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Determinant factors influencing the spatial distributions of subtropical lianas are correlated with components of functional trait spectra

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Abstract Lianas are important vegetation components that control structure and function, especially in tropical and subtropical forests. To explore the spatial assembly mechanisms of a subtropical liana community, we tested the following hypotheses: spatial distributions of subtropical lianas are determined by forest structures and topographic features, which are surrogates for host/light availability and edaphic/water conditions, respectively, and these effects are mediated through species functional traits. We examined the spatial distribution of lianas in two plots (areas 9 and 16 ha) representing landscapes in an intact forest and a secondary forest, and analyzed spatial distribution pattern at the species level using a simple, spatially explicit model. We also examined the correlations between determinant factors for species distribution and species functional traits, including climbing habits, leaf traits and wood density. The spatial distribution of lianas was controlled mainly by topographic gradient. Most species had preferences for concave topographies, i.e., valley habitats. Any covariates related to the host (or to light) had little influence on the distribution of most liana species. Distributional responses to topography were different among species, and associated significantly with leaf nitrogen content and climbing habit, but not with wood density. The correlation between variation in habitat preferences and leaf economic spectrum suggests that an environmental

filter for physiological response to topography is the important mechanism shaping the spatial patterns of this subtropical liana community.

Keywords Environmental filter · Habitat preference · Leaf economic spectrum · Spatially explicit model · Topography

Introduction

Woody climbing plants (lianas) are important vegetation components that control forest structure and function especially in tropical and subtropical forests (Schnitzer and Bongers 2002). Lianas are most diverse in tropical forests, where they account for about 25 % of woody plant species (Gentry 1991). High leaf production rates in these climbing plants also contribute substantially to forest productivity (Hegarty 1991). Meanwhile, they have detrimental impact on tree communities by suppressing tree growth and elevating the mortality risk of canopy trees (Ingwell et al. 2010). Potential mechanisms determining assembly patterns (e.g., spatial distribution) of lianas should be explored to improve our understanding of the ecological roles of lianas in forests.

Climbing habits and physiological traits are key functional traits that structure liana communities (Bell et al. 1988; Hegarty and Caballé 1991). Climbing habit is generally classified into the following categories: twiner (twining by movement of branch shoots), root climber (clinging by adventitious roots), tendrillar (grasping by tendrils) and scrambler (leaning on surrounding structures). These climbing habits are related closely to the host tree-forms supporting the lianas; the upper tree-diameter limit for support is greatest for root climbers and smallest for tendrillar forms (Putz and Holbrook 1991). Establishment and growth of lianas are affected strongly by the availability of host trees (Putz 1984), a surrogate for forest structure (e.g., van der Heijden and Phillips 2008). Indeed, several studies have demonstrated that host preference among different climbing

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habits results in nonrandom patterns of distribution or abundances of lianas (DeWalt et al. 2000; Carrasco-Urra and Gianoli 2009).

Lianas generally have high light and nutritional demands. They are more abundant in well-lit spaces, such as those in canopy gaps and younger forests (Putz 1984; DeWalt et al. 2000); they grow in water- and nutrient-rich sites, such as those in forest stands located in the valleys of mountainous landscapes (Putz and Chai 1987; Kusumoto et al. 2008). In contrast, other studies have demonstrated that lianas include a range of species with diverse shade tolerances (Sanches and Valio 2002; Gilbert et al. 2006) and habitat preferences (Chettri et al. 2010). As in tree species, leaf traits, including leaf area and nitrogen content, which reflects acquisition and conservation of resources, are important explanatory factors in habitat differentiation among lianas (Ichihashi et al. 2010). These earlier studies indicated that the climbing growth form is not associated with any particular habitat, such as those that are well-lit (Gianoli et al. 2010), and a combination of climbing habit and physiological traits contributes to the diversification of a habitat preference spectrum among lianas. Therefore, quantification of species responses to environmental conditions that are likely associated with their functional traits is essential for improved understanding the spatial assembly mechanisms of these plants.

The mechanism that shapes the spatial distribution of liana species can be decomposed into three distinct, spatially structured causes: host tree availability, light availability and nutrient and/or water availability within a forest. The availability of host trees and light is determined by aboveground structures of tree vegetation, while availability of nutrients and/or water is determined by environmental heterogeneity, which is often a function of landscape topography. The relative importance of these causes is expected to differ among species with different functional traits. Such spatially structured ecological processes probably generate spatial autocorrelation in liana occurrence. Models that ignore spatial autocorrelation promote inaccurate parameter estimation and inadequate quantification of uncertainty (ver Hoef et al. 2001). Hierarchical modelling with inclusion of spatial dependent random effects largely contributes to the disentanglement of such confounding mechanisms while at the same time taking account of spatial autocorrelations (Ogle et al. 2006).

Subtropical forests in southern Japan occur in landscapes with complex topographies, frequent typhoon disturbance, and a history of silviculture. Within such settings, gradients of biotic and abiotic conditions allow us to analyze the spatial distributions of lianas in naturally occurring combinations of forest structures and topographic features. In the present study, we hypothesized that the spatial distribution of subtropical lianas is determined by host and light availabilities, and by edaphic/water conditions mediated through species

functional traits relating to plant economics. To test this prediction, we modelled spatial distributions of liana species using a simple, spatially explicit model that incorporates spatial random effects and species-dependent random effects to specify the relative importance of forest structure and topography on the occurrence probabilities of lianas in intact and secondary forests. We investigated functional traits including leaf traits (specific leaf area and leaf nitrogen content) and wood density, which can determine plant economics of resource acquisition and conservation (Wright et al. 2004; Chave et al. 2009), as well as climbing habit. Using the correlations between determinant factors for species distributions and functional trait spectra, we explored the spatial assembly mechanisms of the subtropical liana community.

Methods

Study site

The study was conducted in intact and secondary forests (3.2 km apart from each other) located in the northern part of Okinawa Island, in southern Japan. The climate of the region is maritime, subtropical; average annual precipitation is 2,535 mm, and monthly mean maximum and minimum temperatures are 27.1 and 14.9 °C, respectively, according to the nearest observatory (Oku Observatory, Japan Meteorological Agency), approximately 14 km apart from the study sites. Typhoons strikes are especially frequent during summer and autumn (June–October). Monsoon winds in winter are also a chronic stress for the forests. The old stage mountainous topography of the region has a high valley density. Total soil nitrogen contents and C:N ratios (0–5 cm depth) at the study site were 0.38–0.49 % and 19–11 on ridges and in valleys, respectively (T. E., unpublished data).

The vegetation was subtropical, evergreen, broad-leaved forest dominated by the evergreen oak species *Castanopsis sieboldii* and other broad-leaved species (Kubota et al. 2005). A large part of the woodland comprised unevenly aged secondary forest that developed after logging (Anonymous 1953); a few undisturbed stands were also present. The intact forest we studied was located in the Mount Yonaha Cultural Properties Area (26°43'N, 128°13'E). The canopy layer of the intact forest was dominated largely by *C. sieboldii* and *Distylium racemosum*; the canopy height was maximally 13.5 m (Kubota et al. 2005). A secondary forest we examined was located in the Yona Experimental Forest, University of the Ryukyus, Japan (26°45'N, 128°14'E). According to records of the Experimental Forest, small-scale clear-cutting or selective logging for fuel had occurred at this site, but no commercial logging or other artificial disturbance had been recorded in the previous 60 years. The canopy layer in this secondary forest was dominated largely by *C. sieboldii* and *Schima*

wallichii; the canopy height was maximally less than 20 m (Enoki 2003).

Data collection

Stem censuses were conducted in two study plots, i.e., the intact (8.0625 ha) and secondary forests (16.0625 ha). All liana stems ≥ 2 cm in diameter were tagged and recorded. The criteria of diameter measurement was the recommended maximum size to evaluate canopy lianas suggested by Gerwing et al. (2006). Diameters were measured using diameter tape following Gerwing et al. (2006), which involved measurements 1.3 m above the main root or 0.5 m above the highest adventitious root when adventitious roots emerged > 1.3 m from the main root. When branching occurred close to the ground, each branch was measured separately at 1.3 m height and recorded as “multiple stems”. Root positions (coordinates of latitude and longitude) of lianas were determined by a location survey with a global positioning system (GPS) device and a digital location survey device combining a compass, laser distance meter, and an inclinometer (LaserAce 300; Trimble, CA). More details of the survey location are provided by Kusumoto et al. (2008). We conducted the stem censuses for lianas in 2007 in the secondary forest (Kusumoto et al. 2008) and in 2008 in the intact forest. To obtain data on forest structure, we measured and recorded positions of tree stems ≥ 30 cm in diameter at breast height using methods that we used previously in 2008. Species nomenclature used here follows Yonekura and Kajita (2003).

Leaf sampling was conducted near the study plots in August 2008 and April 2009. Living leaves were collected from an average of five individuals per liana species recorded in the stem census. Fully expanded intact leaves were taken from the tops of the crowns by cutting off ordinary shoots using tree pruners or wire saws with the aid of a large slingshot (BIG SHOT[®]; Sherrilltree, NC). Using LIA32 software (ver.0.376 β 1, K. Yamamoto, Nagoya University, Nagoya, Japan), we calculated leaf lamina areas for 4–10 leaves per each individual. Subsequently, leaves were oven-dried at 70 °C for 48 h, after which dry mass was measured. After mass measurement, we measured leaf nitrogen concentration at the individual leaf level using a CN analyzer (Yanaco CN coder MT-700; J-Science Lab, Osaka, Japan).

To measure wood density, wood sampling was conducted near the study plots in March 2012. We collected wood samples by cutting lignified liana stems (1–3 cm in diameter) near the roots from five individuals per liana species. Wood samples were debarked and soaked in distilled water for 12 h to allow water absorption to the potentially maximum limit; we then measured wet mass. Wood volume was determined for wet samples by volume displacement of distilled water in a sealable glass bottle. Subsequently, we dried the wood at 70 °C for at

least 72 h, after which we measured the dry mass to calculate wood density (dry mass/volume; g cm^{-3}). In this manner, we assembled data for four functional traits: climbing habit, specific leaf area (SLA), leaf nitrogen, and wood density.

The plots in the intact and secondary forests were divided into 129 and 257 cells measuring 25×25 m, respectively, based on a rectangular plane coordinate system (Japan Plate Carree JGD 2000 Zone XV; Japan Coordinate System). For each cell, we calculated two topographic indices, a relief index and slope inclination, using a 10×10 -m digital elevation model (DEM; GIS-MAP Terrain ver. 2.0; Hokkaido-Chizu, Hokkaido, Japan). The relief index was calculated using concavity and convexity indices based on the concept of below- and aboveground openness developed by Yokoyama et al. (2002). Concavity and convexity were defined as the sums of maximum and minimum elevation angles, respectively, for eight azimuths. The maximum (or minimum) elevation angle was defined as the angle between a given DEM point and the highest (or lowest) DEM point within 100 m in an azimuth direction. Thus, the relief index was defined as the reverse of the arithmetic average between convexity and concavity; a relief index of zero indicated a flat plane, and positive and negative values indicated convex and concave topographies, respectively. Slope inclination of each DEM point was calculated as the inclination of a plane vector constructed from the surrounding eight DEM points.

Statistical modelling

To explore the effects of the forest structures and topographic features on spatial distributions of liana species, we constructed a hierarchical Bayesian model with spatial autocorrelation incorporated, i.e., spatial random effects. Five variables (tree species richness, tree density, tree basal area, relief index, and slope inclination) were included as covariates. Tree species richness and tree density acting as surrogates for host availability may be interpreted as biotic factors. Total basal area was indicative of biomass development and treated as a surrogate of the light environment (Kohyama 1992); total basal area was also interpreted as a biotic factor. Relief index and slope inclination were interpreted as topographically controlled edaphic factors, i.e., abiotic factors. These covariates were centered by subtracting the respective sample mean of each variable from all of its values.

A random intercept and slope model (Zuur et al. 2009) was used to analyze the occurrence of liana species. We assumed that the occurrence of liana species was a Bernoulli process with occurrence probability P :

$$Y_{ij} \sim \text{Bernoulli}(p_{ij}) \quad (1)$$

where Y_{ij} is the presence or absence (1/0) of liana species j in cell i . Then, we expressed logit of p_{ij} as linear function:

$$\begin{aligned} \log \text{it}(p_{ij}) = & (\beta_0 + b_{0j}) + (\beta_1 + b_{1j})x_{1i} + (\beta_2 + b_{2j})x_{2i} \\ & + (\beta_3 + b_{3j})x_{3i} + (\beta_4 + b_{4j})x_{4i} + (\beta_5 + b_{5j})x_{5i} \\ & + (\gamma + c_j)z_i + \varepsilon_i \end{aligned} \quad (1)$$

where x_{iS} (x_{1i} , x_{2i} , x_{3i} , x_{4i} , x_{5i}) are values of the covariates in cell i (x_1 = tree species richness, x_2 = tree stem density, x_3 = tree basal area, x_4 = relief index, x_5 = slope inclination). β_S (β_0 , β_1 , β_2 , β_3 , β_4 , β_5) are the overall component parameters representing the averaging trend of lianas associated with the predictors (β_0 = intercept, β_1 = effect of tree species richness, β_2 = effect of tree stem density, β_3 = effect of tree basal area, β_4 = effect of relief index, and β_5 = effect of slope inclination). b_{jS} (b_{0j} , b_{1j} , b_{2j} , b_{3j} , b_{4j} , b_{5j}) are species-dependent parameters corresponding to the overall component parameters. z_i , γ , and c are the variable and parameters associated with plot differences in the occurrence probability of liana species. In the model, z_i are logical values indicating whether cell i is located in the intact forest (= 0) or secondary forest (= 1). γ is a parameter that represents the averaging trend of plot differences. c_j is species-dependent plot differences, and ε_i are the spatial random effects at the cell level.

For the overall components (β_0 , β_1 , β_2 , β_3 , β_4 , β_5 , γ), we assigned non-informative normal priors with means of zero and large variance [normal (0, 10^4)]. For the species-dependent parameters (b_{0j} , b_{1j} , b_{2j} , b_{3j} , b_{4j} , b_{5j} , c_j), we assigned normal priors with means of zero and specified variance representing degree of species difference ($\sigma_{b_0}^2, \sigma_{b_1}^2, \sigma_{b_2}^2, \sigma_{b_3}^2, \sigma_{b_4}^2, \sigma_{b_5}^2, \sigma_{c_j}^2$). For these variance parameters, we assigned non-informative uniform priors [uniform (0, 10^4)].

The occurrence probability of lianas depended on values in a spatial neighbourhood. The intrinsic conditional autoregressive (CAR) model can examine spatial autocorrelation simply as spatial random effects at cell level using neighbourhood information and unknown variance parameters (Besag 1974). Spatial random effects were estimated independently for the two plots; i.e., the vector of spatial random effects for each cell was divided into ε_{1-129} (cells in the intact forest) and $\varepsilon_{130-386}$ (cells in the secondary forest). In the CAR model, the spatial random effect ε in cell i in each plot is represented by a distribution conditioned by all other cells $m \neq i$. Assuming that ε_i depends only on the neighbours (the eight immediately adjacent cells surrounding cell i), which we designate as $\{n_i\}$ consisting of n_i cells, then the conditional distribution for ε_i was specified as;

$$\varepsilon_i | \{\varepsilon_m, m \in \{n_i\}\} \sim \text{Normal} \left(\sum_{m \in \{n_i\}} w_{im} \varepsilon_m / n_i, v_i^2 / n_i \right) \quad (3)$$

where w_{im} represent the weight of each neighbourhood cell, which is assumed to be 1 in this study. Therefore, conditional means of the CAR are equal to the mean of

the random effects for the neighbours, while conditional variances are inversely proportional to the number of neighbours, n_i . Variance parameters, v_l^2 ($l = 1, 2$), control amount of variation in random effect, i.e., intensity of spatial autocorrelation. For v_l^2 , we assigned non-informative uniform priors [uniform (0, 10^4)].

Posteriors of the model parameters were estimated by the Markov chain Monte Carlo (MCMC) method using WinBUGS software (ver. 1.4.3; Lunn et al. 2000). We ran the MCMC sampling for 60,000 iterations of three chains with a thinning interval of 20 iterations. We discarded the first 30,000 samples as burn-in. We judged the convergence of the chains by whether the Gelman–Rubin statistic (Gelman and Rubin 1992) was smaller than 1.1.

After parameter estimation, we calculated for each combination the correlation coefficient between the species-dependent parameter corresponding to the covariates (tree species richness, tree density, total basal area, relief index, and slope inclination) and species functional traits (climbing habit, SLA, leaf nitrogen content, and wood density). For climbing habit as a categorical variable, we calculated the coefficient of determination ($1 - \text{sum of the within-group sum-of-squares} / \text{total sum-of-squares}$) and used its square root as the correlation ratio. The significances of these correlations were judged by a P value with 5 % significance level. These analyses were performed using R software (ver. 2.14, R Development Core Team, Vienna, Austria).

Results

Liana community structure and functional traits

We recorded a total of 2,894 trees (≥ 30 cm in diameter) belonging to 35 species in the two study plots (see Table S1 and S2 in the online supplements). We observed 1,528 stems of lianas representing 22 species in total, incorporating data for lianas in the secondary forest provided by Kusumoto et al. (2008) (Table 1). The spatial distributions of trees and lianas are shown in Fig. 1. *Morinda umbellata* was the dominant species in terms of total stem counts. Four climbing habits were identified, i.e., twiner, root climber, scrambler, and tendrillar.

Functional traits of each species were also shown in Table 1. SLA values ranged from 8.0 to 26.6 $\text{mm}^2 \text{mg}^{-1}$. Five root climber species had lower SLA values than other climbers. Leaf nitrogen content ranged from 1.15 to 4.01 % and was especially high in *Trichosanthes miyagii*, *Elaeagnus glabra*, and *Mucuna macrocarpa*. Root climbers and some twiner species had lower leaf nitrogen than the other species. Wood density ranged from 0.27 to 0.55 g cm^{-3} . *Erycibe henryi* and *Jasminanthes mucronata*, were not sampled and were excluded from the modelling because of their extremely low occurrence frequencies (each was present in only one cell).

Table 1 List of liana species recorded in the study plots, numbers of stems, and species functional traits

Species	Family	Stems ^b	CH	SLA (mm ² mg ⁻¹)	LN (%)	WD (g cm ⁻³)
<i>Morinda umbellata</i>	Rubiaceae	91/304	TW	18.5 ± 2.4	1.79 ± 0.07	0.34 ± 0.04
<i>Actinidia rufa</i>	Actinidiaceae	62/201	TW	18.0 ± 2.9	1.99 ± 0.31	0.39 ± 0.02
<i>Pileostegia viburnoides</i>	Hydrangeaceae	183/35	RC	10.8 ± 1.5	1.45 ± 0.21	0.27 ± 0.03
<i>Anodendron affine</i>	Apocynaceae	28/89	TW	8.3 ± 1.6	1.29 ± 0.24	0.40 ± 0.05
<i>Trachelospermum gracilipes</i>	Apocynaceae	67/25	RC	9.6 ± 1.9	1.31 ± 0.20	0.39 ± 0.02
<i>Mucuna macrocarpa</i>	Fabaceae	0/67	TW	20.8 ± 6.7	3.11 ± 0.57	0.45 ± 0.05
<i>Ficus thunbergii</i>	Moraceae	41/21	RC	9.4 ± 1.4	1.49 ± 0.17	0.48 ± 0.04
<i>Mussaenda parviflora</i>	Rubiaceae	29/29	TW	20.1 ± 3.7	1.86 ± 0.28	0.41 ± 0.02
<i>Coptosapelta diffusa</i>	Rubiaceae	1/48	TW	15.8 ± 4.0	1.28 ± 0.23	0.55 ± 0.01
<i>Lonicera affinis</i>	Caprifoliaceae	27/7	TW	14.2 ± 3.1	1.40 ± 0.17	0.45 ± 0.01
<i>Rubus × utchinensis</i>	Rosaceae	17/13	SC	15.4 ± 1.4	1.93 ± 0.42	0.44 ± 0.01
<i>Kadsura japonica</i>	Schisandraceae	3/24	TW	24.8 ± 8.2	1.89 ± 0.42	0.46 ± 0.04
<i>Ficus nipponica</i>	Moraceae	11/15	RC	8.0 ± 1.7	1.34 ± 0.09	0.48 ± 0.02
<i>Trichosanthes miyagii</i>	Cucurbitaceae	7/17	TD	23.8 ± 5.6	4.01 ± 0.49	0.27 ± 0.07
<i>Elaeagnus glabra</i>	Elaeagnaceae	13/6	SC	17.5 ± 2.1	3.47 ± 0.36	0.50 ± 0.06
<i>Berchemia racemosa</i>	Rhamnaceae	6/9	TW	26.6 ± 5.2	2.00 ± 0.31	0.27 ± 0.03
<i>Stauntonia hexaphylla</i>	Lardizabalaceae	4/8	TW	11.7 ± 1.7	1.15 ± 0.14	0.36 ± 0.02
<i>Zanthoxylum scandens</i>	Rutaceae	5/5	SC	16.7 ± 1.2	2.02 ± 0.34	0.41 ± 0.00
<i>Psychotria serpens</i>	Rubiaceae	0/5	RC	9.3 ± 0.6	1.30 ± 0.19	0.35 ± 0.03
<i>Aristolochia liukuensis</i>	Aristolochiaceae	0/2	TW	17.6 ± 1.2	1.76 ± 0.14	0.39 ± 0.02
<i>Erycibe henryi</i> ^a	Convolvulaceae	2/0	TW			
<i>Jasminanthes mucronata</i> ^a	Asclepiadaceae	1/0	TW			

Number of stems in the intact forest (left) and the secondary forest (right) were shown

Functional traits were climbing habit (CH) (*TW* twiner, *RC* root climber, *SC* scrambler, *TD* tendrillar), specific leaf area (SLA), leaf nitrogen content (LN), and wood density (WD). Values of the numerical functional traits are mean ± standard deviation

^aThese species were not used in statistical modelling because they occurred in only one cell; their leaves and stems were not sampled

^bData of the secondary forest were cited from Kusumoto et al. (2008)

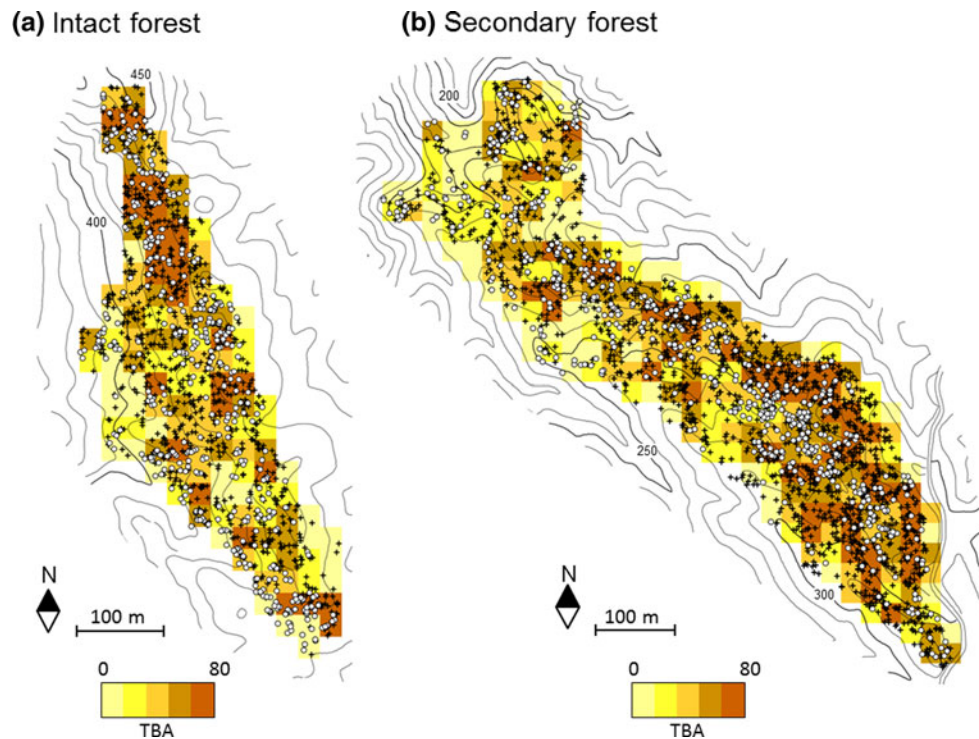


Fig. 1 Spatial maps of lianas and trees in the two study plots. The *white circles* and *cross symbols* represent individual lianas (≥ 2 cm in diameter at breast height) and trees (≥ 30 cm in diameter at breast height), respectively. Contour intervals are 10 m. Cells (25 × 25 m

grids) are colored according to total tree basal area (TBA m² ha⁻¹). Data for lianas in the secondary forest are from Kusumoto et al. (2008). **a** Intact forest, **b** secondary forest

Spatial distribution of liana species

The Gelman–Rubin statistic was less than 1.1 (see Fig. S1 in the online supplements) for all parameters of the hierarchical Bayesian model incorporating with

spatial random effect, indicating that three parallel MCMC chains converged the same estimate. The spatial random effect had no significant correlation with covariates other than slope inclination (Fig. 2; a spatial map of random effects is provided in Fig. S2 in the

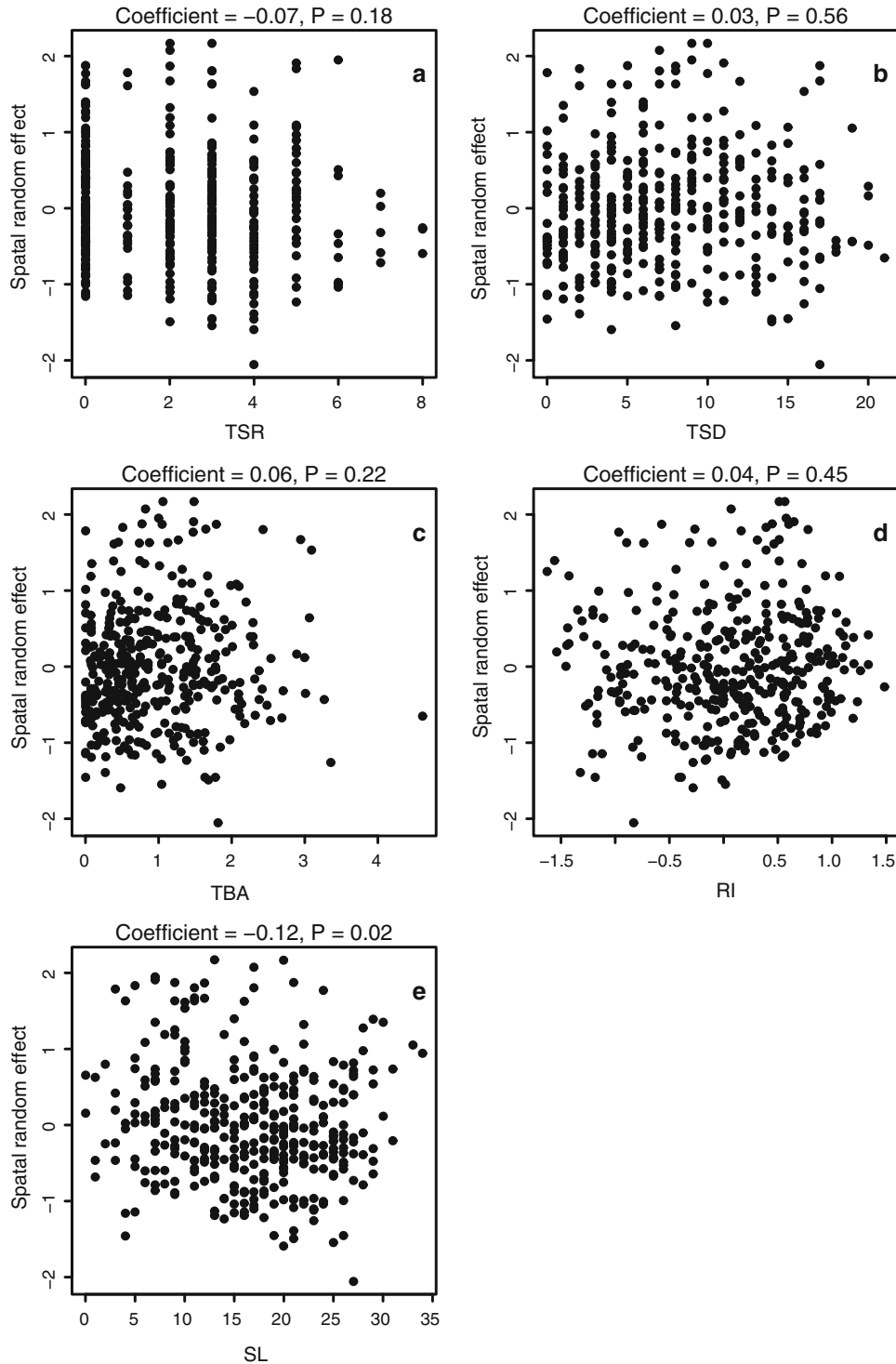


Fig. 2 Relationships between spatial random effects and covariates, and results of correlation analyses. The covariates are **a** tree species richness (TSR), **b** tree stem density (TSD), **c** tree basal area

(TBA), **d** index of ground surface relief (RI), and **e** slope inclination (SL). The spatial random effects were estimated using the intrinsic conditional autoregressive (CAR) model

Table 2 Summary statistics [mean, standard deviation (SD), 2.5, 50 and 97.5 %] of posteriors for the overall components

Parameter ^a	Mean	SD	2.5 %	50 %	97.5 %
β_0	-3.242	0.462	-4.188	-3.229	-2.364
β_1	-0.029	0.063	-0.156	-0.027	0.093
β_2	0.072	0.038	-0.003	0.072	0.146
β_3	-0.028	0.266	-0.546	-0.027	0.484
β_4	-1.496	0.239	-1.985	-1.493	-1.050
β_5	0.014	0.015	-0.015	0.014	0.045

^aParameters indicate common distributional trends among liana species: β_0 , intercept; β_1 , effect of tree species richness; β_2 , effect of tree stem density; β_3 , effect of tree basal area; β_4 , effect of relief index; β_5 , effect of slope inclination

online supplements). Conditional variances (v^2 , determining strength of spatial autocorrelation) were similar between the two plots: posterior means were 5.1 and 4.1 for intact and secondary forests, respectively.

Most of the posterior distributions for the overall components (β) that represented common distributional trends between liana species included zero in their 95 % confidence intervals (Table 2). Only the relief index had a significant negative relationship with the occurrence probability of lianas.

Posterior distributions of species-dependent parameters related to the relief index did not include zero in the 95 % confidence intervals when the posterior mean of the overall component was added (Fig. 3). Species-dependent parameters for the relief index varied greatly between species: posteriors for some species did not include the posterior mean of the overall component in their 95 % confidence intervals (i.e., were significantly higher or lower than the liana overall mean). Most of the species-dependent parameters for the other covariates included zero in their 95 % confidence intervals and varied little between species. Some species had significant relationships with tree density. Only one species (*Ficus nipponica*) had a significant relationship with slope inclination. No species had significant relationships with tree species richness or tree basal area.

Correlations between the determinant factors of spatial patterns and functional traits

Some significant correlations were observed between variation in species-dependent parameters associated with covariates and species functional traits (Table 3). The variation in species-dependent parameters for the relief index was correlated significantly negatively with leaf nitrogen content and significantly with climbing habit. Other combinations were not significant.

Discussion

Spatial pattern analysis has a long tradition in plant ecology (Schlup and Wagner 2008), and a wide variety

of methods are available as reviewed by Dale (1999). One of the problems in spatially structured ecological data is spatial autocorrelation (Legendre 1993). We applied a hierarchical Bayesian model incorporating spatial random effects to analyze spatial patterns of species for improved understanding of spatial assembly mechanisms in subtropical lianas. Weak and insignificant correlations between covariates and spatial random effects indicate that the hierarchical model successfully separated the effects of spatial autocorrelation from the effects of spatially structured covariates, and thus the model specified species responses to biotic and abiotic factors. Our approach revealed the relative importance of spatially dependent ecological processes on the occurrence probability of each liana in intact and secondary forests; we demonstrated variation in habitat preference among species.

The spatial pattern of liana species can be explained by two distinct mechanisms, i.e., host and light availability associated with forest structure (Carrasco-Urra and Gianoli 2009; Blick and Burns 2011) and nutrient/water availability along topographic gradients (Malizia et al. 2010). For parameters associated with topography, particularly the relief index, we detected a significant effect on the occurrence of lianas in the overall component and also in most of the species-dependent parameters. However, for parameters associated with forest structures, we detected no significant effects in the overall component or in most of the species-dependent parameters. Although the occurrence of some liana species was influenced by tree stem density, the effect was relatively marginal. These results suggest that topographic variation is more important than forest physiognomy in structuring spatial patterns of subtropical liana species. This finding does not rule out the importance of host or light availability, but may be ascribed to a characteristic in canopy structure of the subtropical forest. Several studies, particularly those set in forests with highly heterogeneous vertical structure, have demonstrated the influence of host structures and light conditions on the distribution and abundance patterns of lianas (e.g., DeWalt et al. 2000; Carrasco-Urra and Gianoli 2009). On Okinawa, chronic wind stresses, including those inflicted by typhoons, prevent the development of vertical structure in forests, so that canopies are shaped into homogeneous and continuous surfaces without emergent trees (Kubota et al. 2004). Such a reduced gradient of heterogeneity in canopy structure may obscure spatial partitioning of liana species among levels of host or light availability.

Ground surface relief was related negatively to the occurrence probability of all liana species. Thus, subtropical lianas are distributed preferentially in concave topographies, i.e., valley habitats. Interestingly, no liana species occurred preferentially on convex topographies. The valley habitat is often characterized by high soil water content, nutrient availability (Gessler et al. 2000), and low susceptibility to wind disturbance (e.g., Bellingham 1991). In subtropical forests, spatial heterogeneity

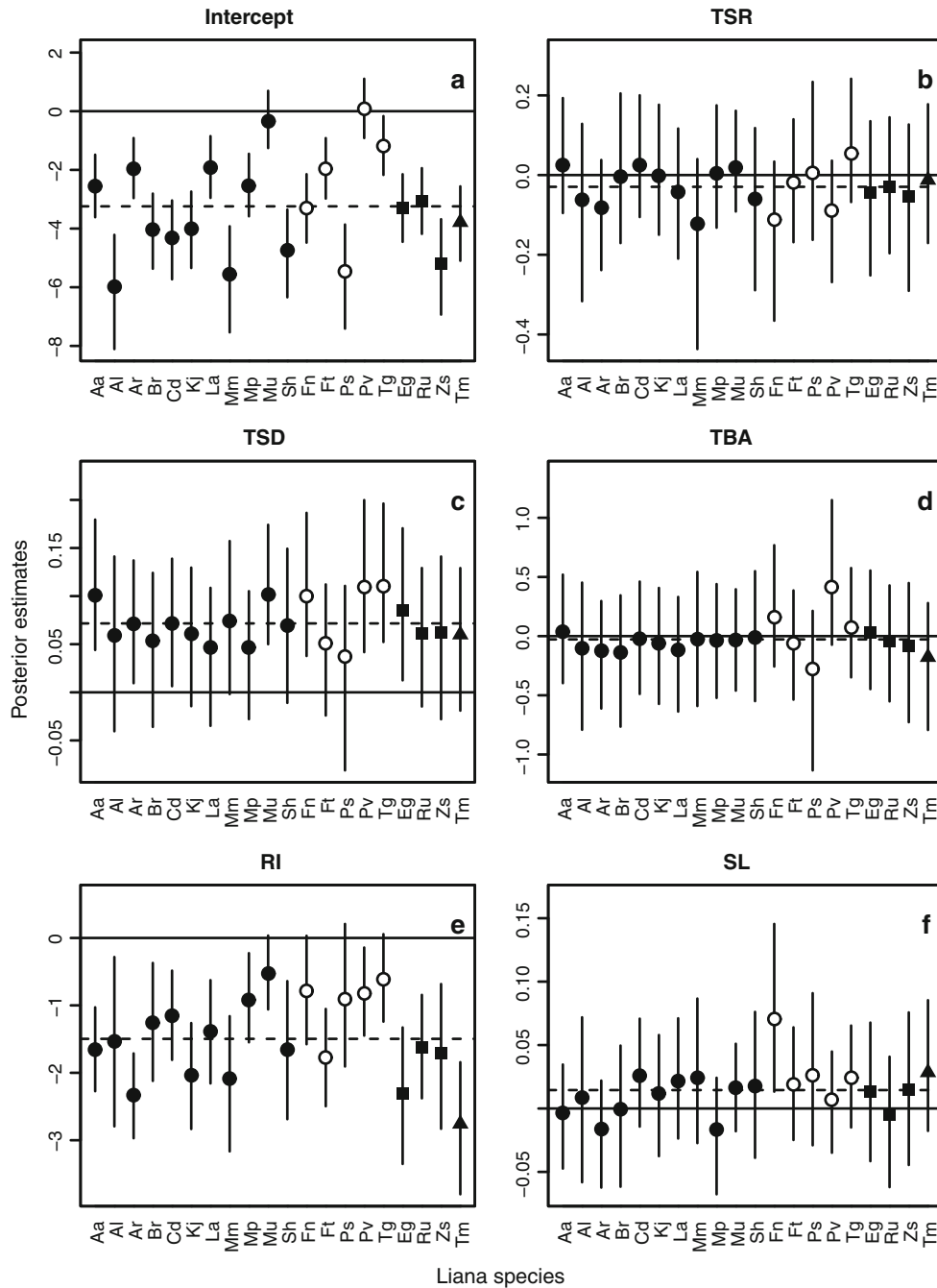


Fig. 3 Posteriors of species-dependent parameters for predictors. Note that the posterior means of overall components were added to the posteriors of species-dependent parameters. *Line segments* represent 95 % confidence intervals for estimates of the parameters. *Filled circles, open circles, filled squares, and filled triangles* represent posterior means of the parameters for twining, root climbers, scramblers, and tendrillers, respectively. *Horizontal solid lines and dashed lines* represent zero and posterior means, respectively, of overall components: **a** intercept, **b** tree species richness (TSR), **c** tree density (TSD), **d** tree basal area (TBA),

e index of ground surface relief (RI), and **f** slope inclination (SL). Species abbreviation codes: Aa, *Anodendron affine*; Al, *Aristolochia liukuensis*; Ar, *Actinidia rufa*; Br, *Berchemia racemosa*; Cd, *Coptosapelta diffusa*; Eg, *Elaeagnus glabra*; Fn, *Ficus nipponica*; Ft, *Ficus thunbergii*; KJ, *Kadsura japonica*; La, *Lonicera affinis*; Mm, *Mucuna macrocarpa*; Mp, *Mussaenda parviflora*; Mu, *Morinda umbellata*; Ps, *Psychotria serpens*; Pv, *Pileostegia viburnoides*; Ru, *Rubus ×utchinensis*; Sh, *Stauntonia hexaphylla*; Tg, *Trachelospermum gracilipes*; Tm, *Trichosanthes miyagii*; Zs, *Zanthoxylum scandens*

is observed in edaphic factors, including soil water across topographic gradients (Hara et al. 1996; Kubota et al. 2004). Wind-induced canopy gaps occur most frequently in ridge habitats, making convex topogra-

phies relatively well-lit (Kubota et al. 2004). This study and previous works indicate that spatial patterns of liana species are more influenced by the gradient of edaphic conditions across topographies than by gradi-

Table 3 Correlations between determining factors of distribution and functional traits of liana species

Parameter ^a	CH	SLA	LN	WD
b_1	0.14	0.02	-0.22	-0.06
b_2	0.28	-0.36	-0.12	-0.05
b_3	0.44	-0.39	-0.23	0.01
b_4	0.68*	-0.42	-0.70**	-0.09
b_5	0.52	-0.33	-0.07	0.24

* $p < 0.05$, ** $p < 0.01$

^aPosterior means for species-dependent parameters were used as the determining factors associated with covariates: b_1 = effect of tree species richness, b_2 = effect of tree stem density, b_3 = effect of tree basal area, b_4 = effect of relief index, and b_5 = effect of slope inclination. Functional traits are climbing habit (CH), specific leaf area (SLA), leaf nitrogen content (LN), and wood density (WD). At the calculation, we transformed LN values following equation $\sin^{-1} \sqrt{\text{LN}}$

ents of light environment (canopy gaps) (Malizia et al. 2010).

Our modelling, which incorporated a species-dependent random effect, revealed large variation among liana species in the species-dependent parameters associated with the relief index, even though most species occurred preferentially in valley habitats. Thus, environmental filtering related to topography plays an important role in the spatial assembly patterns of subtropical lianas. Notably, we found that differences in habitat preferences were correlated significantly with the spectrum of leaf nitrogen content and climbing habit. Such functional traits influencing performance (e.g., growth, survival, and reproduction) are widely accepted as indicators of environmental requirements or the tolerances of individual species (Grime 1977; Westoby et al. 2002). Thus, variation in these traits among liana species may be regarded as an economic spectrum (Wright et al. 2004; Chave et al. 2009) responsible for mechanistic links between environmental filtering and habitat differentiation (Keddy 1992; Díaz et al. 1998).

High nitrogen content and/or large SLA reflect competitive ability in terms of net photosynthetic capacity, but also to a low stress-tolerance (Dahlgren et al. 2006). For example, occurrences of *T. miyagii*, *M. macrocarpa*, and *E. glabra*—species characterized by high nitrogen content and large SLA—were restricted strongly to valley habitats. The dominant species, *M. umbellata* had intermediate characteristics in the trait spectrum of subtropical lianas. The high abundance of *M. umbellata* may be derived from leaf functional traits of this generalist species, which does not have specialized traits for specific abiotic conditions that occur in valley or ridge sites. These observations demonstrate that the leaf economic spectrum contributes to habitat differentiation between species. On the other hand, climbing habits reflect a plant's capability for ascending into the canopy layer or for exploring well-lit habitats. The significant correlation between climbing habit and habitat preference resulted from spatial patterns of the root climbers, such as *Trachelospermum gracilipes*,

F. nipponica, *Pileostegia viburnoides*, and *Psychotria serpens*. These species had weaker preferences among topographies than other species characterized as different climbing habits (see Fig. 3) and had low leaf nitrogen concentration and small SLA (see Table 1). These leaf traits jointly promote a low photosynthesis (Reich et al. 1999), which is economically advantageous in shady environment where root climbers usually expand their foliage, i.e., inside the canopy (Ichihashi and Tateo 2011). This convergence of leaf traits may allow root climbers to persist under diverse environmental conditions in subtropical forests. These suggest that habitat differentiation due to environmental filtering may be explained by leaf traits spectrum merged with climbing habits.

In contrast, stem economic spectrum (represented by wood density) did not correlate with habitat preference among liana species. One potential explanation may be that little variation in wood density exists due to (the climber) life-form. Wood density represents investment in mechanical properties and water transport efficiency. Thickening of wood results in mechanical stability (van Gelder et al. 2006), while low wood density is related to high hydraulic efficiency (Poorter et al. 2010). The liana growth form has high water transport efficiency and reduced allocation of biomass to mechanical tissues (Ewers and Fisher 1991). Therefore, lianas do not require the development of dense wood for mechanical support (Selaya and Anten 2008). In fact, the wood densities of subtropical lianas converged to values (mean = 0.26–0.54 g cm⁻³) lower than those of sympatric tree species (mean = 0.63 g cm⁻³ among 46 tree species; Fujii et al. 2009). Convergence in wood density among subtropical lianas may reflect low investment in mechanical support and consequent concentration of habitat preferences (frequently valley distributions) among species, but not diversification of habitat preference.

The correlation between variation in habitat preference and leaf economic spectrum suggests that the topographically associated environmental filter mediated through physiological traits of species is prevalent mechanism shaping spatial patterns of subtropical liana community. Our findings should improve understanding of the response of liana spatial dynamics to forest management in this region. Clear-cut logging in this subtropical forest has had an impact on tree species composition (Fujii et al. 2010), but no studies have reported increases in liana species in response to this logging regime, unlike other forests (e.g., Ding and Zang 2009). This difference may be due to potential mechanisms determining distribution of subtropical lianas that we identified in this study. The spatial distribution of subtropical liana species was shaped strongly by edaphic factors related to topography, rather than by forest structure. Despite silvicultural modification of host structure and light availability, the habitat of most subtropical lianas appears to be restricted mainly by environmental filtering through functional traits, which

may thus prevent species spreading beyond valley habitats.

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