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老挝 Phou Khao Khoauy 国家公园树木分布特征*

Manichanh Satdichanh[1,2,3]，Jérôme Millet[4]，Andreas Heinimann[5,6]，
Khamseng Nanthavong[3]，Rhett D. Harrison[7,8]
（1. 中国科学院西双版纳热带植物园，云南 勐腊 666303；2. 中国科学院大学，北京 100049；
3. 老挝国立大学林学院，老挝；4. Fédération des Conservatoires botaniques nationaux，法国；
5. 瑞士发展与环境中心，瑞士；6. 伯尔尼大学地理研究所，瑞士；7. 世界混农林中心东亚和中亚区域办公室，云南 昆明 650204；
8. 中国科学院东亚植物多样性与生物地理重点实验室，云南 昆明 650204）

摘要：本研究在老挝 Phou Khao Khoauy 国家公园（在万象东北方向 40 km）的两种森林类型取样，以此研究决定树种分布的因素。本研究在海拔为 300～450 m 地区共设置了 11 个 50 m×50 m 样地，并测量了所有胸径大于 10 cm 的树木。调查样地按森林类型（混合落叶林，以山毛榉科为主，干常绿林）分层随机选取，共鉴定 47 个科，70 个属，123 个种。在每个样地的两个位置收集土壤样品，每个样品在两个深度分别为 0～10 cm 和 10～20 cm 处采集，并进行基本土壤参数分析（pH 值，有机质 OM，氮 N 和磷 P，氧化钾 K_2O，颗粒大小以及质地）。通过聚类分析对植物群落进行标识，使用 NMDS 分类法及非参数检验法研究土壤对植物分布的影响，揭示了老挝 Phou Khao Khoauy 国家公园内树种组成与土壤条件的关系。

关键词：植物分布；老挝；土壤；植物群落；物种组成；热带雨林
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Tree distribution in Phou Khao Khoauy National Park，Laos

Manichanh Satdichanh[1,2,3]，Jérôme Millet[4]，Andreas Heinimann[5,6]，
Khamseng Nanthavong[3]，Rhett D. Harrison[7,8]
（1. Xishuangbanna Tropical Botanical Garden，Chinese Academy of Sciences，Mengla Yunnan 666303，P. R. China；
2. University of the Chinese Academy of Sciences，Beijing 100049，P. R. China；3. Faculty of Forestry Science，National University of Laos；
4. Fédération des Conservatoires botaniques nationaux，Frence；5. Centre for Development and Environment，Switzerland；6. Institute of Geography，
University of Bern，Switzerland；7. World Agroforestry Centre，East & Central Asia Regional Office，Kunming Yunnan 650204，P. R. China；
8. Key Laboratory of for Plant Diversity and Biogeography of East Asia，Kunming Institute of Botany，
Chinese Academy of Sciences，Kunming Yunnan 650204，China）

Abstract：To investigate the factors determining tree species distribution，forests sampling at Phou Khao Khoauy National Park（PKK），40 km NE of Vientiane in central Laos was conducted. Eleven 0.25（50 m×50 m）samples were set up between 300～450 m elevation and all trees ⩾10 cm were enumerated. Plot locations were randomly assigned after stratifying by forest type（mixed deciduous forest，dominated by Fagaceae，and dry evergreen diperocarp forest）and 47 families，70 genera and 123 species were identified. Soil samples were collected from two locations，each sample was collected at two depths，between 0～10 cm and 10～20 cm depth and they were analyzed for getting basic soil parameters［pH，organic matter（OM），nitrogen（N）and phosphorus（P），potassium oxide（K_2O），particle size and texture］. By cluster analysis for plant community group identification，and by non-metric multidimensional scaling（NMDS）and a post-hoc non-parametric tests for examine the influence of soil parameters on plant distribution，this study found that in Laos，which located on the northern edge of the tropics，substantial turn-

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Corresponding author：Manichanh Satdichanh，chanh199@gmail.com

over in tree species composition sometimes occurs over short distances, although tree species may be shared among forest types. Moreover, turnover in species composition appears to be associated with soil conditions.

Key words: plant distribution; Laos; soil; plant community; species composition; tropical forest

Plant community ecology is determined by both biotic and abiotic factors [1~2]. Species occurrence in the given plant community is not accidental but a response to climatic factors, soil conditions, species interactions and biogeography. Gradients in soil variables, water pH and other abiotic factors are strongly correlated to species distributions at both small and large scales [3~4]. For example, at a global scale, plant distribution is strongly influenced by climate, topography and soil[5]. At landscape scales, the soil conditions and altitude are the most important environmental variables determining plant distributions and influencing the structure of forest communities [6~8].

The vegetation types in Indo-China have been divided into two basic categories based on elevation, phenology, rainfall patterns, species dominance, floristic relationships and soil types. The first category is tropical rain forest, which includes wet-evergreen forest, dry-evergreen forest, freshwater swamp forest and evergreen montane forest. The second category is deciduous forest, which includes mixed deciduous forest and deciduous dipterocarp forest. Laos is situated on the northern edge of the tropics in Asia and supports a diversity of forest types, including both deciduous and evergreen forests. Deciduous forests mainly occur in lowland areas of southern Laos from 100 m to 800 m in elevation. Evergreen forests in Laos include rain forest, dry evergreen dipterocarp forest (a mixture of deciduous and evergreen species) and mixed coniferous forest [13~16]. Mixed coniferous forest occurs at higher elevations of up to 2 000 m. However, other evergreen forest types and deciduous forest types in Laos may be distributed in very close proximity. Moreover, species often occur in both forest types [17~18]. In particular, mixed deciduous forest and dry evergreen dipterocarp forest overlap in many species but vary in the proportion of evergreen versus deciduous species. The factors determining the distribution of forest types at local scales are still poorly understood. Moreover, most previous work delineating forest categories has been based on qualitative assessments.

The forests in Phou Khao Khoauy National Park (PKK) have been disturbed in the past by logging, infrastructure construction and human activities. Previous studies found that the floristic composition of PKK was significantly associated with altitude and soil conditions [19~20]. However, the disturbance of native forests in PKK had lead to the existence of pioneer deciduous and evergreen vegetation. The aim of our study was to understand the factors determining the distribution of plant species in PKK. We were particularly interested to investigate whether previous suggestions that different forest types sometimes exist in close proximity are supported by a quantitative approach to assessing ecological communities. Our results are an important basis to understanding the drivers of plant distribution at landscape scales within Laos, where basic information on forest ecology is still lacking.

1 Materials and methods

1.1 Study area and data collection

PKK is one of eighteen sites in Laos that were designated as protected areas in 1993. PKK (18°14' ~ 18°32'N;102°38' ~ 102°59'E) is a mountain range about 40 km northeast of Vientiane at its closest point. It encompasses an area of around 2 000 km^2 and covers three provinces including Vientiane province, Vientiane Prefecture and Borlikhamxay province. The forest types found within PKK correspond to the mixed deciduous forest (dominated by Fabaceae), dry evergreen dipterocarp forest and monodominant coniferous forest (mainly Pinaceae), at higher elevation [19]. Elevation varies from ≤100 m to nearly 1 700m. Average rainfall in the rainy season (May-October) is 3 369 mm, while on average only 265 mm of rainfalls from November-April.

Data were collected from 11 permanent forest plots located on the eastern side of PKK. These plots covered mixed deciduous forest (five plots) and dry evergreen

forest (six plots) only, and the elevation of the plots ranged from 300 ~ 450 m. These permanent forest plots were established by the Institude Recherche pour le Developpement (IRD)-France and Faculty of Forestry (FOF) National University of Lao (NUoL) in 2009 [19]. Each plot is 0.25 ha (50 m × 50 m). After stratifying by forest type, the location of plots was randomly assigned. All individual trees with a diameter-at-breast-height (DBH) ≥10 cm were enumerated. Trees with DBH ≥10 cm were chose because "the ecological sorting and soil performance on plant appears to affect trees of all size classes without inducing a shift in the diameter distribution [21]". Tree DBH, height, and position were recorded and the species identified. Herbarium specimens were collected and deposited at the National Herbarium of Laos, NUoL Faculty of Forestry herbarium and NUoL Faculty of Science herbarium. From the 11 permanent plots a total of 1 221 individual trees, including 47 families, 70 genera and 123 species were enumerated.

Soil sample collection and analyses were conducted by the Sud Expert Plantes Initiative Project [19]. In each plot, two soil samples were collected from two locations across the diagonal of each plot using a soil auger; each sample was collected at two depths, between 0 ~ 10 cm and 10 ~ 20 cm depth. Soils were analyzed at the soil analysis laboratory of the National Agriculture and Forestry Research Institute (NAFRI) in Vientiane, Lao PDR. The soil samples were analyzed for pH, organic matter (OM), nitrogen (N) and phosphorus (P), potassium oxide (K_2O), particle size and texture.

1.2 Data analysis

All analyses were implemented in R v. 3.1.3 [22]. We used the data collected from each plot to create a plot vs. species matrix of species abundance. Multivariate analyses were applied on this matrix. The difference in species composition across plots was quantified using Sorenson similarity index (similarity distance) based on abundance data. After that, we used hierarchical agglomerative clustering to assign groups, using the complete linkage method for group identification. To test the statistical significant of clusters we used simprof function in clustsig package in R [23]. To examine the hierarchical classification and analyze the relationship between environmental variables and plant distributions in the given communities, we used non-metric multidimensional scaling (NMDS) using vegan package in R. The NMDS procedure was based on the default parameters in R, which included Bray-Curtis dissimilarity index (abundance based) and a maximum of 100 starts in search of stable solution. The soil parameters were log transformed (log10) to approximate a normal distribution for each parameter. The results of the NMDS analysis and log transformed soil parameters were used to examine the relationship between plant distribution and environmental parameters using the post-hoc non-parametric function envfit in the vegan package, based on 999 permutations.

2 Results

2.1 Species composition

Our cluster analysis classified plant communities in our study site into three groups. Group I covered four plots and was mainly dominated by *Gonocaryum* sp. (13 %), *Lagerstroemia calyculata* (10 %), *Horsfieldiaa amygdalina* (10 %), *Diospyros* sp.2 (6 %) and *Canthium glabrum* (5 %). Group II covered three plots and was dominated by *Horsfieldia amygdalina* (21 %), *Hopea ferrea* (10 %), *Gonocaryum* sp. (6 %) and *Xanthophyllum flavescens* (5 %). Group III covered four plots and dominated by *Hopea ferrea* (20 %), *Horsfieldia amygdalina* (13 %), *Alphonsea gaudichaudiana* (9 %) and *Cratoxylum cochinchinense* (7 %). The relative dominance values of the top 20 species in the plant communities were as follows; Group I ranged from 0.35 ~ 16.14, Group II ranged from 0.03 ~ 10.63 and Group III ranged from 0.12 ~ 23.62 (Table 1). However, Groups II and III were not significantly different using 0.05 as the probability of a Type I error. The NMDS ordination of plant communities also represented these groups (r = 0.98, stress = 0.04) (Figure 1).

Tab. 1　Relative dominance of the top 20 species of each plant community group at PKK. Group I ranged from 0.35 ~ 16.14, Group II ranged from 0.03 ~ 10.63 and Group III ranged from 0.12 ~ 23.62

No.	Group I	Relative dominance	Group II	Relative dominance	Group III	Relative dominance
1	*Hopea ferrea*	16.14	*Hydnocarpus ilicifolia*	8.8	*Hopea ferrea*	23.62
2	*Lagerstroemia calyculata*	6.28	*Hopea ferrea*	8.21	*Hydnocarpus ilicifolia*	8.8
3	*Hydnocarpus ilicifolia*	10.08	*Gonocaryum* sp.	0.033	*Alphonsea gaudichaudiana*	1.73
4	*Diospyros pendula*	3.52	*Xanthophyllum flavescens*	5.97	*Cinnamomum iners*	1.71
5	*Canthium glabrum*	2.44	*Aidia* sp.	1.98	*Xerospermum laoticum*	5.83
6	*Xylia xylocarpa*	3.5	*Syzygium* sp.	10.63	*Gironniera nervosa*	0.4
7	*Syzygium* sp.	2.74	*Microdesmis caseariifolia*	0.74	*Mangifera odorata*	4.5
8	*Rinorea boissieui*	2.49	*Artocarpus* sp.	0.85	*Syzygium syzygioides*	9.32
9	*Canthium* sp.	0.35	*Sindora laotica*	3.29	*Xanthophyllum flavescens*	9.57
10	*Microcos tomentosa*	2.83	*Xerospermum laoticum*	0.98	*Syzygium* sp.	3.17
11	*Memecylon ovatum*	2	*Ormosia cambodiana*	0.51	*Xerospermum noronhianum*	1.63
12	*Lagerstroemia* sp.	1.31	*Vatica harmandiana*	2.22	*Xanthophyllum* sp.	0.3
13	*Euonymus* sp.	0.74	*Alphonsea gaudichaudiana*	0.65	*Buchanania* sp.	2.52
14	*Vitex pinnata*	4.26	*Cratoxylum cochinchinenses*	0.95	*Aphanamixis polystachya*	0.22
15	*Rothmannia attopevensis*	1.78	*Gonocaryum lobbianum*	0.48	*Aidia* sp.	0.36
16	*Streblus taxoides*	0.38	*Styrax* sp.	0.36	*Schima wallichii*	1.3
17	*Peltophorum dasyrrhachis*	3.17	*Walsura* sp.	1.25	*Gonocaryum lobbianum*	0.23
18	*Gardenia annamensis*	1.39	*Streblus ilicifolius*	0.16	*Diospyros mollis*	0.7
19	*Garcinia multiflora*	0.9	*Syzygium syzygioides*	1.82	*Xanthophyllum* sp.	1.19
20	*Cratoxylum formosum*	0.65	*Vatica odorata*	1.13	*Styrax* sp.	0.12

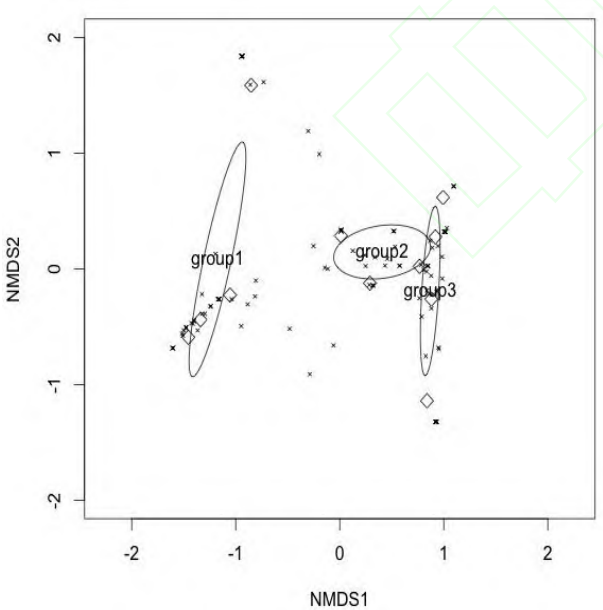

Fig. 1　NMDS ordination of tree distributions in PKK and classification into each community (stress = 0.04, r = 0.98). Cluster analysis classified plant communities in our study site to be three groups. Group I covered four plots. Group II covered three plots and Group III covered four plots. However, Groups I and II were not significantly different.

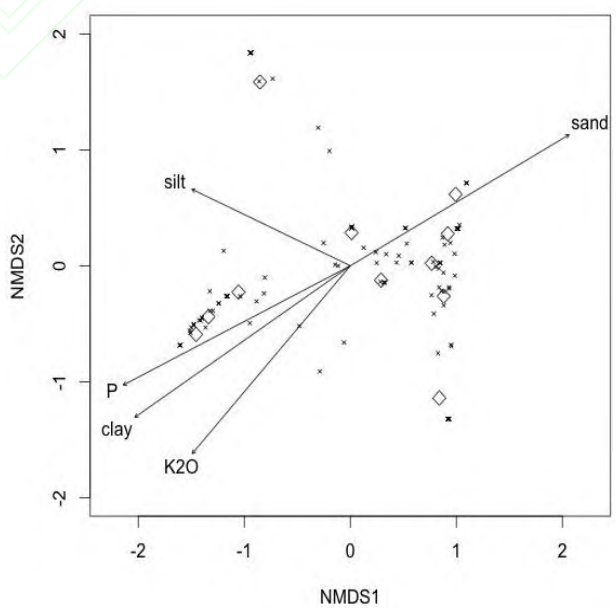

Fig. 2　The NMDS ordination of plant communities and associated soil parameters. The environmental fitted vector test found that P ($p = 0.021$), K_2O ($p = 0.029$), sand (0.007) and clay (0.008), but not silt ($p = 0.091$) were significantly associated with variation in plant composition.

2.2 Plant distribution across soil gradients

The NMDS axes explained 73 % of the total variance in species composition (stress = 0.04, r = 0.98) (Figure 2). The first NMDS axis had positive correlation with sand was negatively correlated with P, K_2O, clay and silt. NMDS axis 2 had a positive correlation with sand and silt while P, clay and K_2O were strongly negatively correlated with this axis. However, as expected following the cluster analyses, the plant communities of Group II overlapped with Group III (Figure 2). The environmental fitted vector test found that P ($p = 0.021$), K_2O ($p = 0.029$), sand (0.007) and clay (0.008), but not silt ($p = 0.091$) were significantly associated with variation in plant community composition. These results suggest that plant communities are sorting out along a gradient from sandy soil with low P and K_2O to clay soil with higher P and K_2O.

3 Discussion

Our results suggest that the tree distribution in the mixed deciduous and dry evergreen dipterocarp forests at PKK is strongly determined by soil gradients. The ordination analysis showed that the distribution of plant species in the given communities was significantly correlated with P, K_2O, and the proportion of sand or clay particles. This suggests that these environmental factors played the key role in determining plant distribution in PKK.

Previous studies elsewhere have reported similar results on the relationship of plant distribution and soil gradients. For example, Chahouki *et al* [24] found that the distribution of vegetation in Poshtkouh Rangelands, Iran was correlated with the soil texture, soil salinity and other characteristics, respectively. They also found that soil texture controlled plant distribution through its effect on soil moisture availability, ventilation and distribution of the roots. Many studies on tropical soil nutrients also showed that phosphorus is an important limiting factor and assumed to limit the productivity in lowland tropical forest [25~29]. Intensive logging was conducted in PKK until 1993 and currently PKK still experiencing disturbance. Logging and other disturbance factors may have contributed to the changes in the species composition and soil chemical characters at out site.

Our cluster analysis demonstrated that it is possible to identify a significant turnover in forest composition among plots located at a similar elevation and in close proximity with one another. Nevertheless, theses analyses also showed that many species were shared among the groups identified. Our results are consistent with other studies on forest types in Laos [13,17,18], and confirmed that different forest types in Laos occur in very close proximity but that a number of plant species may be shared among forest types. Differences in forest associations occurring at the same elevation appear to be driven by variation in soil conditions.

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