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RESEARCH ARTICLE

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

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Abstract

Questions: Lianas are a conspicuous element of tropical forests but have largely been ignored in species-level vegetation surveys. As a result, there is limited understanding of how environmental factors structure liana communities.

Location: A 20-ha forest dynamics plot in Xishuangbanna National Nature Reserve, southwestern China.

Methods: We evaluated the distribution of the 50 most abundant liana species, comprising >18,000 individuals, in the 20-ha forest plot. Ordination analysis and generalized linear mixed models were used to evaluate how species distribution and abundance are associated with soil pH, soil phosphorus (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.

Results: 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.

Conclusions: 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, highlighting 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, below-ground resource availability plays an important role in shaping the assembly of liana communities.

KEYWORDS
community assembly, gap, lianas, phosphorus limitation, soil nutrient availability, species distribution, tropical forest

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 (Guisan & Thuiller, 2005; Araujo & Guisan, 2006).

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 above-ground and below-ground resources (Schnitzer & 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 & Bongers, 2011; van der Heijden et al., 2015; Estrada-Villegas & Schnitzer, 2018). Most studies have evaluated lianas as a single functional group, potentially concealing important interspecific differences in liana responses which are key to understanding community dynamics. Several studies have reported that liana species had habitat preferences, such as low hill areas (Ibarra-Manríquez & Martínez-Ramos, 2002; Addo-Fordjour et al., 2014; Addo-Fordjour & 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 weingto 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 & 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 the 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 tree-fall gaps, where lianas can recruit rapidly and abundantly, but where they decrease in abundance over time when the gap closes (Schnitzer & 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 analyze 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 & Poorter, 2001), and also N mineralization 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 & 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., 2014). We also expect that most lianas will be associated with convex areas and relatively flat areas where irradiance and soil fertility are higher.

2 | METHODS

2.1 | Study site

This research was carried out in Xishuangbanna, Southwest China (101°34′26–47″ E, 21°36′42–58″ N). Xishuangbanna is located on the northern edge of the Asian tropical rain forests and is identified as part of the Indo-Burma biodiversity hotspot (Myers et al., 2000). Mean annual precipitation is 1,532 mm, of which ~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 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.

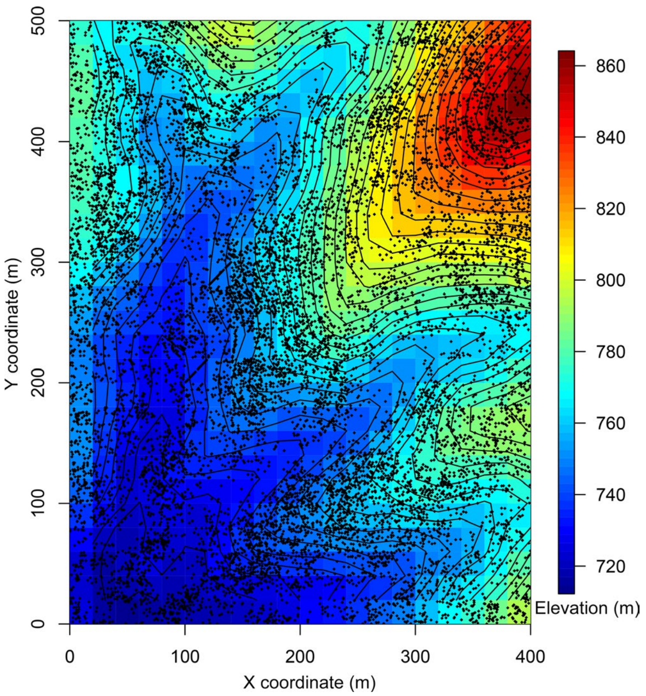

FIGURE 1 The distribution of lianas in relation to topography (elevation) in the Xishuangbanna 20-ha tropical seasonal rain forest dynamics plot. Each dot is a liana individual and colors refer to elevation

2.2 | Species selection

From 2013 to 2015, all rooted lianas ≥1 cm diameter were tagged, mapped, and 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 the 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% (18,581 individuals) of all identified liana individuals (Table 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 × 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.

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 m and 5 m, 2 m and 15 m or 5 m 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 a depth of −10 cm. 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 oxidized 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

TABLE 1 Distribution of optimal (average weight) soil conditions (pH, nitrogen, phosphorus, potassium) and topography (convexity and slope) of 50 liana species

Species	Code	Individuals	pH	Nitrogen	Phosphorus	Potassium	Convexity	Slope
Parameria laevigata	Pa_la	2,387	L	L	L	M	H	M
Byttneria aspera	By_as	1,451	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

(Continues)

TABLE 1 (Continued)

Species	Code	Individuals	pH	Nitrogen	Phosphorus	Potassium	Convexity	Slope
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

Note: 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]) did not deviate significantly from average. Nomenclature of lianas follows Flora of China (http://www.efloras.org/).

TABLE 2 Group differences (gap) and correlations between soil chemical properties across 500 20 m × 20 m quadrats in the tropical rain forest of Xishuangbanna, China

	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**

Note: Median for each variable in gap and non-gap is given. 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 test bto compare gap–group differences, a binary variable for light conditions (gap versus non-gap). $^{**}p < 0.01$; $^{*}p < 0.05$.

distilling unit was used to determine the soil N content in the solution. Microdiffusion 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, Waltham, MA, USA). Extractable P was released from the soil in a solution containing 0.03 mol/l NH_4F and 0.025 mol/l HCl and estimated colorimetrically. Exchangeable K was extracted in a neutral 1 mol/l 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 subquadrats within that quadrat by using the "*geoR*" package in R (see Hu et al., 2012). Based on this data set, for each soil factor, comparisons among element concentrations were done on a volumetric basis (g/cm^3) rather than a mass basis (Ellert & Bettany, 1995) because this 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 bivariate Pearson correlation showed that most soil factors were associated (Table 2). To avoid the bias from measurements (such as extractable P, which depends on the model of extraction, see Qin et al., 2019), only total N, P and K were used in the analyses.

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 were 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.

2.5 | Gaps

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

2.6 | Data analysis

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 × 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*" (R Core Team, R Foundation for Statistical Computing, Vienna, Austria), 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*" (R Core Team).

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 (Neter et al., 1989; Hox et al., 2010). 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 submodels 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) the linear form of the continuous predictors and (3) the gap. We considered models with $\Delta AIC \leq 2$ to have a substantial level of empirical support from the data (Carroll & Ruppert, 1981; Burnham & Anderson, 2002). 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*" (R Core Team, and a threshold value of 3 (Zuur et al., 2010; Appendix S1). 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 better fit. Zero inflation was not detected. We tested for spatial autocorrelation by using the Moran-I test implemented in the package "*ape*" (Paradis & Schliep, 2019) via the package "*DHARMa*" (R Core Team) on the conditional (on the fitted random effects)-scaled residuals simulated from the best-fitted (GLMM) model. Spatial autocorrelation was not detected (Appendix S2). We constructed the GLMMs using the "*glmmTMB*" package (Brooks et al., 2017) and a sample script is provided in the the Supporting Information (Appendix S3).

To evaluate whether liana species have their optimum under significantly higher or lower resource concentrations than the 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 the Wilcoxon–Mann–Whitney U test were performed using SPSS version 23 for Windows (Gouda, 2015).

3 | RESULTS

3.1 | Soil nutrients across the landscape

Across the 500 forest quadrats, total K varied threefold (range 7.7–20.3 g/cm^3, average 12.3), total P varied threefold (range 0.2–0.6 g/cm^3, average 0.4), total N varied onefold (range 1.8–2.4 g/cm^3, average 2.0) and pH varied 1.5-fold (range 4.1–6.3, average 4.9) (Appendix S4). Of these 500 forest quadrats, 31 were defined as gaps.

Soil nutrient concentrations were positively related to each other and pH (Table 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. A 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).

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% of all used explanatory variables (Figure 3).

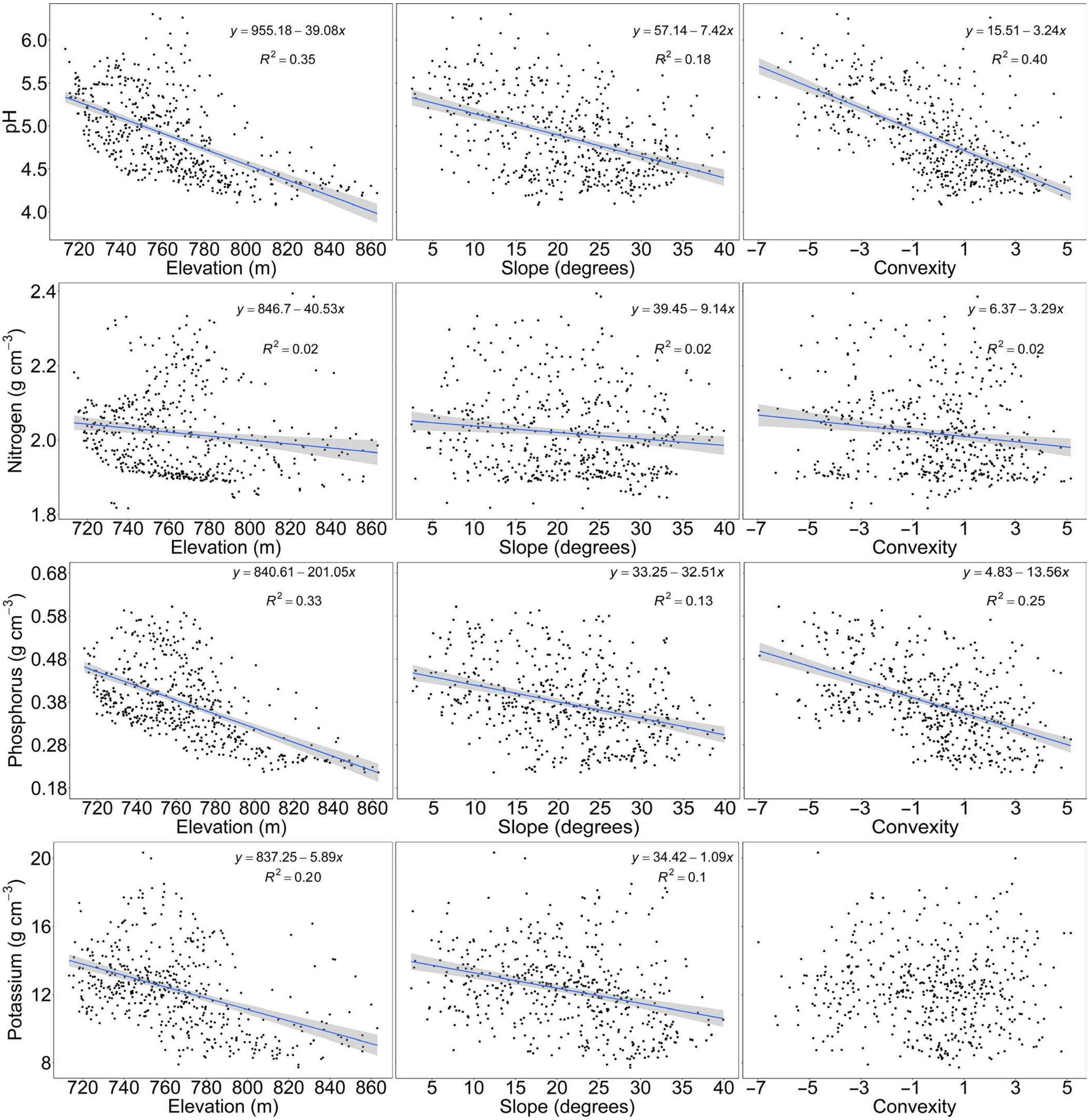

FIGURE 2 Relationships between soil conditions (pH, nitrogen, phosphorus, potassium) and topography (elevation, slope and convexity). Each dot represents the soil pH or nutrient value in each quadrat. Linear regression models were fitted (see the equations) and R^2 values are shown in the subpanels. A regression line is given only for those models which are significant at the 5% level ($p < 0.05$)

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 S5). We found similar results for the main axis of variation when assessing liana community composition with the DCA by using the *envfit* function; soil pH and P showed strong relationships with the first two ordination axes (Appendix S6, S7).

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 4, Appendix S8, S9). 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 high interspecific variation. Liana abundance in gaps was higher than in non-gaps (Appendix S8).

We observed different responses to resource availability across liana species (Figure 4, Appendix S10). Forty-four per cent 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 per cent and sixty-two per cent 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%).

3.3 | Preference of lianas to resource niches

Forty-six out of the 50 species tested occurred at significantly higher or lower resource conditions for one or more soil nutrients than expected at random (Table 1). Nine species (such as *Byttneria aspera*, *Uvaria kweichowensis*, and *Tetrastigma cauliflorum*) were specialized for nutrient-rich conditions (i.e., for 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 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 steep places for their distribution (i.e. high slope).

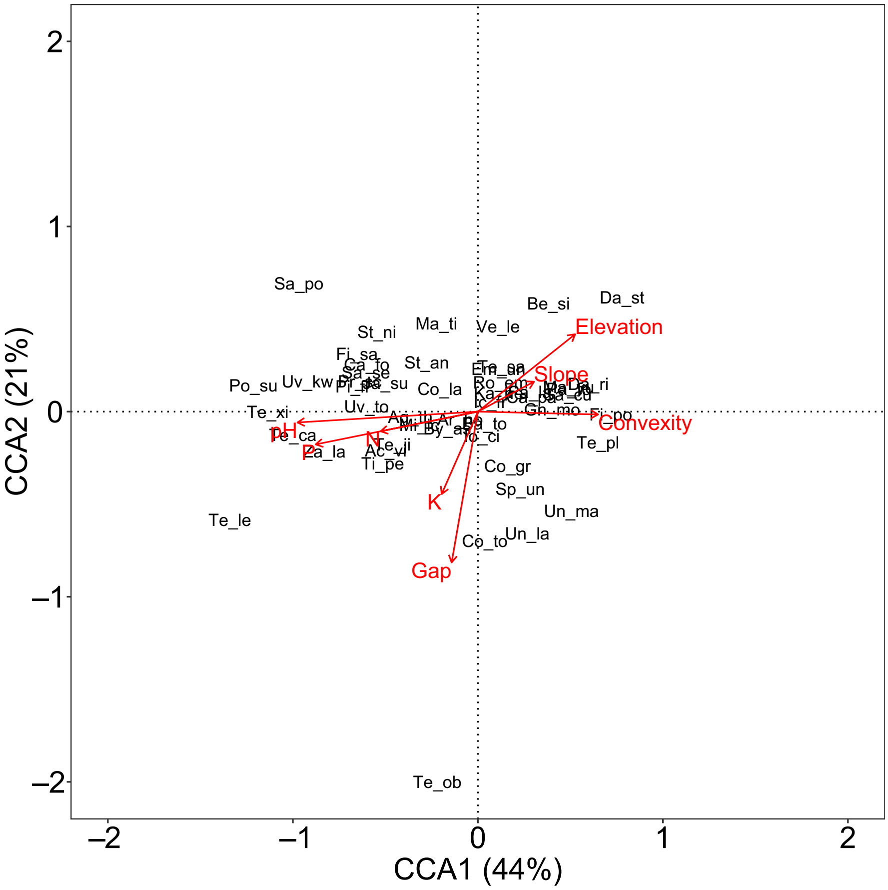

FIGURE 3 Canonical Correspondence analysis (CCA) ordination plots showing the distribution of the 50 dominant liana species and the associations with environmental factors in the Xishuangbanna 20-ha tropical seasonal rain-forest dynamics plot. CCA1 and CCA2 are plotted and the arrows represent the explanatory variables used in the analysis. For species names and codes see Table 1

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 concentrations of N and K, but not of P.

4.1 | Soil nutrient concentrations vary across the landscape, and with topography and gap

We hypothesized that soil nutrient concentrations decrease with elevation because nutrient fertility is high in deep clayey soils on 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), in line with the hypothesis. Moreover, we observed that soil nutrient concentrations decreased with slope (Figure 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 accumulate downslope (Brubaker et al., 1993). Alternatively, transport of soluble elements by the 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). 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., 2014).

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 gaps to establish and lianas tend to have fast growth and inherently high resource requirements (Schnitzer et al., 2014). Our results indicated that soil pH and P were the strongest drivers of liana distribution (Figure 3, Appendix S5), 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 3). The Xishuangbanna forest plot occurs on latosol with pH values of 4.5–5.5, with mean soil pH being 4.9 (Appendix S4), which is slightly acid and quite similar to that in 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 on 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 a high aluminium level 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). 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 contradicted the hypothesis 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 3). Yet, 84% of the liana species showed a unimodal response, 12% a negative response and only 4% a positive response to soil P (Figure 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 still others at high-P sites (Figure 5). Previous studies on nutrients and plant growth have argued that P is more limiting than N in mature lowland tropical forests (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 & Syers, 1976; Brady & 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 5).

We hypothesized that gaps would have a strong effect on liana abundance because most lianas need gaps to establish. We found that gaps did affect species distribution along the second CCA axis

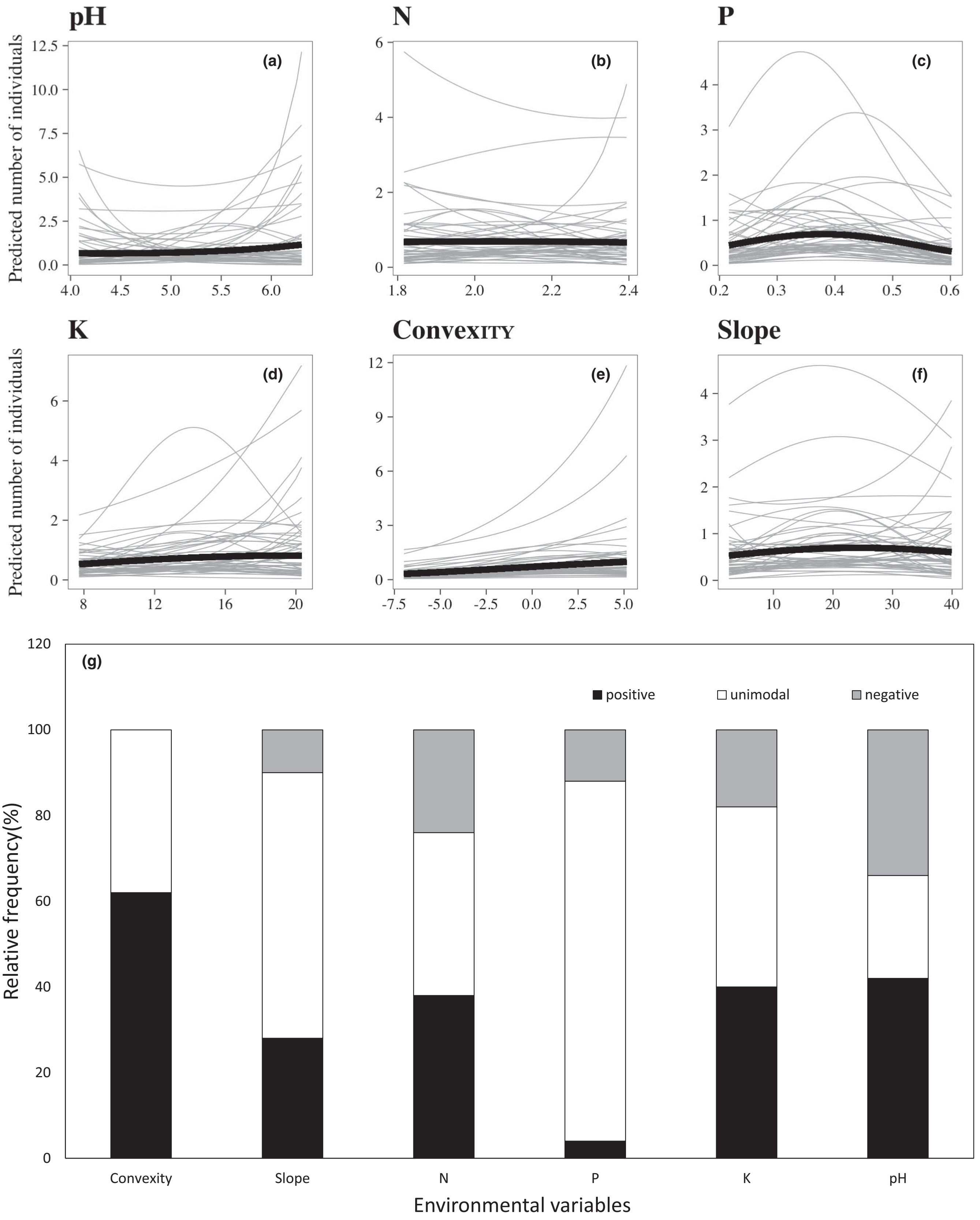

FIGURE 4 Effects of soil nutrients (pH, N, P, K, panels a, b, c, and d, respectively) and topography (convexity and slope, panels e and f respectively) on the community-level and species-level abundance of lianas. The dark black lines represent the community-level predictions and the light gray lines represent the (*n* = 50) species-level predictions from the best-fitting model. For community-level estimates and species-specific estimates see Appendix S4. Panel g indicates the percentage of species displaying the specific response modes (positive, unimodal, or negative) to the considered variables

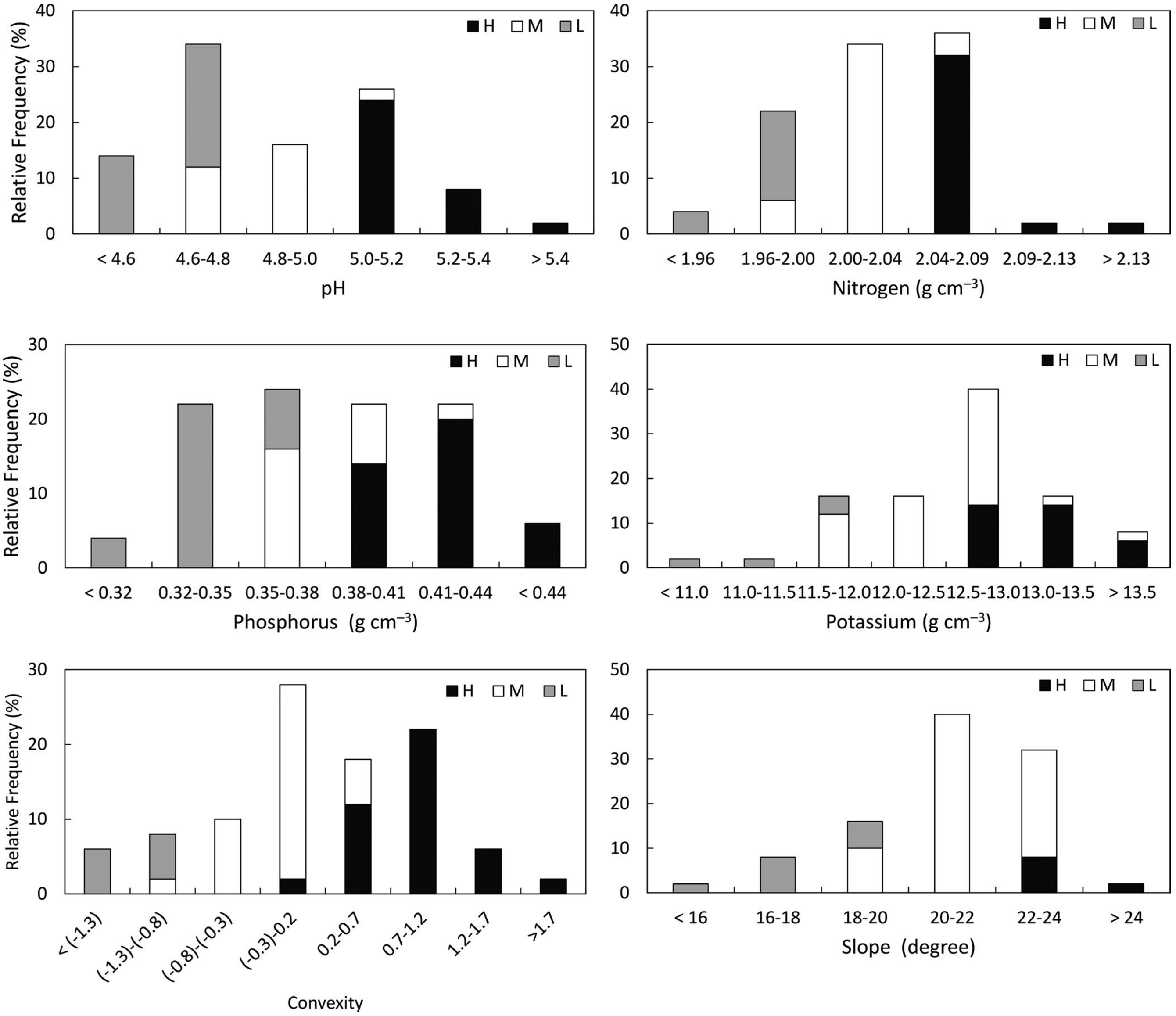

FIGURE 5 Frequency distribution of optimum (average weight) soil nutrient conditions (pH, nitrogen, phosphorus, potassium) and topographic conditions (convexity and slope) of 50 liana species. The figure summarizes the results of the randomization procedures for each species (Table 1), where species 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), or lower (L, gray) resource requirements. For those in the middle (M, white)

(Figure 3) and liana abundance in gaps was indeed higher than in non-gaps (Appendix S8). Other studies also found lianas respond favourably to canopy disturbance (Putz, 1984; Schnitzer et al., 2000; Malizia & 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 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 the DCA analysis (Appendix S6). Several reasons may explain the relatively 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 the 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.

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., 2014) and we found that liana optima of most species were located at higher soil resource availability for K and N (Figure 5), which indicates that those species specialize for high resources. Probably lianas need a 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). 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 1, Figures 3, 5). At the same time, liana preferred higher convexity and lower slope where more light was available and soil moisture and nutrients accumulated (Figure 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), thus rejecting the idea that all lianas behave as acquisitive species.

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 goes together with their fast growth and acquisitive strategy of resource use. Overall, these results highlight that below-ground resource availability plays an important role in shaping liana community assembly, partially independently of the known effects of higher light conditions.

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AUTHOR CONTRIBUTIONS

QL, FS, JLZ, and LP conceived the ideas and designed methodology; QL, LQS, and MC collected the data; QL and JMV analyzed the data; QL, JMV, JLZ, FS, and LP led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data used in this study are provided in Appendix S11 of the Supporting Information.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1 Variance Inflation Factors (VIF) for the covariates included in the generalized linear mixed-effects models (GLMMs)

Appendix S2 DHARMa Moran's I test for spatial autocorrelation

Appendix S3 Sample code for generalized linear mixed-effects models (GLMMs) R script

Appendix S4 Statistical description of soil variables

Appendix S5 Canonical correspondence analysis output for explanatory variables

Appendix S6 Associations between the liana community composition (using the ordination axes of a detrended correspondence analysis [DCA]) and environmental variables

Appendix S7 Detrended correspondence analysis (DCA) ordination plot

Appendix S8. Output for the best-fitted generalized linear mixed-effects models (GLMMs) at the community level

Appendix S9 Group level coefficients (random effects) for the abundance of lianas (>1 cm stem diameter) as a function of soil nutrients, topography, and gap

Appendix S10 Output for the best-fitted generalized linear mixed-effects models (GLMMs) at the species level

Appendix S11 Data set

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