding abiotic environmental factors, positive relationships between elevation and liana recruitment and growth were retained. In this analysis, competition by trees decreased the liana basal area growth rate (Appendix S4.4).

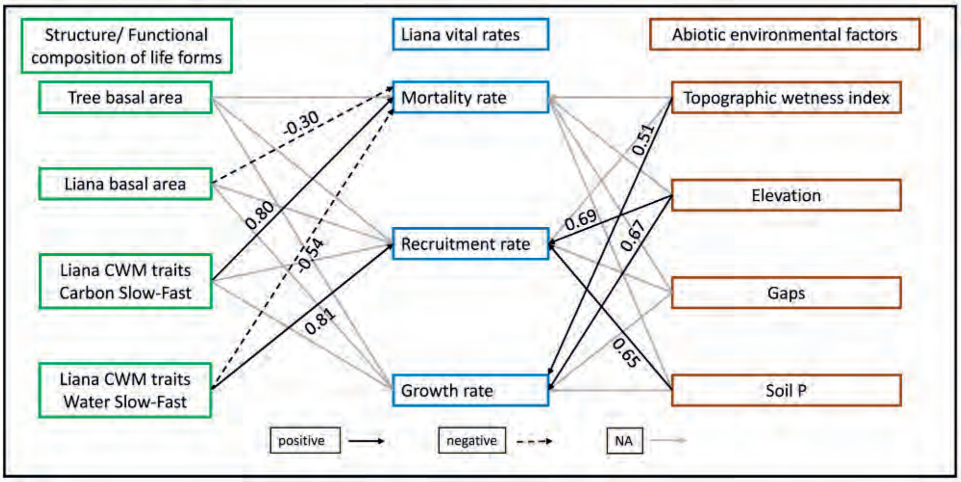


Figure 4.6 Regression models predicting the effects of competition (i.e., tree basal area and liana basal area; green boxes), liana functional traits (i.e., PC1 and PC2, green boxes), and abiotic variables (i.e., Elevation, Gaps, soil P, Topographic Wetness Index, brown boxes)) on liana performance (i.e., mortality rate, recruitment rate, and growth rate, blue boxes), based on all possible subset combinations of all variables. The best models are selected with the lowest AICc. Liana vital rates were calculated based on liana density; 20 1–ha plots are used as units of replication. The values next to the arrows indicate the regression coefficients of the variables. Positive effects are indicated by black solid lines and negative effects are indicated by black dashes lines. NA indicates no significant effect (grey solid lines).

4.4 DISCUSSION

We evaluated how liana communities changed over time and assessed the underlying putative mechanisms. During the 5 years period, liana density decreased, liana basal area increased, and liana communities became more acquisitive. The decline in liana density was strongly driven by mortality rate and occurred in the smallest size classes, whereas liana density increased in large size classes. Abiotic environmental factors (i.e., elevation and soil resources) and liana functional composition influenced liana demographic processes, whereas competition by lianas and trees seemed to have little effect.

4.4.1 Liana community changes in Xishuangbanna

Lianas are found to increase in abundance in Neotropical forests, which may be driven by an increase in forest disturbances, CO_2 or nutrient fertilization, or drought (Schnitzer and Bongers 2011, Schnitzer 2015). In our Asian forest the liana community was also changing, but with a significant decrease in density and increase in basal area (Figure 4.2). These changes in liana structure suggest that the liana community is undergoing succession, with a decrease of lianas in the lower size classes because of a lack of recruitment and self–thinning, and an increase in lianas in the larger size classes due to basal area growth (Figure 4.4). The decline in liana density was mostly driven by increased mortality rate.

Mortality rate is the vital rate with the strongest impact on liana density, because it can affect lianas from all size classes, and hence, the whole population, whereas recruitment can only affect the youngest size classes, and has therefore less effect on the whole population.

Disturbance – At first sight, the observed changes in liana structure suggest that the community is undergoing regular succession after disturbance, where growth leads to an increase in liana basal area but mainly in larger individuals (Figure 4.2 and 4.4, Appendix S4.1) which, in turn results in shading and self–thinning of smaller individuals and a decrease in overall liana density (Figure 4.2 and 4.4, Appendix S4.1). Yet, succession after disturbance would also lead to a shift in liana community composition, where fast–growing light demanding lianas with acquisitive trait values are replaced by slow growing shade tolerant lianas with conservative trait values. Instead, our results indicate that liana communities are shifting towards *faster resource use* strategies, not only in terms of light and carbon (PC1, Figure 4.5), but also in terms of water use (PC2, Figure 4.5). This suggests that in our forest liana change is not driven by local disturbances (cf. Bongers et al. 2020), but by global change, and that the largest lianas benefit most from this global change.

Droughts – Increased frequency of droughts is often mentioned as a reason for global liana increase. Lianas are thought to have a dry season growth advantage over trees (Schnitzer 2005), because they have to invest less in a self–supporting stem and could instead invest that carbon in deeper roots, thus getting access to water from deeper soil layers during drought (Schnitzer 2018). In our forest, drought is not likely to have played a role; else communities with conservative water use would have benefited most. Instead, we found that liana communities with fast water use (PC axis 2) benefited most as they had a stronger increase in recruitment and decrease in mortality (Figure 4.6), and liana communities showed an increase in water use traits over time (Figure 4.5, Appendix S4.2 and S4.3). Water availability is especially important for tall lianas that are in the canopy, have longer hydraulic pathlengths, and face stronger atmospheric drought. Maybe strong droughts are less important in our forest because their effect is mitigated by the occurrence of fogs during the dry season.

CO_2 and N fertilization – Fertilization through increased CO_2 concentration and N deposition could indeed have led to increased basal area growth and could explain why the communities have become more acquisitive over time. Generally, increases in nitrogen results in shifts towards more acquisitive resource use strategies, including greater leaf area, specific leaf area, and lower leaf dry matter content (Shovon et al., 2020). Although the communities became more acquisitive in carbon and nutrient use (PC 1), two lines of evidence suggest that it is more likely that increased water availability, or improved water use efficiency under higher CO_2 could explain liana change. First it was the communities with slow water use (lower right quadrant of the PCA) that showed especially large increases in water use (PC2), second, communities that had already fast water use (upper right quadrant) were especially able to show large increases in carbon use (PC1), third, communities with faster water use had both a higher recruitment and a lower mortality (Figure 4.6).

4.4.2 Resource conditions and community strategies determine liana dynamics

***Topography and soil resources play a major role in explaining liana dynamic*s** – We hypothesized that abiotic environmental factors are strong drivers in shaping liana vital rates. Elevation indeed increased liana growth and recruitment (Figure 4.6), possibly because closer to the crest there is more irradiance. Hills in Xishuangbanna are relatively tall (836 m) and steep (751 – 795 m within the plot), and because of the relatively high latitude the sun occurs at relatively low angles (21 degrees N). Elevation may therefore strongly modify the available irradiance. In addition, near to the crest soils tend to be shallow, which in combination with high wind speed leads to a more stunted vegetation (Lawton and Putz 1988) where many small trees may provide more trellis for lianas. Shallow soils and high windspeed also lead to more canopy gap formation (Poorter et al. 1994) and light, and hence more opportunities for liana recruitment and growth. Surprisingly, gaps did not significantly influence liana performance, possibly because the lianas were fairly large (diameter > 1 cm), and probably already in the canopy, or because the gap data were collected in 2011, before the liana monitoring period (2014–2019).

Elevation and slope position are also good proxies for soil resource availability, where nutrient concentrations and soil water content increase towards the valley (Liu et al. 2020). P is a strong determinant of liana distribution in Xishuangbanna (Liu et al. 2020), which may explain why high P increases liana recruitment, although it is surprising that it does not affect growth and survival (Figure 4.6). In addition, we found that soil water availability, as reflected in the topographic wetness index, increased liana growth (Figure 4.6).

Forest structure and liana dynamics – We hypothesized that competition by trees and lianas would negatively affect liana performance (Figure 4.1) but found little evidence; tree basal area indeed had a negative effect on recruitment of liana basal area (Appendix S4.4), possibly because light competition is asymmetric, and trees cast a dense shade on small, regenerating lianas, but not on established lianas that have an extensive leaf layer on top of the tree crowns (Medina–Vega et al.

2020). Lianas are therefore more likely to inhibit trees (Schnitzer et al. 2000, Peña–Claros et al. 2008) than the other way around mainly because lianas compete effectively for light (Schnitzer et al 2005, Chen et al. 2008), but also sometimes for water and nutrients (Pérez–Salicrup and Barker 2000). Possibly, large lianas can partly avoid competition with trees in the same subplot, by rooting in multiple locations. Apparently, lianas, as a life form, hardly compete with themselves (Figure 4.6). Lianas only survived better in sites with a high liana basal area, perhaps because these are the microsites where lianas thrive well and have attained a high dominance.

Fast carbon and nutrient use increase mortality, but fast water use leads to a better performance – We hypothesized that liana communities with acquisitive trait values would have a shorter lifespan and faster turnover, with higher growth, mortality, and recruitment rate. We indeed found that liana communities with faster carbon and nutrient use (i.e., high values of PC1) had higher mortality rate and, therefore, a stronger decline in density (Figure 4.3, Figure 4.6). Surprisingly, we found that liana communities with a faster water–use (i.e., high values of PC2) not only had a higher recruitment rate but also a lower mortality rate, leading to a significant increase in liana density (Figure 4.3, Figure 4.6). This indicates that, currently, acquisitive lianas with fast water use gain in dominance in Xishuangbanna, which is possibly facilitated by the typical climatic conditions of Xishuangbanna, where the presence of fogs reduce atmospheric drought in the critical dry season.

4.5 CONCLUSIONS

Since liana increase in tropical forests has been put forward as a generic phenomenon (Phillips et al. 2002, Schnitzer and Bongers 2011), multiple studies have shown that in multiple forests lianas were actually decreasing (Gerolamo et al. 2018), suggesting that those changes in lianas are context dependent (Bongers et al. 2020). For a tropical forest at relatively high latitude in China, our study showed that lianas decreased in density mainly by high mortality of smaller individuals but increased in basal area by high survival and growth of larger individuals, and that the liana community changed toward more, large, acquisitive lianas, which are particularly well suited for rapid water use. We speculate that the success of these large, water spending lianas resulted from foggy conditions during the dry season, which largely mitigates atmospheric drought, in combination with CO_2 fertilization increasing water use efficiency. Thus, although fertilization by either CO_2 or nutrients and (warming related) droughts increase globally (Schnitzer 2015), not all liana communities may respond in the same way to such global changes (Marvin et al. 2015, Wright et al. 2015). We conclude that understanding these different responses of liana communities across forests to global change thus requires more inventory data and interpretations from resource gradients and functional trait spectra.

4.6 ACKNOWLEDGEMENTS

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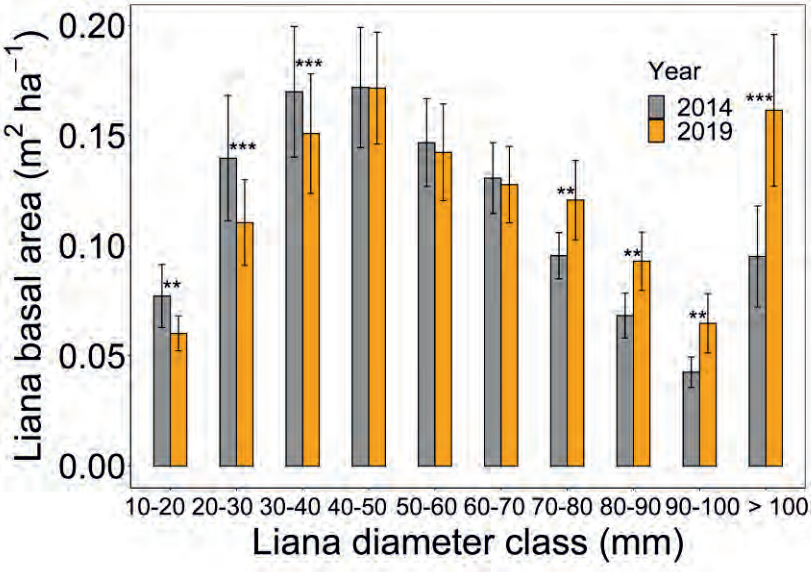
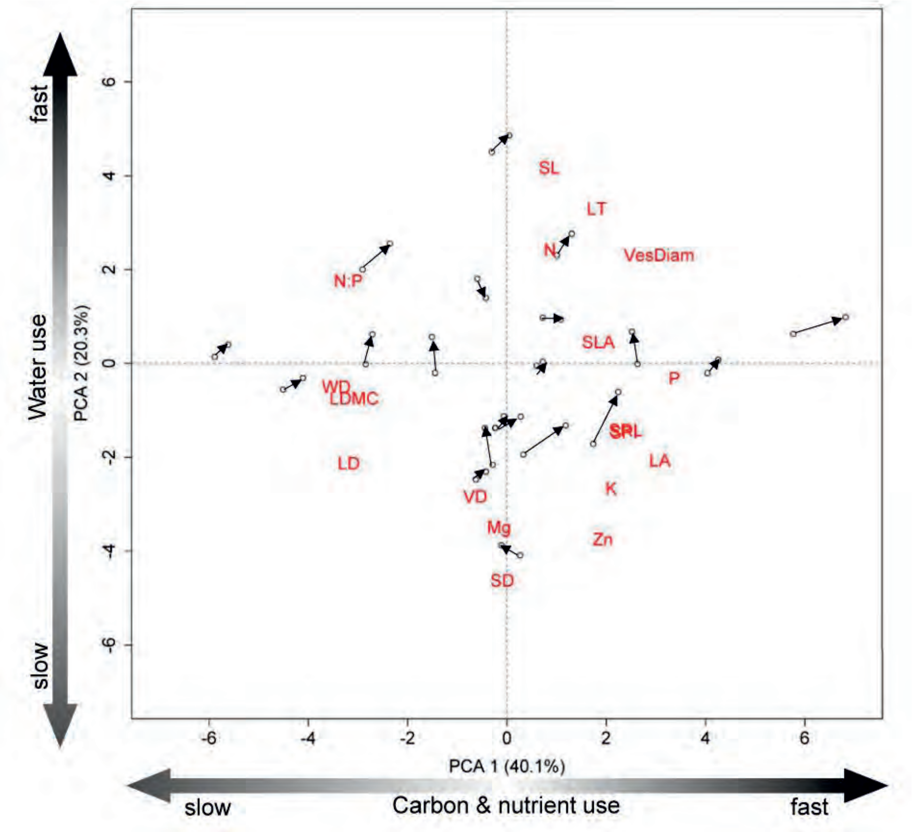
4.7 SUPPORTING INFORMATION

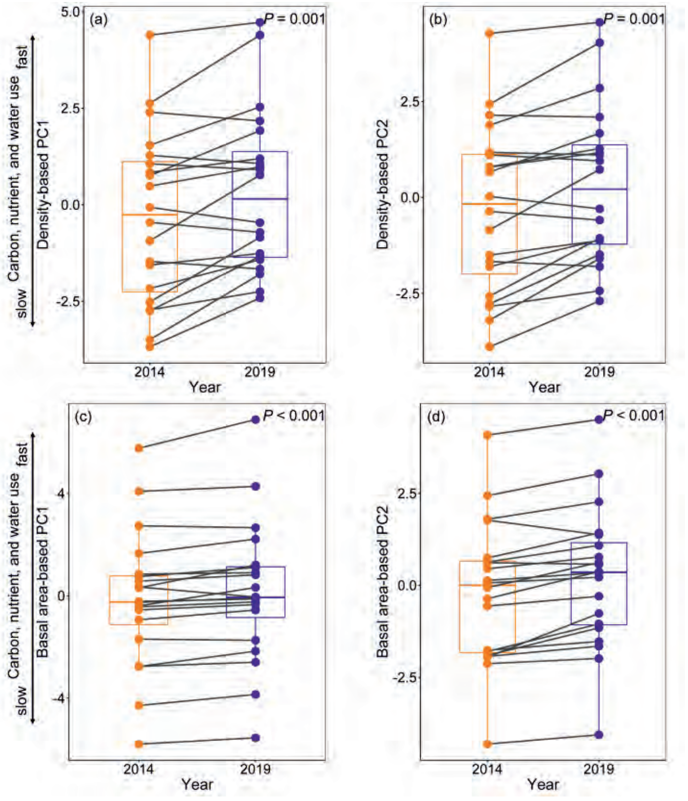
Appendix S4.1 Mean (± 95% confidence interval) of liana basal area per diameter class in 20 1–ha plots in Xishuangbanna tropical seasonal rain forest, SW China. In white, data from the first census (2014, n = 23155); in grey, data for the second census (2019, n = 20231). Asterisk indicates significant differences between censuses of a paired samples T–test. ** indicates $p < 0.01$, *** indicates $p < 0.001$, ns indicates $p > 0.05$.



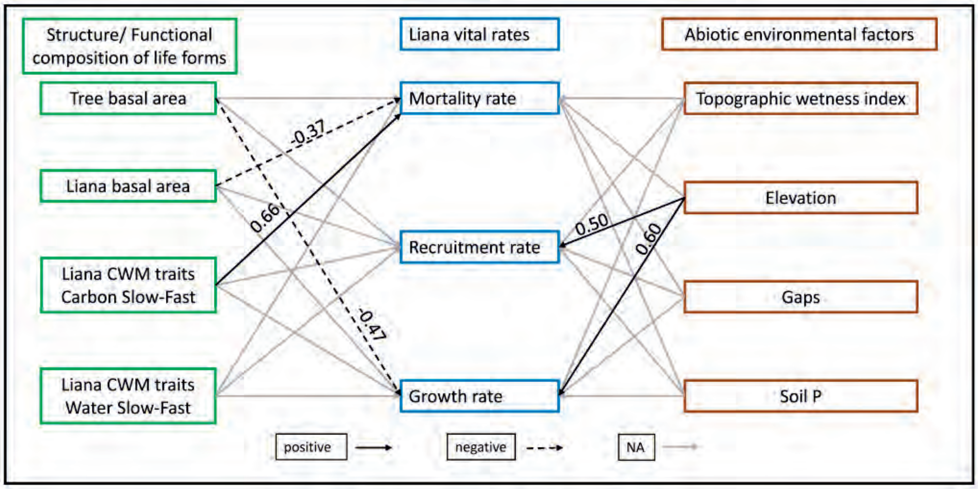
Appendix S4.2 Principal component analysis (PCA) of basal area–based community weighted mean (CWM) traits of liana communities in 2014 and 2019 in a tropical seasonal rain forest in Xishuangbanna, SW China. The first two PCA axes are shown, reflecting variation in slow to fast carbon and nutrient use (PC1) and water use (PC2). Each dot represents the regression score of a 1–ha plot (N = 20). The arrows show for each plot the change of PCA axes loading scores over the 5–years period. Red labels represent CWM traits loadings. For trait abbreviations see Table 4.1.

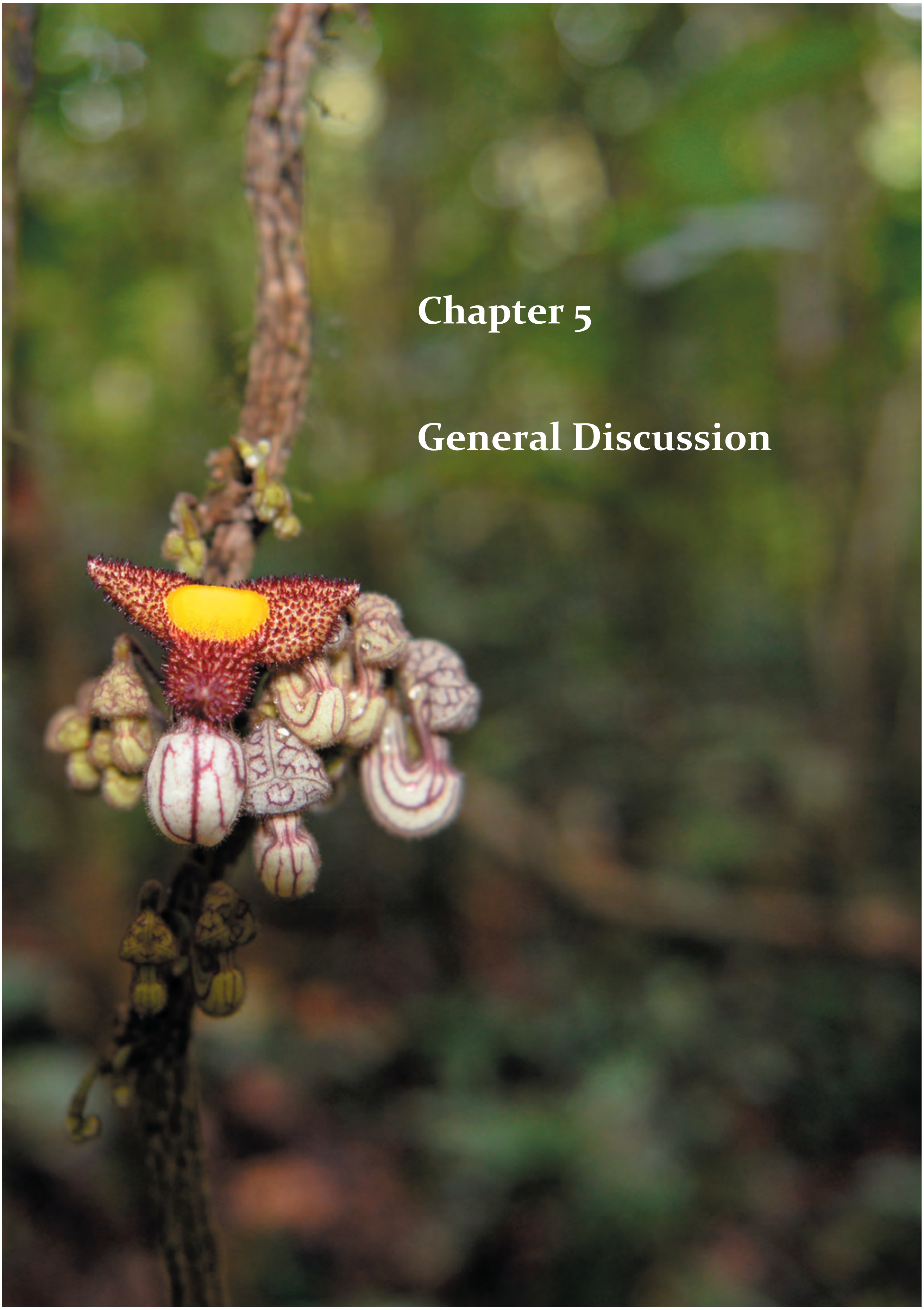


Appendix S4.3 Changes in liana community weighted mean (CWM) traits compostion (first two Principal component analysis axes loading scores) in a seasonal tropical rain forest in Xishuangbanna, SW China. PC1 (panel a) and PC2 (panel b) indicate the density–based CWM traits compostion for two censuses (2014 and 2019). Basal area–based CWM trait compostions were showed as PC1_BA (panel c) and PC2_BA (panel d). Each dot represents loading scores of the first two axes of PCA analysis of a 1–ha plots (N = 20). Light grey lines connect the measurements of the same plot. Significance level (*p*) of a paired samples T–test is shown.



Appendix S4.4 Regression models predicting the effects of competition (tree basal area, liana basal area; green boxes), liana functional traits (PC1 and PC2, green boxes), and abiotic variables (Elevation, Gap, soil P, Topographic Wetness Index, brown boxes)) on liana performance (mortality rate, recruitment rate, and growth rate, blue boxes), based on all possible subset combinations of all variables. The best models are selected with the lowest AICc. Liana vital rates were calculated based on liana basal area; 20 1–ha plots are used as units of replication. The values next to the arrows indicate the regression coefficients of the variables. Positive effects are indicated by black solid lines and negative effects are indicated by black dashes lines. NA indicates no significant effect (grey solid lines).





Chapter 5

General Discussion

Lianas are a dominant life form in tropical forests, and play an important role in the diversity, structure and functioning of these forests. A better understanding of lianas is required to provide new insights into the mechanisms that control the dynamics of lianas, and in turn their effects on tropical forests (Schnitzer 2018). To date, we lack studies in which the joined effects of abiotic and biotic factors on liana communities are investigated. In this thesis, I evaluated how biotic and abiotic environmental conditions influence liana functional traits, and how environmental conditions and traits shape together liana community dynamics and species distribution in a Chinese tropical forest.

The studied abiotic effects included the major resource gradients, including soil fertility, soil moisture and light availability, which are expected to shape the niches dimensions for liana species. In addition, I quantified terrain conditions ("topography" in Figure 5.1) that partially control these resource gradients in hilly landscapes, such as elevation, slope, and convexity. I quantified biotic conditions using community weighted mean (CWM) trait values that characterize the liana community, and forest structural measures such as stem density and basal area. Biotic and abiotic conditions were quantified for 500 sub–plots within a 20–ha forest plot. In addition, all lianas (> 20,000 individuals) were inventoried in this plot in 2013 and 2019, which allowed me to quantify the establishment, growth, and survival of liana species in this forest. In addition, for the 29 most abundant liana species, I quantified functional traits and their resources niche dimensions (i.e., resource gradients: light, water, and soil nutrient). With this data set, I could show how abiotic and biotic environmental conditions associate with liana functional traits, and how conditions and traits together shape the local dynamics and distributions of liana species (see also Figure 5.1). Following this, I addressed the main questions of this thesis (see also Figure 1.3):

1. How do abiotic conditions structure liana species distributions? (*Chapter 2*)
2. How do functional trait associations shape abiotic niche dimensions? (*Chapter 3*)
3. How do abiotic and biotic conditions explain liana dynamics and community changes over time? (*Chapter 4*)

In this final chapter (*Chapter 5*), I synthesize the results of this thesis and other studies to answer my research questions. I will discuss the implications of my results for temporal changes in liana abundance and composition and provide research recommendations for future studies on lianas.

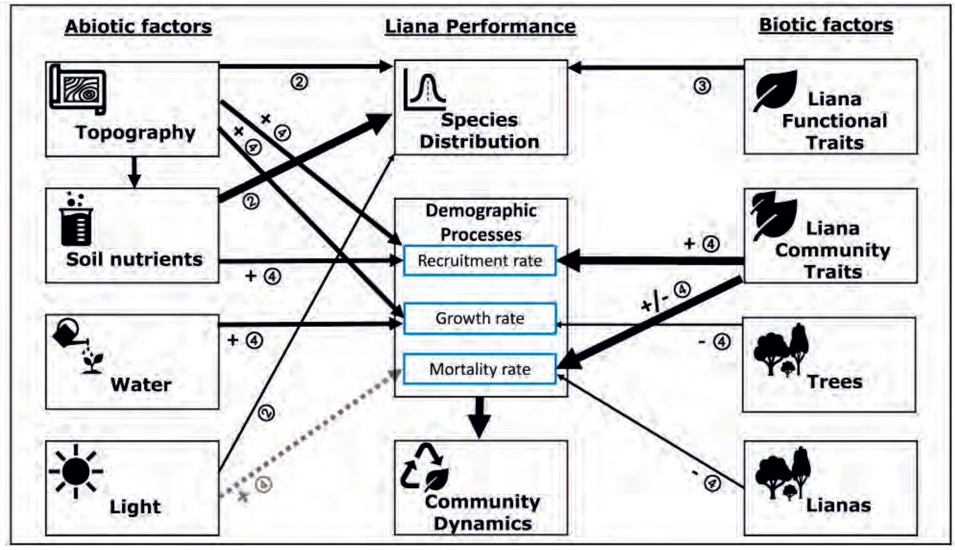


Figure 5.1 Conceptual model showing how abiotic factors (left column) and biotic factors (right column) affect liana performance (central column) in terms of species distribution, demographic processes (i.e., recruitment, growth, and mortality), and community dynamics. Hypothesized relations that were confirmed by this study are given in black continuous arrows), and hypothesized relationships that were not confirmed are indicated by grey dotted arrows. The texts next to the arrows indicate the effects are positive (+) or negative (–) and chapter numbers. The thickness of the arrow indicates the relative importance of the factors for liana performance (based on the results in Chapter 2–4). Multiple effects in chapter 2 and 3 are not shown here.

5.1 How do abiotic conditions structure liana species distributions?

Topography modifies soil resource availability (i.e., water and nutrients, DeWalt et al. 2006), light conditions and even seed dispersal (Lawton and Putz 1988) and may therefore have a strong impact on liana recruitment and growth, and ultimately species distributions. I found that soil nutrients significantly decreased with elevation and slope (Figure 5.1, ***Chapter 2***). This result is in line with the observations that steep slopes can cause erosion and loss of nutrients from a shallow topsoil layer, as the nutrient–rich topsoil may be washed down the slope and accumulated downslope (Brubaker et al. 1993). Alternatively, transport of soluble elements through movement of soil water, or accumulation of deeper organic soil horizons, may lead to higher nutrient concentrations in downslope locations (Foster et al. 1985). Accordingly, elevation was a good predictor of soil nutrient availability in my study (Figure 2.2).

It was predicted that lianas have an acquisitive nature and therefore would occupy nutrient–rich niches in the forest. This prediction was only partially supported by my results (***Chapter 2***). For soil P, probably the most limiting soil nutrient in this forest, liana species partitioned the available gradient, indicating that there are also liana species specialized for low P levels. This is remarkable because it implies that some liana species occupy low soil fertility sites, which was against my expectation. Across the warm and wet tropics, phosphorus is often considered a limiting nutrient because old, strongly weathered, and leached soils dominate many wet tropical areas (Vitousek et al. 2010). My results suggest lianas can still be successful on such poor soil conditions, which questions the assumption that they always have an acquisitive nature.

For most species, optimal resource conditions (quantified by the abundance weighted mean of abiotic factor values for sites where the species occur) was found at higher soil resource availability for N and K (Figure 2.5, Figure 5.1, ***Chapter 2***), which indicates that those species specialize for high availability of N and K. Probably many lianas need higher leaf N concentration to support higher Rubisco concentrations for their higher photosynthetic rates (Cai et al. 2009) and higher leaf K to regulate their gas exchange more tightly (Benlloch–González et al. 2008).

Different abiotic conditions could drive liana distribution synergistically. Canopy gaps affects liana distributions. I found that liana abundance in gaps was indeed higher than in non–gaps (Appendix S2.8, Figure 5.1), but also that liana species specialized for different levels of light or soil moisture and thus partially partition these resources too (Schnitzer and Carson 2001). Also, lianas preferred higher convexity and lower slopes where soil moisture and nutrients may accumulate. Overall, my study thus confirm that high light spots create beneficial conditions for lianas, but at the same time that some liana species are also successful in sites characterized by low light levels and/or low soil fertility.

5.2 How do functional trait associations shape abiotic niche dimensions?

Plant functional traits and strategies hold the promise to explain species distributions, but my results indicate that this was not in the straightforward way as I hypothesized. A primary spectrum in toughness and water use was found in my study (***Chapter 3***), which showed a range from liana species with traits referring to a more water–conservation strategy with tough tissues (i.e., high leaf density, leaf dry matter content, wood density), to liana species with a more water–spending strategy with soft tissues (i.e., greater vessel diameter and stomatal length). The second spectrum, however, showed changes across liana species in leaf nutrient concentrations, SRL and SLA, which reflected resource acquisition of soil nutrients and carbon. Intriguingly, the two spectra are associated with different, orthogonal PCA axes (Figure 3.1). I thus observed two independent spectra, and each of those spectra partly reflects the conservative–acquisitive paradigm.

Similar life history trade-offs are found for the two different life forms (lianas and trees) (Gilbert et al. 2006). Apart from the obvious difference between lianas and trees with lianas climbing trees with implications for their biomechanics (Zhang et al. 2019), lianas and trees may share similar trade–offs in construction cost and functioning, but lianas are supposed to be in general more acquisitive than trees, with easy access to light and therefore faster growth rate in a competitive context with trees. I found that lianas species that occupied higher light niches had a higher maximum vessel diameter (Table 3.3). This suggests that in an exposed high–light environment, these lianas benefit from a high–water transport capacity. Increasing vessel diameter is an anatomically cheap and efficient way to increase the water transport capacity of the stem (Schnitzer 2005, van der Sande et al. 2019) as hydraulic conductance scales with the fourth power of vessel diameter (Lambers et al. 2008). While trees can increase their water transport capacity by increasing their stem diameter, this is not an option for lianas because their climbing habit requires relatively flexible, slender stems (Hoffmann et al. 2000).

Different functional traits shaped different niche dimensions and multivariate trait strategies also play a role in shaping liana distribution (Figure 3.3, Figure 5.1), indicating that liana species with more acquisitive trait values (softer tissues, higher water use) occupy niches characterized by higher soil resource availability. When resource niches were predicted based on individual traits, acquisitive trait values (i.e., vessel diameter, stomatal pore index and Zn concentrations increased different resource niches) often increased the resource niche, but not always (e.g., a high specific root length predicted a lower soil N level). This suggests that different components of the multivariate strategy axes are important for different niche dimensions. I thus showed that liana communities can cover an acquisitive versus conservative gradient by themselves, rather than that they (only) form a homogeneous acquisitive group compared to trees.

5.3 How do abiotic and biotic conditions explain liana dynamics and community changes over time

Most evidence for liana increase comes from the Neotropics (e.g., Laurance et al. 2014, Phillips et al. 2002, Schnitzer et al. 2012, Yorke et al. 2013), however, recently there were some studies that reported that liana did not change (Londré and Schnitzer 2006) or even decreased, for example in seedlings (Umaña et al. 2020). Studies in Africa provided a startling contrast in liana dynamics (e.g., Bongers et al. 2020, Caballé and Martin 2001, Thomas et al. 2015). Both abundance and biomass decreased in these study areas, which could be explained by the high hunting pressure, leading to less disturbance by big mammals such as forest elephants, and forest closure (Bongers et al. 2020). For the Xishuangbanna tropical seasonal rain forest, I observed that lianas decreased in density mainly because of high mortality of smaller individuals but increased in basal area because of high survival and faster growth of larger individuals. Moreover, the liana community was changing towards more, large, acquisitive lianas, which are particularly well suited for rapid water use (***Chapter 4***). These findings suggest that the liana community is undergoing succession This indicates that, currently, acquisitive lianas with fast water use gain in dominance in the Xishuangbanna forest. I speculate that the success of these large, water spending lianas resulted from the foggy conditions that characterize the dry season, which largely mitigate the atmospheric drought, in combination with CO_2 fertilization increasing water use efficiency. Although fertilization by either CO_2 or nutrients and (warming related) droughts increase globally (Schnitzer 2015), not all liana communities may respond in the same way to such global changes (Marvin et al. 2015, Wright et al. 2015), as with any perturbation to a natural system, the underlying mechanisms and their effects on ecosystems are likely to be complex and interactive. For example, elevated CO_2 may indirectly influence liana abundance by increasing tree productivity and mortality, which could result in higher forest-level disturbance (Phillips and Gentry 1994).

Liana dynamics in Xishuangbanna are very much depending on very local conditions, which could be explained by several abiotic and biotic conditions. I found that topography had a strong effect on liana dynamics and that liana growth and recruitment increased at higher elevations (Figure 4.6, Figure 5.1). Hills in Xishuangbanna are relatively tall (836 m) and steep (751 – 795 m within the plot), and because of the relatively high latitude (21 degrees N), the sun occurs at relatively low angles. Elevation may therefore strongly modify the available irradiance. In addition, near to the crest soils tend to be shallow, which in combination with high wind speed leads to a more stunted vegetation (Lawton and Putz 1988) where many small trees may provide more trellis for lianas. Shallow soils and high windspeed also lead to more canopy gap formation (Poorter et al. 1994) and light, and hence more opportunities for liana recruitment and growth.

High soil P increases liana recruitment (Figure 4.6, Figure 5.1), which can also explain why P is a strong determinant of liana distribution in Xishuangbanna (Liu et al. 2020), although it is surprising that it does not affect growth and survival. In addition, I found that soil water availability, as reflected in the topographic wetness index, increased liana growth. These results indicate that despite the better light availability, liana recruitment and growth will also benefit from fertile soil and high–water availability.

I expected that competition by trees and lianas would negatively affect liana performance but found little evidence for this. Tree basal area indeed had a negative effect on recruitment of liana basal area (Figure 4.6, Figure 5.1), possibly because light competition is asymmetric, and trees cast a dense shade on small, regenerating lianas, but not on established lianas that have an extensive leaf layer on top of the tree crowns (Medina–Vega et al. 2020). On the other hand, large lianas may partly avoid competition with trees in the same subplot, by rooting in multiple locations. Apparently, lianas, as a life form, hardly compete with themselves; lianas only survived better in sites with a high liana basal area (Figure 4.6, Figure 5.1), perhaps because these are the microsites where lianas thrive well and have attained a high dominance.

My study indicates that liana community changes are not only driven by abiotic factors and forest structure but also by functional trait strategies. Global change is leading to shifts in forest dynamics and species composition because of environmental changes such as increased drought stress and disturbances (van der Sande et al. 2016). The relative importance of these changes can be inferred from analyzing changes in functional traits values. However, most studies only focus on the relations between performance and individual traits (e.g. Poorter and Bongers 2006, Wright et al. 2010, but see van der Sande et al. 2016), and none of them focus on liana communities. Functional trait data of lianas are more often used in the comparison between trees and lianas (e.g., Zhang et al. 2019, Dias et al. 2019, Medina–Vega et al. 2020), which limits our understanding of the roles of functional traits in liana community changes. I found that liana communities with faster carbon and nutrient use had higher mortality rate and, therefore, a stronger decline in density. Meanwhile, I found that liana communities with a faster water–use not only had a higher recruitment rate but also a lower mortality rate, leading to a significant increase in liana density (Figure 4.6). These compositional changes may lead to shifts in community composition, with acquisitive lianas with fast water use gaining in dominance, and hence affect ecosystem processes in terms of carbon sequestration and forest dynamics. Thus, I conclude that understanding responses of liana communities to global change requires more inventory data and interpretations from functional trait spectra.

5.4 Research recommendations to improve measurements

This research had several limitations and based on these limitations I make three research recommendations, that may improve future liana research.

1. Quantifying liana light environments. Lianas are an inherently light demanding life form, and quantification of light conditions is therefore important to assess their performance and light niche. Given that lianas are tall and slender, most lianas have their leaves up in the forest canopy, which makes the quantification of the light environment difficult. I used a categorical quantification of the light environment as 'closed' forest or as canopy gaps, where a gap is defined as a quadrat where the canopy cover was less than 50%. Future studies could infer the light environment from a 3D forest structure, as quantified using Light Detection and Ranging (LiDAR), or measure light environment directly with light sensors, using a canopy crane, or hemispherical photographs. I expect that such finer–grain measures will better allow for showing how, and whether, liana species occupy different light niches, and how those niches are associated with other resources.

2. Root traits. In my study, I measured many above ground functional traits (stem and leaf properties) but only one root trait (i.e., specific root length), and therefore still miss key underground properties. Above– and belowground traits cannot be considered analogues because they function differently and might not be related to resource uptake in a similar manner (Weemstra et al. 2016). My result indicate that lianas really depend on soil nutrients (Figure 4.6, Figure 5.1) and increased water increases growth (Figure 4.6, Figure 5.1). More specifically, since soil P is considered very limiting in my study area, the role of mycorrhizal associations and/or root exudates that release P should be included in future studies. The very strong effect of soil P indeed indicates that we might miss key hidden traits in the soil, i.e., root distribution and dynamics (Weemstra et al. 2020). Root traits, for example, SRL reflects the root uptake length at a given biomass cost. In addition, root N content and respiration rate are expected to be associated with net soil resource acquisition rate, and root lifespan reflects the degree of biomass conservation (Weemstra et al. 2016). More root traits, therefore, should be included in further liana studies, which may indeed be a next frontier to understand liana functioning and performance.

3. Include smaller lianas in inventories. Good inventories of lianas are relatively rare compared to those of trees, and they require other criteria. As lianas are structural parasites, they are relatively slender, and at small diameters (1 cm) they tend already to be in the canopy. The minimum diameter limit of lianas included varies from 1 cm (e.g., this study; Thomas et al. 2015) to 10 cm (e.g., Phillips et al. 2002) across studies. The use of a lower diameter limit would allow to include a larger number of lianas, to better quantify liana dynamics, and also detect different patterns. For example, in my study, small lianas were decreasing in numbers whereas tall lianas were increasing in size. Moreover, smaller liana seedlings are more sensitive to canopy gaps compared to taller lianas that are in the canopy (Dewalt et al. 2000). In this thesis, I thus probably underestimated the role of gaps compared to the role of soil nutrients. Standard liana census methods suggest a stem diameter of 0.5 cm (Gerwing et al. 2006, Schnitzer et al. 2008) as a minimum diameter limit to study liana community dynamics, regeneration, and succession.

This would better capture the dynamics of the liana community (i.e., growth, mortality, recruitment) than only focusing on larger size–classes. However, most studies only record liana individuals ≥ 1 cm in diameter (e.g., this study, Schnitzer et al. 2012, Thomas et al. 2015). Basing on my results explained above and my experience during the field work periods, I highly recommended 0.5 cm as a minimum diameter for studies on liana community dynamics.

5.5 Research challenges in liana ecology

The study of liana ecology has advanced our understanding of ecological theory (Schnitzer, 2018). This thesis presents the first study that simultaneously evaluates the relative importance of abiotic and biotic environmental factors on liana community dynamics. I show that changes in liana abundance and biomass (quantified as basal area in my study) do not run in parallel, and that local environmental conditions and functional traits play an important role in liana performance, and that those local conditions largely drive liana community dynamics and shape distribution patterns. However, our understanding of lianas ecology is still incomplete. Here I give three recommendations to improve our understanding of liana communities.

1. Lianas in Paleotropical and Neotropical forests. Forest dynamics and tree species composition vary substantially between Paleotropical and Neotropical forests, but these broad biogeographic regions are treated uniformly in many studies (Taylor et al. 2019). What is the key difference between Neotropical forests where lianas tend to increase, and Paleotropical forests where lianas are not clearly changing or even decreasing? Compared to Neotropical forests, Paleotropical forests are characterized by trees that are on average taller (Feldpausch et al. 2011), leading to less light for liana establishment. Several studies have compared the stem growth, wood allocation, and aboveground biomass of trees in Paleotropical forests and Neotropical forests, and found both stem growth and the ratio of stem growth to litterfall were higher in Paleotropical forests compared to Neotropical forests (e.g., Hertel et al. 2009, Taylor et al. 2019). It would be interesting to see whether these regional differences in tree dynamics also translate into regional differences in liana dynamics.

2. Long–term monitoring is needed. Long–term monitoring of lianas (i.e., decades to centuries) are necessary to detect temporal patterns and underlying mechanisms, as this is the timescale that corresponds to the life cycle of liana and competing trees during which environmental change, acclimation, and natural large–scale disturbances may take place (Zuidema et al. 2013). In this thesis, I used a 5–year period to discuss liana dynamics. This may be sufficient to address questions related to spatial variation in abiotic and biotic conditions and ecosystem processes, but this is rather short for addressing questions related to global change. There is a need to monitor both trees and lianas in new plots networks set up over longer time scales around the global for showing decadal changes instead of multiple–year changes. Such a long–term perspective is key to better grasp the impact of global change on forest dynamics. Without the information on such liana dynamics, we will miss one of the key drivers of changes in tree communities and entire forests (Phillips et al. 2002, Laurance et al. 2014). Additionally, we should not only focus on liana abundance, but also on liana biomass and seedling dynamics, because they may show different patterns compared to abundance.

5.6 Concluding remarks

In this dissertation, I have evaluated the relative importance of abiotic and biotic environmental factors for liana community dynamics and how they shape the spatial distributions of lianas. Abiotic resource conditions and biotic conditions (including forest structure and species traits) indeed determine the species performance (i.e., recruitment, growth, and mortality) and shape species distribution and niches. I showed that lianas benefit more from high–light conditions, but that especially below–ground resource conditions, such as soil P and water availability, act as important drivers in liana community change. Lianas in

Xishuangbanna forest show a significant decrease in abundance and increase in basal area, which indicates that the liana community is undergoing succession, probably driven by CO_2 or N fertilization. This result is partly in contrast with the widely documented liana increase over the last decades. Additional and new studies on liana communities in multiple forests are needed to better understand the implications of lianas for the dynamics of tropical forests with ongoing climate change.

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Summary

Tropical forests are global hotspots of biodiversity and important for the global carbon and water cycle. Lianas form a conspicuous element of tropical forests but have largely been ignored in species-level vegetation surveys. As a result, their ecology, in terms of functional traits, dynamics, and distribution are not fully understood. This study aims to improve our understanding of liana community ecology by analyzing species differences in functional traits, liana dynamics, and liana distributions in a tropical rainforest in SW China. I addressed three main questions in this thesis.

In ***chapter 2***, I address the question how species distribution and abundance are associated with soil nutrients, canopy gaps, and topography. I evaluated in a 20-ha forest plot the distribution of the 50 most abundant liana species, comprising > 18,000 individuals. Soil pH and P were the strongest drivers of liana species distribution and also strongly correlated with each other. Most liana species occurred under significantly higher or lower soil nutrient conditions than expected at random. Lianas mainly separated along the P gradient, whereas for N and K most liana species tended to occupy locations with high soil nutrient concentrations. This study highlights the importance of soil nutrient status, and especially phosphorus for liana niche partitioning in wet tropical forests on highly

weathered soils. Most liana species had high resource requirements for N, K, and light, which come along with their fast growth and acquisitive resource use strategy. Hence, belowground resource availability plays an important role in shaping the assembly of liana communities.

In ***chapter 3*** I evaluate how functional trait associations shape abiotic niche dimensions. Eighteen functional traits related to light, water, or nutrient acquisition, storage and use were measured, and liana niche dimensions were quantified for 29 species, based on their distributions. I found two trait spectra; a tissue toughness spectrum ranging from soft to hard tissues, along which species also vary from acquisitive to conservative water use, and a resource acquisition spectrum ranging from low to high light and nutrient acquisition and use. Different traits were important for different niche dimensions. These studies indicate that plant functional traits and strategies can indeed explain species distributions. Lianas show a broad spectrum from conservative to acquisitive trait strategies which allows them to partition soil fertility gradients (in line with ***chapter 2***).

In ***chapter 4,*** I ask how abiotic and biotic conditions explain liana dynamics and community changes over time. I monitored from 2013-2019 >20,000 lianas and analyzed how changes in liana communities within twenty 1-ha plots were driven by underlying vital rates (i.e., recruitment, growth and survival), abiotic factors (i.e., topography, light gaps, water, and soil phosphorus), biotic factors (tree and liana basal area), and the functional composition of liana communities based on 18 traits. I found that liana abundance decreased because of high mortality of small lianas, whereas liana basal area increased because of high survival and growth of large lianas. Liana communities showed a spectrum of slow to fast carbon and nutrient use, and a spectrum from slow to fast water use. Abiotic environmental factors (i.e., elevation and soil phosphorous and water) and liana functional composition influenced liana demographic processes, whereas competition by lianas and trees had little effect. Over the 5 years period, the liana community changed toward more, large, acquisitive lianas with rapid water use. This indicates that the liana community is undergoing succession, possibly driven by increased CO_2 fertilization.

In this thesis, I show and discuss that abiotic resource conditions and biotic conditions (including forest structure and species traits) indeed determine the species performance (i.e., recruitment, growth, and mortality) and shape liana species distribution and niches. The observed decrease in liana abundance and increase in basal area in this SW Chinese rainforest partly contrasts with the widely documented liana increase across various Neotropical forests, which indicates that local drivers can overrule global change drivers. New studies across multiple forests are needed to better understand how ongoing climate change affects the dynamics of lianas communities and tropical forests.

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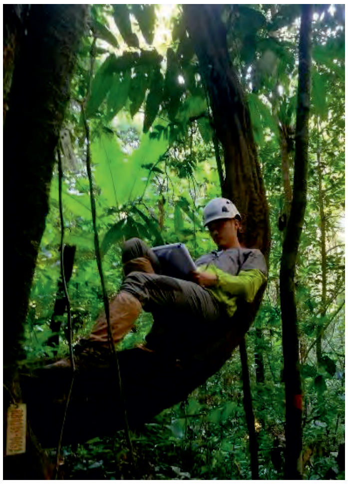
Short biography



Qi Liu was born on 15th of March 1990 in Chizhou, China. He grew up and attended primary, middle, and high school in Chizhou. In 2008, he decided to pursue a BSc. in Biological Science at Anhui Normal University.

In 2011, it was the first time he heard of the Xishuangbanna Tropical Botanical Garden, Chinese Academy of Science (XTBG-CAS), a beautiful place with scientists who are passionate about nature. After a four-year enjoyable journey in Plant Eco-physiological Group (PEG), he completed his MSc. in ecology at XTBG-CAS in 2016. In XTBG, his research aimed to explore the species composition and diversity of the liana community. His interest in liana communities grew and he decided to continue this field of study. He secured a scholarship from the Chinese Scholarship Council, which contributed to the successful application for a PhD position at the Forest Ecology and Forest Management Group (FEM) at Wageningen University in the Netherlands from 2017 to 2021. His liana research could now continue, and now as a collaboration between FEM and PEG. He has conducted experiments regarding the distribution, functional ecology, and dynamics of liana communities. For this, he measured a series of functional traits related to leaf, stem, and root functions. Meanwhile, he also surveyed liana populations across a 20-ha plot in Xishuangbanna. During his PhD, he presented his research finding in multiple international seminars and conferences and his work has been published in peer-reviewed scientific journals. Moreover, he supervised two MSc students from Wageningen University with their thesis research in the Netherlands and China.

Now, having finished his PhD thesis, Qi Liu is ready to move on in science. By doing so he aims and hopes to contribute to the understanding of forest dynamics and complexity, which is crucially important to assure the community ecology and conservation.

Publications

Bai, X. L., Zhang, Y. B., **Liu, Q.**, Wang, Y. S. D., Yang, D., and Zhang, J. L. (2020). Leaf and stem traits are linked to liana growth rate in a subtropical cloud forest. Forests, 11(10), 1120.

Liu, Q., Sterck, F.J., Medina–Vega, J.A., Sha, L., Cao, M., Bongers, F., Zhang, J. and Poorter, L. (2021). Soil nutrients, canopy gaps and topography affect liana distribution in a tropical seasonal rain forest in SW China. Journal of Vegetation Science, 32: e12951.

PE&RC Training and Education Statement

With the training and education activities listed below the PhD candidate has complied with the requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)

Review of literature (6 ECTS)

- Community assembly ecology of lianas in South China rainforest: distribution, functional traits and dynamics

Post-graduate courses (6.4 ECTS)

- Structural equation modelling; WUR (2018)
- The 2nd international workshop on response and adaptation of terrestrial ecosystem carbon, nitrogen and water cycles to climate change; China (2019)
- The 4th Xishuangbanna international symposium; China (2019)
- Dynamic models in R; WUR (2021)

Deficiency, refresh, brush-up courses (12 ECTS)

- Basic statistics; WUR (2017)
- Ecological methods 2; WUR (2017)
- Forest ecology and forest management; WUR (2018)

Laboratory training and working visits (3 ECTS)

- Anatomy of lianas; Xishuangbanna Tropical Botanical Garden Chinese Academy of Science (2018)

Competence strengthening / skills courses (2.4 ECTS)

- The choice: un-box your PhD process & take charge of your performance; WUR (2018)
- Project & time management; WUR (2020)
- Last stretch of the PhD Programme; WUR (2020)
- Writing propositions for your PhD; WUR (2020)
- Workshop on data visualization: the information is beautiful way; WUR (2020)

Scientific integrity / ethics in science activity (0.15 ECTS)

- Scientific integrity meetings FEM; WUR (2020)
-

PE&RC Annual meetings, seminars and the PE&RC weekend (1.5 ECTS)

- PE&RC First year weekend (2017)
- PE&RC Midterm year weekend (2019)

National scientific meetings / local seminars / discussion groups (4.5 ECTS)

- Journal club FEM (2017-2021)
- XTBG Xishuangbanna tropical botanical garden CAS seminar (2018-2019)
- R Club FEM (2020-2021)
-

International symposia, workshops and conferences (4.1 ECTS)

- Netherlands Annual Ecology Meeting (NAEM); the Netherlands (2020)
- British Ecological Society (BES) annual general meeting online; the United Kingdom (2020)
-

MSc thesis supervision (6 ECTS)

- How do functional traits of liana species shape their light and nutrient niches?
- How plant traits shape liana water niches in the tropical seasonal rainforest of Xishuangbanna, China

Colophon

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