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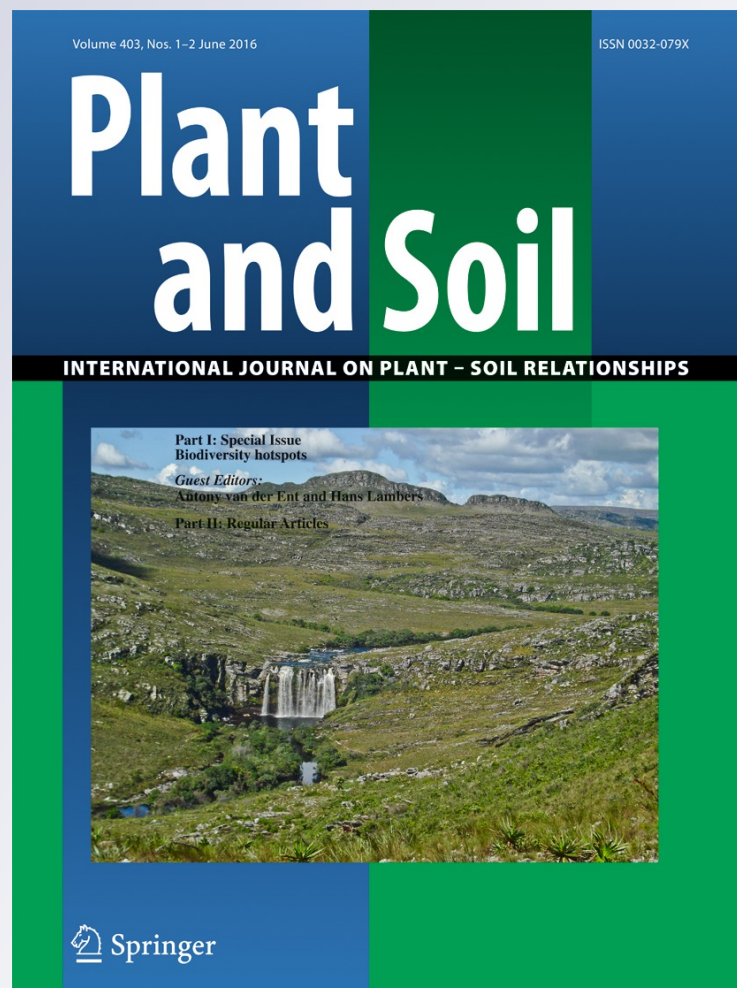
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G. Letcher, Yi Ding, Yunfeng Huang,
Xinghui Lu, Jihong Huang, Wande Liu &
Zhidong Zhang**

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Associations between plant composition/diversity and the abiotic environment across six vegetation types in a biodiversity hotspot of Hainan Island, China

Yong Jiang · Runguo Zang · Susan G. Letcher · Yi Ding ·
Yunfeng Huang · Xinghui Lu · Jihong Huang · Wande Liu ·
Zhidong Zhang

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Abstract

Aims Exploring the associations between vegetation and abiotic environments might increase our understanding of biodiversity formation mechanisms. Here, we explore variation in plant composition/diversity and their abiotic determinants across six vegetation types in a biodiversity hotspot of Hainan Island, China.

Methods We established twelve 1-ha permanent plots, two in each of the six old-growth forest types. All woody stems ($\text{dbh} \geq 1$ cm) and six soil and two microclimatic factors were measured. Associations between the abiotic factors and plant composition/diversity were analyzed by a spatial regressive model.

Results Plant diversity/composition changed with forest types. The key factors correlated with species

composition in deciduous monsoon forest were canopy openness and soil water content. Soil total nitrogen and pH were the vital determinants of diversity in coniferous forest. Soil water content, phosphorus and canopy openness were associated with higher diversities in lowland- and montane- rain forests. Soil organic matter and pH were the major factors influencing composition in the montane evergreen forest, whereas air temperature and soil total nitrogen were associated with the lowest diversity of the stunting statured montane dwarf forest.

Conclusions Variation patterns of plant composition/diversity across different forest types were closely associated with the changes in the six soil and two microclimatic factors within each forest.

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Y. Jiang
Key Laboratory of Ecology of Rare and Endangered Species and Environmental Protection of Ministry of Education; College of Life Science Guangxi Normal University, Guilin 541004, China

Y. Jiang · R. Zang (✉) · Y. Ding · Y. Huang · X. Lu ·
J. Huang · W. Liu · Z. Zhang
Key Laboratory of Forest Ecology and Environment of the State Forestry Administration; Institute of Forest Ecology, Environment and Protection, Chinese Academy of Forestry, Beijing 100091, China
e-mail: zangrung@caf.ac.cn

R. Zang
e-mail: zangrung@163.com

Y. Jiang · R. Zang · Y. Ding · Y. Huang · X. Lu ·
J. Huang · W. Liu · Z. Zhang
Co-Innovation Center for Sustainable Forestry in Southern China, Nanjing Forestry University, Nanjing 210000, China

S. G. Letcher
Department of Environmental Studies, School of Natural and Social Sciences, Purchase College (SUNY), Purchase, NY 10577, USA

Keywords Abiotic environment · Soil regimes · Biodiversity distribution · Tropical forests · Bawangling National Nature Reserve

Abbreviations

TDMRF	Tropical deciduous monsoon rain forest
TCF	Tropical coniferous forest
TLRF	Tropical lowland rain forest
TMRF	Tropical montane rain forest
TMEF	Tropical montane evergreen forest
T MDF	Tropical montane dwarf forest
CO	Canopy openness
SWC	Soil water content
SOM	Soil organic matter
TN	Soil total nitrogen
TP	Soil total phosphorus
AP	Soil available phosphorus
AT	Air temperature
CCA	Canonical correspondence analysis
SAR	Spatial simultaneous autoregressive error model estimation

Introduction

Under global change the increase in human-mediated modifications of ecosystems could lead to substantial losses of biodiversity (Cardinale et al. 2012). Reductions in biodiversity may alter the quality and number of ecosystem functions and services provided by terrestrial ecosystems (e.g., Isbell et al. 2011). Tropical forests are a highly diverse but also highly threatened ecosystem (Wang et al. 2006; Loreau and de Mazancourt 2013), where variation in forest structure and species diversity has been associated with differences in abiotic conditions (Segura et al. 2002; Slik et al. 2009; Ding et al. 2012). At regional or local scales, soil type and topography play an important role in shaping diversity as both of them influence water and nutrient availability (Miyamoto et al. 2003; Phillips et al. 2003; Potts 2003). Plant diversity may decline with increasing soil fertility in tropical forests of varied conditions (Peña-Claros et al. 2012). Variation in canopy openness also leads to marked gradients in irradiance, which, accordingly, results in a change in diversity (Slik 2004). Other studies report that species diversity does not vary (Clinebell et al. 1995) or even increases with soil fertility (Duivenvoorden 1996; Poulsen et al. 2006). Given these contrasting results,

there is still much to learn about how abiotic conditions affect tree species diversity in the tropics.

Until now, knowledge of diversity patterns and environmental factors in different vegetation types at the landscape scale (such as a forest management unit or a nature reserve) are still lacking (Ledo et al. 2013; Opdam and Wascher 2004; Sundaram and Hiremath 2012). Focusing on plant species diversity patterns among distinct vegetation types in a region is important. Clarifying the distribution of biodiversity in relation to vegetation types may enhance our understanding of the ecological functions of a landscape (Toledo et al. 2012). Vegetation developed under different environmental conditions in the same region can also be compared so that the role of recent environmental factors in determining the assembly of plant communities can be assessed (Onipchenko and Semenova 1995). Analysis of species diversity variation across different vegetation types at the landscape scale may provide a scientific basis for the proper management, sustainable utilization and sound conservation of resources in different vegetation types.

Here we present a detailed investigation of woody plants across six vegetation types and their environmental conditions in the Bawangling National Nature Reserve on Hainan Island, China. Abiotic factors strongly influence vegetation structure and diversity in different forest types across the tropical landscape, specifically, we hypothesize that the following factors are important in determining the variation patterns of plant composition/diversity across different forest types: 1) Low soil water content and high canopy openness correlate with species composition (especially the proportion of the deciduous species) in the deciduous monsoon forest; 2) The low soil pH and nutrients (including nitrogen and phosphorus) affect the species composition (especially the relative proportion of the broadleaved species) in the coniferous forest; 3) High soil water content, low soil nutrients and low canopy openness correlate with the highest diversity in the montane rain forest; 4) The low canopy openness, low soil nutrients (especially phosphorus), low soil water content affect the species diversity in the lowland rain forest; 5) Low soil pH, low canopy openness and high soil organic matter correlate with species composition in the montane evergreen forest, whereas low air temperature, low soil pH and high soil organic matter correlate with the lowest diversity of the stunting statured montane dwarf forest. Through this study we wanted to know which abiotic

environmental factors are associated with the composition/diversity of each old-growth forest type.

Materials and methods

Study site

The study site is located in the Bawangling Forest Region on Hainan Island, south China (Fig. 1). Hainan island is floristically rich and has been listed as an internationally significant biodiversity ‘hotspot’ in conservation (Myers et al. 2000; Chen et al. 1993). It is located at the northern edge of tropical Asia, with a total area of 33,920 km². Comprising less than 0.5 % of China’s land area, over 4600 plant species have been recorded on the island, equal to 15 % of the nation’s total, and approximately 500 of those plant species are endemic to the island (Wang et al. 2012). In addition, the island is characterized by a complete tropical vegetation belt stretching from mangroves along the coast, to rainforests in the mountains, and cloud forests on the high peaks. The diversity of vegetation zones makes this an appropriate place to study vegetation-environment relationship.

Bawangling National Nature Reserve (BNNR, 18°57′–19°11′N, 109°03′–109°17′E) is a protected area on the western side of Hainan Island (Fig. 1) The vegetation distributions in the BNNR are shown in Fig. 1, which have combined our former work of ground systematic sample plot survey, remote sensing, and local forester’s experiences (Zhang et al. 2013). A summary of site characteristics of the six old-growth forest vegetation types in Bawangling National Nature Reserve is listed in Table 1. The low elevation tropical forests (tropical deciduous monsoon rain forest, the coniferous forest, and lowland rain forest) are similar in terms of precipitation; however, the local terrain and soils for each of the forest types are highly variable. Tropical deciduous monsoon rain forest (deciduous monsoon forest) occurs in drought (due to low water holding capacities of the soils and the topography) and hot (high temperature) habitats and tree species are characterized by deciduousness and thorny stems. Tropical coniferous forest (coniferous forest) is located in habitats with low soil nutrient and low water holding-capacity, where environmental conditions are stressful for broadleaved trees, *Pinus latteri* becomes a mono-dominant. Due to the special geological, environmental and floristic conditions, coniferous forest often has a distinct community

structure and contains a different biodiversity. Tropical lowland rain forest (lowland rain forest) occupies the largest area compared with the former two forest types at low elevation (≤ 800 m) areas on Hainan Island. The investigated soil in the low elevation of Hainan belongs to the laterite in accordance with the older nomenclature. Modern terminology in the latest international classification system (FAO 2006) defines these soils as Ferralsols or Plinthosols. Tropical montane rain forest (montane rain forest) is the zonal vegetation type at intermediate elevation and has montane alfisol whose features are less leached and have lower acidity than Ultisols and Oxisols, but they exhibit high base saturation and their fertility is low to moderate (FAO 2006). Tropical montane evergreen forest (montane evergreen forest) and tropical montane dwarf forest (montane dwarf forest) usually dominate above 1300 m elevation (Zang et al. 2010), the environmental conditions within these two vegetation types are quite different compared to other forests (Long et al. 2011), which is characterized by lower air temperatures, stronger winds, more frequent fogs, and higher levels of ultraviolet radiation (Bruijnzeel and Hamilton 2000). Soils under the montane evergreen forest and the montane dwarf forest are Acrisols and Cambisols, respectively (FAO 2006).

Investigation of the vegetation

We established twelve 1-ha (100×100 m) permanent forest dynamics plots in the old-growth stands of the six forest vegetation types in the Bawangling National Nature Reserve during 2007–2010. Each vegetation type had two replicates of the 1-ha plots. All woody stems (including trees, shrubs and lianas) with a DBH (diameter at breast height) ≥ 1 cm were identified to the species level, tagged, mapped and their DBHs were measured. The nomenclature follows Flora of China (English edition; <http://www.efloras.org>). The sampling technique and survey methods follow CTFS standard protocols (Condit 1998).

Measurement of environmental factors

Each of the 1-ha plot was divided into 25 20×20 m subplots. Soil samples were randomly taken at three points in each of the 20×20 m subplots. A core of the top 20 cm of soil was taken at each point. Soil samples were air-dried and then were ground to fine powder with a

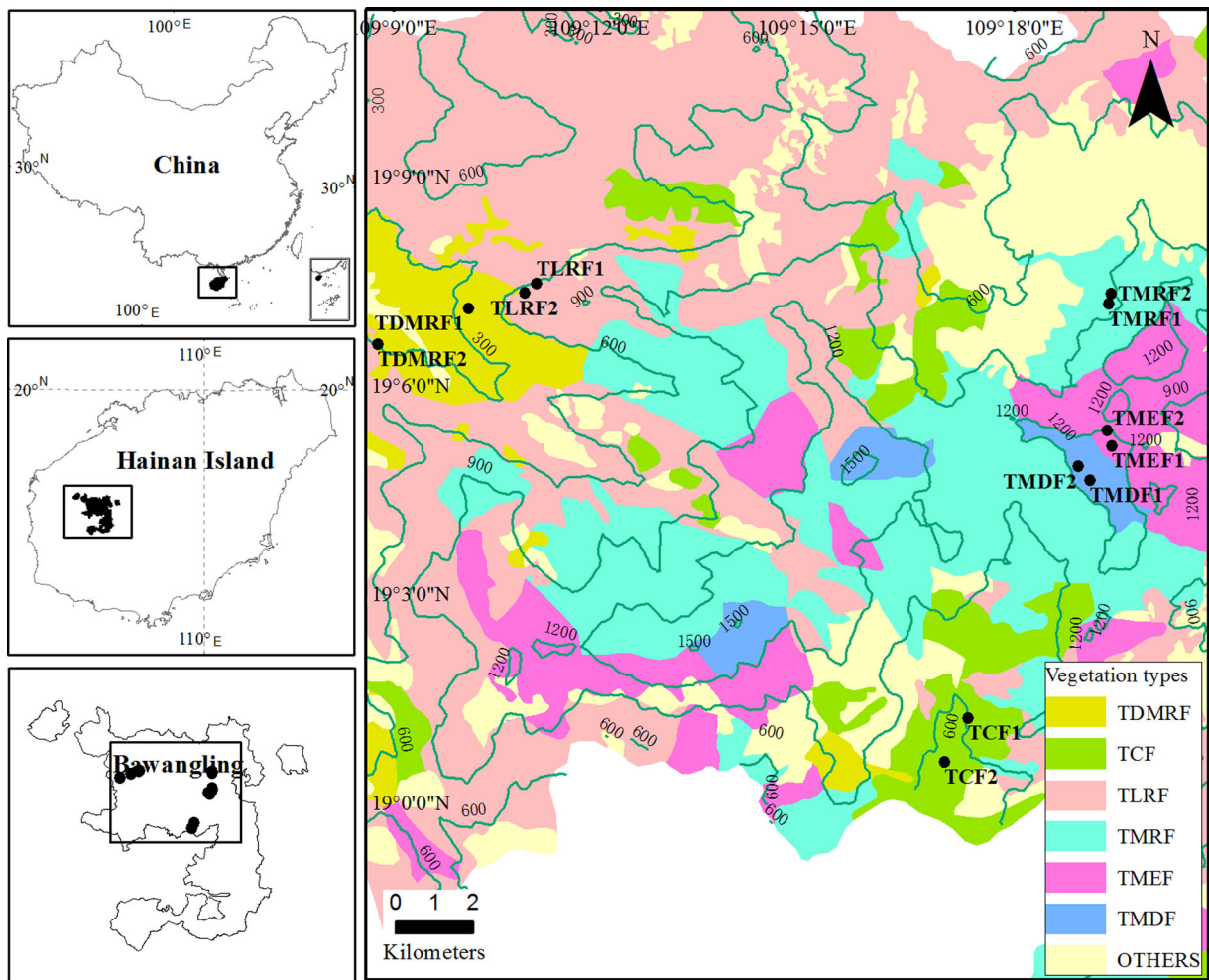


Fig. 1 Sketch map of different vegetation types in the Bawangling National Nature Reserve on Hainan Island, China. The dots indicate the locations of the plots. *TDMRF* represents tropical deciduous monsoon rain forest; *TCF* represents tropical coniferous

forest; *TLRF* represents tropical lowland rain forest; *TMRF* represents tropical montane rain forest; *TMEF* represents tropical montane evergreen forest; *TMDF* represents tropical montane dwarf forest

mill; finally samples were hand-sieved and analyzed. The soil water content (SWC, %) was calculated by subtracting the dry weight from the fresh weight of each sample during the dry season. After taking this moisture value, the three samples were thoroughly mixed before analyzing to represent the soil properties of each 20×20 m subplot. The soil pH, soil organic matter (SOM, g kg^{-1}), total nitrogen (TN, g kg^{-1}), total phosphorus (TP, g kg^{-1}) and available phosphorus (AP, mg kg^{-1}) were analyzed in the laboratory according to standard methods.

Soil for pH analysis was ground to ~ 1 mm. Firstly 25.0 g soil sample was added to deionized water, and stirred and mixed well. After calibration of a combined Electrode with buffer solutions at pH 4.0 and 7.0, the pH

of the soil suspension was measured with the electrode after 30 s equilibration (Anderson and Ingram 1989).

Soil for organic matter (g kg^{-1}) analysis was ground to ~ 0.15 mm. Firstly 0.5 g soil sample was added to a 1 N potassium dichromate solution and 98 % H_2SO_4 ; this mixture was allowed to stand and react for 30 min. Secondly deionized water and concentrated H_3PO_4 was added to the mixture that was thereafter allowed to cool. Thirdly the mixture was titrated with 0.5 mol L^{-1} ferrous ammonium sulfate solution until the color changed from violet-blue to green.

Soil for total nitrogen (g kg^{-1}) analysis was ground to ~ 0.15 mm. Firstly 1 g soil sample was digested in 98 % H_2SO_4 with $\text{K}_2\text{SO}_4\text{-CuSO}_4\cdot 5\text{H}_2\text{O-Se}$. Secondly the

Table 1 Summary of site characteristics of the six old-growth forest vegetation types in Bawangling National Nature Reserve

Characteristics	Forest types											
	TDMRF		TCF		TLRF		TMRF		TMEF		TMDF	
Replicates	plot1	plot2	plot1	plot2	plot1	plot2	plot1	plot2	plot1	plot2	plot1	plot2
Altitude (m)	340	265	579	668	577	668	904	923	1200	1200	1305	1360
Precipitation (mm/month)	160±0.9	155±0.8	167±0.9	170±0.1	168±0.1	164±0.2	175±0.1	178±0.1	179±0.1	180±0.4	180±0.4	181±0.1
Air temperature (°C)	22±0.1	23±0.1	21±0.01	21±0.02	21±0.1	21±0.3	19±0.04	19±0.01	17±0.02	17±0.04	17±0.2	16±0.1
Number of species	139	150	167	146	194	172	230	194	126	140	105	110
Number of stems	15,477	13,603	4974	4167	8195	6892	9186	9925				

Species data are based on trees with diameter at breast height ≥ 1 cm. Precipitation and air temperature were expressed as the mean \pm SD. TDMRF represents tropical deciduous monsoon rain forest; TCF represents tropical coniferous forest; TLRF represents tropical lowland rain forest; TMRF represents tropical montane rain forest; TMEF represents tropical montane evergreen forest; TMDF represents tropical montane dwarf forest

ammonium-N from the digest was obtained by steam distillation, using 0.1 mol L⁻¹ NaOH in excess to raise the pH. Thirdly the distillate was collected in 2 % H₃BO₃, and then titrated with a 0.05 mol L⁻¹ H₂SO₄ to pH 5.0. Finally total nitrogen concentration for the unknown sample was calculated according to changes in volume of 0.05 mol L⁻¹ H₂SO₄.

Soil for total phosphorus (g kg⁻¹) analysis was ground to ~0.15 mm. Firstly 0.25 g soil sample was digested with 60 % HClO₄. Secondly the sample digest was diluted with an ammoniumvanadomolybdate reagent. Thirdly a standard curve was prepared by reading the absorbance of blank with an ammoniumvanadomolybdate reagent, standards and samples at 700-nm wavelength. Finally total phosphorus concentration for the unknown sample from the calibration curve was read.

Soil for available phosphorus (mg kg⁻¹) analysis was ground to ~1 mm. Firstly 3.0 g soil sample was digested with 0.03 N NH₄F–0.025 N HCl solution. Secondly the sample digest was diluted with 0.06 mol L⁻¹ boric acid solution, deionized water and an ammonium-vanadomolybdate reagent, and 0.25 % p-nitrophenol indicator was added. Thirdly a standard curve was prepared by reading the absorbance of blank with an ammonium-vanadomolybdate reagent, standards and samples at 700 nm wavelength. Finally available phosphorus concentration for the unknown sample from the calibration curve was read.

We estimated the air temperature using the empirical regression equation: Air temperature (AT, °C) = 25.0 – 0.006 elevation; precipitation (precipitation: mm) = 65.4 + 37.1 × log (elevation) (Jiang and Liu 1991) based on all of the measured elevations in each of the 20 × 20 m subplots (300 subplots in total). To determine the understory irradiance, each 20 × 20 m subplot was subdivided into four 10 × 10 m quadrates; at each quadrate center, hemispherical canopy photographs were taken at 1.5 m above ground level using a fish-eye lens (HMV1v8, Delta-T Devices Ltd, Cambridge, UK) mounted on a tripod. The canopy cover was calculated from each photograph as the percentage of closed-canopy pixels using the Gap Light Analyzer software (Frazer et al. 1999). Canopy Openness (CO, %) was then obtained from the formula Canopy Openness = 1 - Canopy Cover.

Statistical analysis

We compared the environmental factors across the six old-growth forest vegetation types by an ANOVA. If the

variation was significant ($P \leq 0.05$), we performed multiple comparisons using Tukey Honest significant differences (HSD) to determine which vegetation differed significantly. Individual-based rarefaction and species rank-abundance curves were generated to compare species richness across the six old-growth forest vegetation types.

Sørensen's similarity index was calculated for each pair of vegetation type based on the presence-absence data. Furthermore, we performed an ANOSIM (analysis of similarities) to test whether species compositions are significantly different among the vegetation types. An ANOSIM was implemented with a maximum of 999 permutations. To test the spatial autocorrelation, we performed a Mantel test in the "ade4" package in R version 2.12.0 (R Development Core Team 2011) comparing the matrix of species composition dissimilarity values to the matrix of geographic distances among the 12 plots. The test showed that the differences in species composition among the 12 plots were not a product of underlying geographic gradients in species distributions (i.e., no significant spatial autocorrelations existed for the vegetation types.).

To assess the relationships between diversity and environmental factors we built two matrices, the species abundance matrix (species abundance based on 20×20 m subplot) and the environmental variables matrix (also soil data based on 20×20 m subplot). Detrended correspondence analysis showed that axes lengths were > 3 unit in species abundance matrix. So canonical constrained analyses (CCA) were performed (Sekulová et al. 2013). The significance of the relationship between environmental variables and species abundance was tested with 999 Monte Carlo permutations, and only predictors that significantly ($P < 0.05$) influenced the variation in species composition were marked in the CCA model. The analyses were performed using the vegan package in R version 2.12.0 (R Development Core Team 2011). Further, we explored the relationships between species richness (20×20 m subplots) in each vegetation type and the environmental variables using spatial simultaneous autoregressive error model estimation (SAR) (Kissling and Carl 2008). Given the spatially clustered nature of some of the subplots, we calculated Moran's I values of the raw species richness data and the residuals of simultaneous autoregression models at three distance classes, respectively. There is no detectable spatial autocorrelation in the residuals (Moran's I values is close to zero) in our data (to see Appendix 2), then the species richness pattern can be safely explained by the

environmental variables in the models. SAR models were generated using the R package 'spdep' (Dray et al. 2012).

Results

Variation of species diversity across the six vegetation types

The species-abundance accumulation curve showed that montane rain forest had the highest diversity, whereas montane dwarf forest had the lowest diversity among these six vegetation types; however, some crossing occurred between the curves for some plots such as those of montane rain forest vs. lowland rain forest and coniferous forest vs. deciduous monsoon forest (Fig. 2). The general mean order of species diversity comparison for the six vegetation types is montane rain forest $>$ lowland rain forest $>$ coniferous forest $>$ deciduous monsoon forest $>$ montane evergreen forest $>$ montane dwarf forest. The rank-abundance plots (Fig. 3) showed a similar order of diversity change with the accumulation curves. There

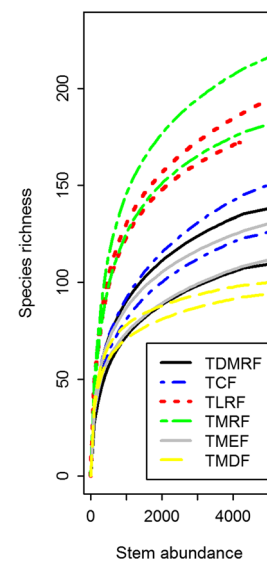


Fig. 2 The species-individual accumulation curves across the six old-growth forest types. The *black solid lines* represent tropical deciduous monsoon rain forest (TDMRF); the *blue dot and dash lines* represent (TCF); the *red dotted lines* represent tropical lowland rain forest (TLRF); the *green short and long dashed lines* represent tropical montane rain forest (TMRF); the *grey solid lines* represent tropical montane evergreen forest (TMEF); and the *yellow long dashed lines* represent tropical montane dwarf forest (TMDF)

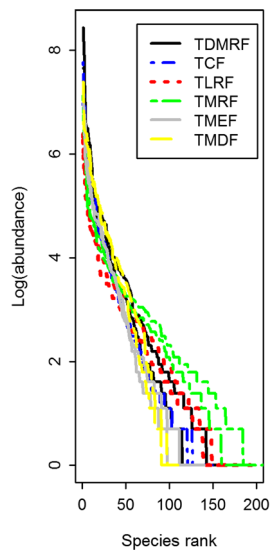


Fig. 3 The species rank-abundance curves across the six old-growth forest types. The *black solid lines* represent tropical deciduous monsoon rain forest (*TDMRF*); the *blue dot and dash lines* represent tropical coniferous forest (*TCF*); the *red dotted lines* represent tropical lowland rain forest (*TLRF*); the *green short and long dashed lines* represent tropical montane rain forest (*TMRF*); the *grey solid lines* represent tropical montane evergreen forest (*TMEF*); and the *yellow long dashed lines* represent tropical montane dwarf forest (*TMDF*)

were significant differences in species composition for the six old-growth forest vegetation types (ANOSIM test, $R=0.9222$, $P=0.001$). We found no relationship between geographic distance and dissimilarity in species composition for the six old-growth forest vegetation types (Mantel test, $P>0.05$ in all cases). The floristic similarity between woody plants was the highest between montane rain forest and lowland rain forest (Table 2).

Changes in environmental factors across the six vegetation types

Table 3 shows that the canopy openness was highest in the montane dwarf forest, followed by the deciduous monsoon forest. The montane rain forest had the highest soil water content and exhibits significant differences with each of the other five vegetation types. Both the air temperature and soil pH showed a similar pattern of variation across the six vegetation types. The soil organic matter was highest in the deciduous monsoon forest, montane dwarf forest and montane evergreen forest and

the lowest in the coniferous forest, whereas the lowland rain forest and montane rain forest had a soil organic matter in-between. The soil total nitrogen was highest in the deciduous monsoon forest and significantly different from the other five forest types (coniferous forest, lowland rain forest, montane rain forest, montane evergreen forest and montane dwarf forest). The soil total phosphorus had a higher value in the montane evergreen forest and was significantly different from the other five forest types, whereas the deciduous monsoon forest and the other four forest types (coniferous forest, lowland rain forest, montane rain forest and montane dwarf forest) exhibited significant differences in soil total phosphorus. The available phosphorus was highest in the montane dwarf forest and montane evergreen forest and lowest in the coniferous forest and lowland rain forest, whereas the montane rain forest and deciduous monsoon forest ranked second and third in their available phosphorus values among the six forest types.

Relationships between environmental conditions and species composition/diversity

Relationships between environmental conditions and forest types of differing species composition are represented by CCA in Fig. 4. The significant environmental variables of pH, soil water content, soil total nitrogen, soil organic matter and soil total phosphorus were effectively selected by the Monte Carlo permutation test ($F=2.26$, $P<0.01$, overall test). The first ordination axis accounted for 47.92 % of the total variation, and together the first two ordination axes accounted for 78.36 % of the total variation. The first ordination axis was significantly correlated with the soil pH and soil water content; the second canonical axis showed strong correlations with the soil organic matter, soil total phosphorus and soil total nitrogen.

The SAR model indicated that correlations between species richness and the measured environmental factors varied with the vegetation types (Table 4). In the deciduous monsoon forest, variability in soil water content and canopy openness emerged as important predictors of species richness. In the coniferous forest, soil total nitrogen and soil pH were the main determinant of species richness. In the lowland rain forest, soil water content and soil available phosphorus were the most important environmental variable explaining species richness. In the montane rain forest, soil total phosphorus and canopy openness played an important role in the

Table 2 Sørensen's percent similarities among the vegetation types

Sørensen's percent similarity						
Vegetation types	TDMRF	TCF	TLRF	TMRF	TMEF	T MDF
TDMRF	1					
TCF	37.52	1				
TLRF	22.71	42.63	1			
TMRF	13.61	32.12	60.08	1		
TMEF	9.31	16.15	35.06	44.12	1	
T MDF	5.84	14.75	26.67	35.49	65.05	1

TDMRF represents tropical deciduous monsoon rain forest; *TCF* represents tropical coniferous forest; *TLRF* represents tropical lowland rain forest; *TMRF* represents tropical montane rain forest; *TMEF* represents tropical montane evergreen forest; *T MDF* represents tropical montane dwarf forest

shape of species richness. In the montane evergreen forest, soil organic matter and soil pH were the predictors of species richness while soil total nitrogen and air temperature were also the predictors of species richness in the montane dwarf forest.

Based on Table 3, we can see that plant diversity in different vegetation types is associated with different environmental factors. The deciduous monsoon forest is characterized by high air temperature, soil organic matter and soil pH, but low soil total phosphorus, available phosphorus, canopy openness and soil water content habitat; the coniferous forest is associated with high air temperature, canopy openness and soil pH, but low soil water content and soil nutrients. The lowland rain forest has low soil water content, canopy openness, soil nutrients (especially P), and has moderate air temperature and soil pH; the montane rain forest is associated

with high soil water content and moderate canopy openness, soil nutrients and soil pH. The two vegetation types at the highest elevations (montane evergreen forest and montane dwarf forest) have high canopy openness, soil phosphorus, and soil organic matter, low soil nitrogen and air temperature, and moderate soil water content.

Discussion

Changes in species diversity across the six vegetation types

Species richness was highest in the montane rain forest, lowest in the montane dwarf forest, and intermediate in the other four vegetation types. The montane rain forest ranked first in species richness likely owing to its

Table 3 Average±SD values for environmental factors of the six old-growth forest vegetation types

Vegetations	Abiotic factors							
	CO (%)	SWC (%)	pH	SOM (g kg ⁻¹)	TN (g kg ⁻¹)	TP (g kg ⁻¹)	AP (mg kg ⁻¹)	AT (°C)
TDMRF	21.92±10.19 ^a	14.64±4.45 ^a	5.80±0.37 ^a	56.90±6.24 ^a	2.82±0.84 ^a	0.61±0.31 ^a	9.28±8.00 ^a	24.76±3.37 ^a
TCF	16.81±2.52 ^b	14.07±2.80 ^a	4.74±0.17 ^b	24.28±4.45 ^b	1.26±0.26 ^b	0.25±0.04 ^c	5.63±2.58 ^b	23.45±2.88 ^{ab}
TLRF	6.70±1.87 ^c	13.49±2.70 ^a	4.74±0.19 ^b	31.86±5.68 ^c	1.06±0.18 ^b	0.20±0.09 ^c	4.10±1.22 ^b	22.08±3.17 ^c
TMRF	11.76±3.30 ^d	29.10±4.68 ^b	4.47±0.28 ^c	43.46±6.04 ^d	1.87±0.45 ^b	0.33±0.10 ^c	13.60±7.64 ^c	21.03±2.89 ^{bc}
TMEF	10.59±3.91 ^d	20.21±5.94 ^c	4.19±0.16 ^d	54.79±9.07 ^a	1.71±0.50 ^b	0.88±0.73 ^b	18.22±6.58 ^d	18.42±1.72 ^{cd}
T MDF	42.59±11.51 ^c	20.08±6.67 ^c	3.95±0.35 ^c	53.68±28.35 ^a	1.65±0.53 ^b	0.35±0.17 ^c	19.12±6.80 ^d	16.61±3.37 ^d

Data with different letters are significantly different at $p < 0.05$; *TDMRF* represents tropical deciduous monsoon rain forest; *TCF* represents tropical coniferous forest; *TLRF* represents tropical lowland rain forest; *TMRF* represents tropical montane rain forest; *TMEF* represents tropical montane evergreen forest; *T MDF* represents tropical montane dwarf forest. Canopy openness (CO, %), Soil water content (SWC, %), Soil organic matter (SOM, g kg⁻¹), Soil total nitrogen (TN, g kg⁻¹), Soil total phosphorus (TP, g kg⁻¹), Soil available phosphorus (AP, mg kg⁻¹) and Air temperature (AT, °C)

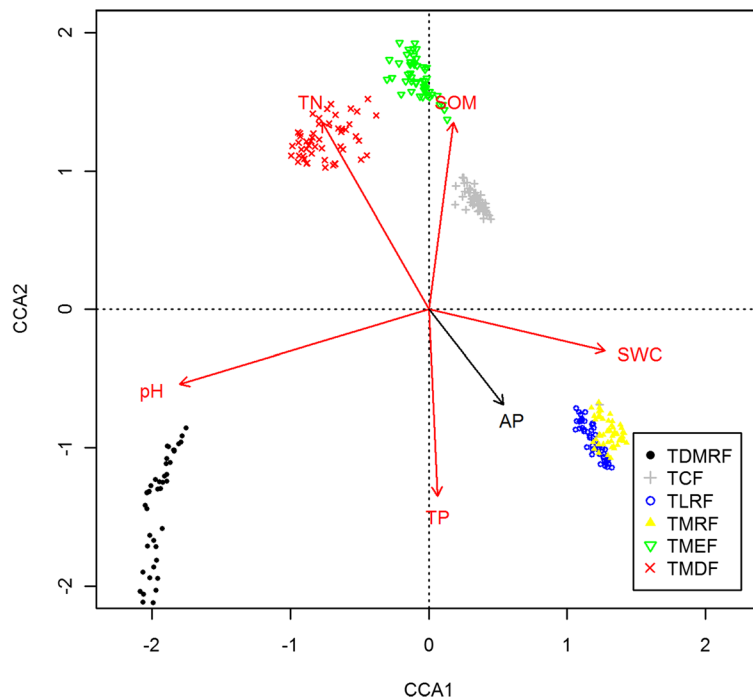


Fig. 4 Canonical correspondence analysis showing the relationships between the 6 soil variables and species abundance across the six old-growth forest types (data from all the 300 plots combined). The *black solid dots* represent tropical deciduous monsoon rain forest (*TDMRF*); the *grey plus signs* represent tropical coniferous forest (*TCF*); the *blue hollow dots* represent tropical lowland rain forest (*TLRF*); the *yellow solid triangles* represent tropical

montane rain forest (*TMRF*); the *green hollow triangles* represent tropical montane evergreen forest (*TMEF*); The *red multiplication signs* represent tropical montane dwarf forest (*TMDF*). Canopy openness (*CO*, %), Soil water content (*SWC*, %), Soil organic matter (*SOM*, g kg^{-1}), Soil total nitrogen (*TN*, g kg^{-1}), Soil total phosphorus (*TP*, g kg^{-1}), Soil available phosphorus (*AP*, mg kg^{-1}) and Air temperature (*AT*, $^{\circ}\text{C}$)

complex community structure and relatively moderate microenvironment, which means more niches available for the survival and growth of many types of plants. By comparison with the montane rain forest, the vegetation types distributed at higher and lower elevations displayed lower diversity. The explanations for this pattern of diversity change across the vegetation types could be hypothesized in this ways in view of vegetation originations: Since montane rain forest occupies the largest area in the study region, it can be supposed to be the largest regional species pool, which had important influences on the composition and structure of the adjacent vegetation types. Montane rain forest locates in mid elevational areas with the most moderate environmental conditions (i.e., high soil water content and moderate canopy openness, soil nutrients and soil pH). When the species in the montane rain forest pool migrated lower or upper wards, the environmental conditions they encountered would be less favorable, some combinations of more stressful factors might present. For example: when lower ward, low nitrogen or soil

water might be influencing some species, meanwhile when upper ward, low temperature or high air humidity could be affecting for some other species. Lowland rain forest occupies the second largest area in the study region, it still has relatively favorable conditions for many species even though some stressful environmental factors filtering out some proportions of species from the montane rain forest, however, these stressful environmental factors could afford niches for some species differing from those in the montane rain forest. Consequently, lowland rain forest, in spite of some different dominant species and fewer uncommon species still has a diversity a bit lower than the montane rain forest. Compared with the lowland rain forest, deciduous monsoon forest and coniferous forest exhibited lower value but slightly higher than montane evergreen forest and montane dwarf forest in species richness. Although deciduous monsoon forest and coniferous forest distribute in the same elevational ranges as the lowland rain forest, they only presented in some very special geological or edaphic conditions. When species from the

Table 4 SAR of environmental variables predicting species richness in the six vegetation types

Variables	Standardized regression coefficient	Estimated value	<i>P</i>
TDMRF			
Canopy openness	-0.34	-0.55	0.00
Soil water content	0.30	0.03	0.01
TCF			
Total nitrogen	0.25	3.63	0.00
Soil pH	0.10	0.54	0.00
TLRF			
Soil water content	0.43	0.89	0.00
Available phosphorus	0.22	1.15	0.00
TMRF			
Total phosphorus	0.09	0.23	0.02
Canopy openness	0.25	0.75	0.00
TMEF			
Soil pH	-0.11	-2.15	0.00
Soil organic matter	0.17	0.24	0.00
TMDF			
Total nitrogen	0.35	3.22	0.00
Air temperature	0.23	1.94	0.00

TDMRF represents tropical deciduous monsoon rain forest, *TCF* represents tropical coniferous forest, *TLRF* represents tropical lowland rain forest, *TMRF* represents tropical montane rain forest, *TMEF* represents tropical montane evergreen forest, *TMDF* represents tropical montane dwarf forest

montane rain forest pool spread down ward into these special habitats. Some new speciation should develop to adapt these stressful niches. Since many species could not survive the dry season soil drought and other edaphic stresses, so the species richness of these two types of lowland elevation were greatly reduced. Some study showed that the high sensitivity to water limited by a relative high temperature and high-pH soil are two of the major causes to determine patterns of low values in species richness in deciduous monsoon forest (Maestre et al. 2012). Besides drought stress and rocky habitat, prevailing acidic base-poor soil results in the coniferous forest with a decreased number of species (Chytrý et al. 2008). When species from the montane rain forest pool moved upper ward, low temperature, low soil pH, more frequent fog and strong wind in the montane evergreen forest and montane dwarf forest would become strong selective forces for many typical tropical species (Letts and Mulligan 2005). And the lower community height

would afford fewer niche spaces for species; thus, the species richness in these two forests reached the lowest values among the six forest vegetation types. During the upward moving process only a few species can adapt to the unique habitat to survive and growth while only a very low proportion of new speciation developed to survive these extremely stressful environment, which are consistent with of the results of Stadtmüller (1987) and Hamilton (1995), who suggested that species richness decreased in the upper montane “cloud” forest.

Environmental effects on the distribution of species diversity across the different vegetation types

Species richness is linked to different combination of environmental factors across the six vegetation types (Table 4). There are statistically significant relationships between species richness and environmental factors (canopy openness and soil water content) in the deciduous monsoon forest. A large proportion of the species in this forest are deciduous and thorny, contributing to a distinct physiognomy for this vegetation type compared with the surrounding forest types. Since the deciduous species in this forest adapt the conditions of high light, high soil nutrients and low soil water content, which might differ in their periods of leafless or even lifespan; light was excessive for some shade tolerant species in the forest, resulting in a negative correlation between species richness and canopy openness. In addition, many species-rich tropical forests, such as: seasonally dry tropical forests, experience a prolonged dry season during which little or no rain falls and the upper soil layers undergo severe drying (Wright 1996). Topography in this forest is rugged due to the great number of exposed big stone and rocks on the ground, leading to low soil water-holding capacity.

The combination of soil total nitrogen and soil pH had significant influences on species richness in the coniferous forest. Species in this forest are mainly located in habitats with poor soil nutrients, short water supply, relative high pH and air temperature. The dominant species in this vegetation is the conifer *Pinus latteri*, which should take a growth rate advantage over other broadleaved tropical species under conditions of low nutrient availability (Zhang et al. 2014). Nitrogen has been shown to influence the growth of plants or vegetation distribution (Neeteson et al. 1998). However, in this forest nitrogen levels is very low compared with the other forest vegetation types (Table 3) and losses of

nitrogen from forests can have potentially serious consequences for soils, receiving waters and species composition (Lovett et al. 2002). Thus, we should improve N level to increase species richness in the coniferous forest. On the other hand, conifers need an acid soil (Franklin and Bergman 2011). Our results also showed a positive correlation between soil pH and species richness.

In the lowland rain forest, available phosphorus and soil water content was strongly correlated with species richness. Phosphorous has been proposed as the nutrient most likely to be limiting in lowland tropical forests (Cleveland et al. 2011) owing to relatively small amounts of available P in the soils (Sollins 1998). Our result showed that available phosphorus in the lowland rain forest was the lowest across the six vegetation types. Thus, the increase in phosphorus supply could positively improve species richness. The soil water content in the lowland rain forest was surprisingly low, maybe owing to be located at a drought habitat in low elevation in study field, making the soil water content becoming a limiting factor to influence the growth of most plants in this forest, leading to significant correlation with species richness.

Our result showed that canopy openness and total phosphorus were positively correlated with species richness in the montane rain forest. Light is a highly temporally and spatially heterogeneous resource in forests (Gravel et al. 2010). The canopy structure in the montane rain forest is extremely complex and dense, which increases species competition for vertical space and reduces canopy openness in this forest types (Denslow and Guzman 2000). The well-developed and complicated architectural features of the montane rain forest community structures allow a very small proportion of light to penetrate into the under storey; thus light becomes a very limiting factor for the growth and regeneration of many species, resulting in a positive correlation between canopy openness and species richness. Many studies showed that phosphorus is an important soil limiting factor in tropical ecosystems, in particular, tends to be the main limiting factor in tropical montane areas (Vitousek and Sanford 1986; Cleveland et al. 2011; Wright et al. 2011). The phosphorus content in the soils of montane rain forest was so low that it limited the growth of most plants in this forest and affected the species richness.

Under the specific environmental conditions of montane evergreen forests, soils are acidic (our data presentation) and, consequently, decomposition of soil organic

matter and soil concentration of exchangeable bases and base saturation are usually low (Ledo et al. 2013). In the montane evergreen forest, our results indicated that among the selected environmental factors, pH and soil organic matter were significantly related to species richness. The acidic soil might restrict the decomposition and absorption of soil organic matter, causing the lack of nutrition, so although soil organic matter was high in montane evergreen forest, it still had a positive effect on species richness.

In the montane dwarf forest, species richness was positively related to both air temperature and total nitrogen. Low-temperature tolerance in the forest probably plays a role in species richness along altitudinal gradients. In addition, low temperature constraints resulted in a comparatively short period of growing season, slow growth and relatively smaller plant sizes (Callaway et al. 2002), and limited the existence of many tropical species.

Conclusions

Plant diversity/composition changed with forest types across the tropical forest landscape. The key abiotic factors correlated with species composition in deciduous monsoon forest were canopy openness and soil water content. Soil total nitrogen and pH were the vital determinants of diversity in coniferous forest. Soil water content, phosphorus and canopy openness were associated with higher diversities in lowland- and montane- rain forests. Soil organic matter and pH were the major factors influencing species composition in the montane evergreen forest, whereas air temperature and soil total nitrogen were associated with the lowest diversity of the stunting statured montane dwarf forest. Our study suggests that the abiotic factors influencing plant growth and community structure in each vegetation type were the most important determinants of overall diversity patterns among different vegetation types across the tropical forest landscape.

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Appendix 1

Table 5 The dominance of 54 species were selected using calculating importance values (IV = Relative frequency + Relative density + Relative dominance) across the six vegetation types

Vegetation types	Species names	Family	IV
TDMRF	<i>Terminalia hainanensis</i>	Combretaceae	0.174
TDMRF	<i>Streblus ilicifolius</i>	Moraceae	0.14
TDMRF	<i>Streblus taxoides</i>	Moraceae	0.036
TDMRF	<i>Albizia odoratissima</i>	Mimosaceae	0.029
TDMRF	<i>Lannea coromandelica</i>	Anacardiaceae	0.028
TDMRF	<i>Catunaregam spinosa</i>	Rubiaceae	0.025
TDMRF	<i>Syzygium cumini</i>	Myrtaceae	0.021
TDMRF	<i>Diospyros strigosa</i>	Ebenaceae	0.02
TDMRF	<i>Alchornea rugosa</i>	Euphorbiaceae	0.019
TCF	<i>Pinus latteri</i> Mason	Pinaceae	0.361
TCF	<i>Aporosa dioica</i>	Euphorbiaceae	0.107
TCF	<i>Melastoma sanguineum</i>	Melastomataceae	0.043
TCF	<i>Toxicodendron succedaneum</i>	Anacardiaceae	0.04
TCF	<i>Cinnamomum porrectum</i>	Lauraceae	0.032
TCF	<i>Decaspermum gracilentum</i>	Myrtaceae	0.025
TCF	<i>Symplocos poilanei</i>	Symplocaceae	0.022
TCF	<i>Adinandra hainanensis</i>	Theaceae	0.022
TCF	<i>Glochidion sphaerogynum</i>	Euphorbiaceae	0.02
TLRF	<i>Vatica mangachapoi</i>	Dipterocarpaceae	0.053
TLRF	<i>Ardisia quinquegona</i>	Myrsinaceae	0.05
TLRF	<i>Koilodepas hainanense</i>	Euphorbiaceae	0.032
TLRF	<i>Machilus suaveolens</i>	Lauraceae	0.028
TLRF	<i>Winchia calophylla</i>	Apocynaceae	0.026
TLRF	<i>Castanopsis tonkinensis</i>	Fagaceae	0.026
TLRF	<i>Syzygium hancei</i>	Myrtaceae	0.02
TLRF	<i>Lasianthus chinensis</i>	Rubiaceae	0.018
TLRF	<i>Peltophorum tonkinense</i>	Fabaceae	0.014
TMRF	<i>Mallotus hookerianus</i>	Euphorbiaceae	0.071
TMRF	<i>Saprosma ternatum</i>	Rubiaceae	0.033
TMRF	<i>Lithocarpus fenzelianus</i>	Fagaceae	0.032
TMRF	<i>Castanopsis carlesii</i>	Fagaceae	0.03
TMRF	<i>Prismatomeris tetrandra</i>	Rubiaceae	0.03
TMRF	<i>Cyclobalanopsis patelliformis</i>	Fagaceae	0.029
TMRF		Polygalaceae	0.025

Table 5 (continued)

Vegetation types	Species names	Family	IV
	<i>Xanthophyllum hainanense</i>		
TMRF	<i>Memecylon ligustrifolium</i>	Melastomataceae	0.023
TMRF	<i>Canarium album</i>	Burseraceae	0.022
TMEF	<i>Syzygium araiocladum</i>	Syzygium	0.074
TMEF	<i>Distylium racemosum</i>	Distylium	0.065
TMEF	<i>Cyclobalanopsis disciformis</i>	Cyclobalanopsis	0.06
TMEF	<i>Psychotria rubra</i>	Psychotria	0.057
TMEF	<i>Syzygium buxifolium</i>	Syzygium	0.055
TMEF	<i>Ternstroemia gymnanthera</i>	Ternstroemia	0.04
TMEF	<i>Dacrydium pierrei</i>	Dacrydium	0.038
TMEF	<i>Symplocos poilanei</i>	Symplocos	0.026
TMEF	<i>Cyclobalanopsis championii</i>	Cyclobalanopsis	0.022
TMDF	<i>Syzygium buxifolium</i>	Syzygium	0.074
TMDF	<i>Engelhardtia roxburghiana</i>	Engelhardtia	0.051
TMDF	<i>Symplocos lancifolia</i>	Symplocos	0.031
TMDF	<i>Psychotria rubra</i>	Psychotria	0.031
TMDF	<i>Cinnamomum tsoi</i>	Cinnamomum	0.031
TMDF	<i>Symplocos poilanei</i>	Symplocos	0.027
TMDF	<i>Michelia mediocris</i>	Michelia	0.024
TMDF	<i>Machilus velutina</i>	Machilus	0.023
TMDF	<i>Rhododendron moulmainense</i>	Ericaceae	0.022

Appendix 2

Appendix 2 showed species richness data for different environmental variables 'spatial autocorrelation at 3 distance classes, and the spatial autocorrelations among the three spatial lag order were exist to some extent across the six vegetation types (capital letter). Spatial autocorrelation in the residuals was almost removed from the species richness data of the addition 8 environmental variables, suggesting that there was no statistical bias in the SAR models (small letter).

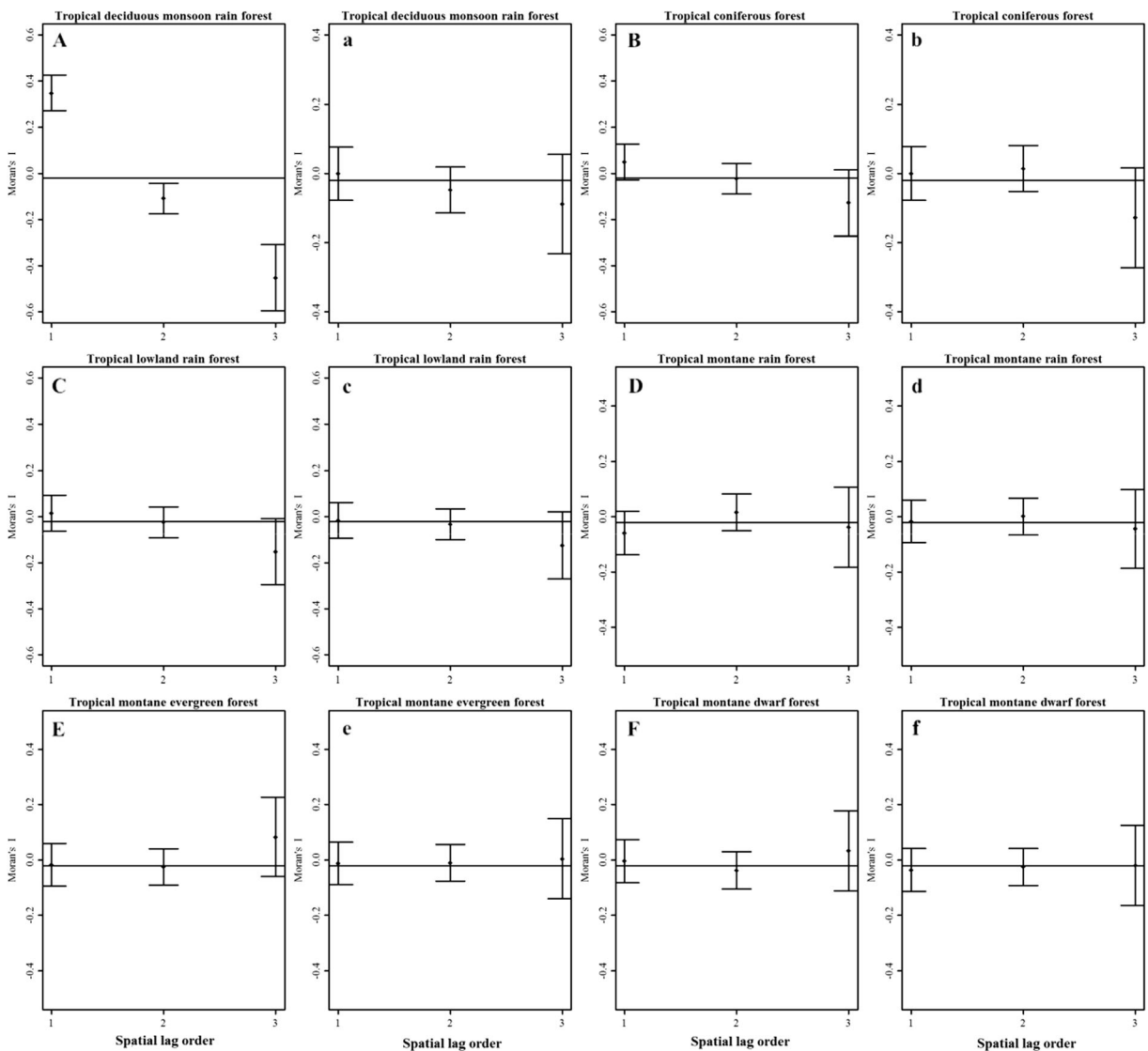


Fig. 5 Correlograms for original richness (*capital letter*) and residuals (*small letter*) of the SAR models for different environmental factors across the six old-growth forest types

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