ENVIRONMENTAL AND HUMAN INFLUENCE ON FOREST COMPOSITION, STRUCTURE AND DIVERSITY IN LAOS

C Lucas[1], K Nanthavong[2] & J Millet[3]

[1]*Faculté des Sciences de Montpellier, Université de Montpellier II, Place Eugène Bataillon, 34095 Montpellier Cedex 5, France*
[2]*Faculty of Forestry, National University of Laos, Campus DongDok Vientiane, Lao PDR*
[3]*Faculty of Sciences, National University of Laos, Campus DongDok Vientiane, Lao PDR; milletjerome@yahoo.fr*

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LUCAS C, NANTHAVONG K & MILLET J. 2013. Environmental and human influence on forest composition, structure and diversity in Laos. This paper concerns the Phou Khao Khouay protected area in Laos which in the past was intensively logged and where infrastructure construction and human activities continue to threaten its forest biodiversity. Phou Khao Khouay comprises rough mountain slopes, steep sandstone cliffs, hilly terrain and flat uplands. A total of 32 permanent plots of 0.25 ha each were established along an altitudinal gradient to characterise and understand the forest composition, structure and diversity. From the co-inertia analyses, six forest types were identified and described in terms of floristic composition, structure and soil preference, allowing evaluation of ecology of species and evolution of forests after disturbance. These results provide knowledge for better management of forests in Phou Khao Khouay National Park.

Keywords: Secondary tropical forest, Phou Khao Khouay protected area

LUCAS C, NANTHAVONG K & MILLET J. 2013. Kesan sekitaran dan manusia terhadap komposisi, struktur dan kepelbagaian hutan di Laos. Kertas ini adalah tentang kawasan terlindung di Phou Khao Khouay yang pernah dibalak dengan giat tetapi kepelbagaian biologi hutannya masih diancam oleh pembinaan prasarana dan aktiviti manusia. Phou Khao Khouay mempunyai cerun gunung yang kasar, cenuram batu pasir yang curam, rupa bumi berbukit dan tanah darat yang rata. Sebanyak 32 plot kekal masing-masing berukuran 0.25 ha diasaskan sepanjang cerun altitud untuk menciri dan memahami komposisi, struktur dan kepelbagaian hutan. Daripada analisis koinersia, enam jenis hutan dikenal pasti dan dihuraikan mengikut komposisi flora, struktur hutan dan tanah. Ini membolehkan penilaian ekologi spesies dan evolusi hutan selepas gangguan dijalankan. Keputusan kajian dapat digunakan untuk menambah baik pengurusan hutan di Taman Negara Phou Khao Khouay.

INTRODUCTION

Lao People's Democratic Republic (PDR) is a country of plateaus, hills and mountainous terrain over 70% of its territory. It has approximately 42% of the total land area under forest cover (FAO 2001). Lao PDR has the most remaining pristine tropical rainforests in South-East Asia, with 9% of the forest being classified as primary forest. In recent decades, tropical forests have been highly disturbed and primary forests continue to decrease (Asner et al. 2005, Ashton 2008). Secondary forests and logged-over forests cover an area of 600 mil ha and an average of a further 9 mil ha is created every year (Brown & Lugo 1990, Emrich et al. 2000). In particular, South-East Asia has the highest deforestation rate (1.3%) in the world, about twice that of Africa or South America (Achard et al. 2002, Lepers et al. 2005). In Laos, the forest cover is estimated to have declined from 70% in 1943 to about 42% in early 21st century (WREA 2008). At this rate of deforestation, the forest cover would be approaching 30% by year 2020. To combat the rapid loss of forest cover, Lao PDR began a reform programme in natural resource management in the early 1990s. Illegal logging is a major concern, especially logging on the mountainous border with Vietnam. In addition, Lao PDR is experiencing a rapid and largely uncontrolled expansion of industrial plantation, in particular, rubber cultivation. This expansion has been driven by the strong demand for natural rubber in key rubber producing and processing countries such as China, Vietnam and India. Some industry experts predict that the estimated 28,000 ha of rubber plantations in Lao at present will grow to some 300,000 ha by 2020 (Hicks et al. 2009). In general, the policy to protect biodiversity in Laos is at variance with actuality.

The Tropical Forestry Action Plan for Lao PDR (Douglas 1989) classifies the forest into four categories: evergreen, mixed deciduous, deciduous and others (pine, bamboo). In the early 1990s, sustainable use and land management of forests intensified within the national agenda of Laos and National Biodiversity Conservation Areas (NBCAs) were established under the Prime Minister Decree No. 164. Laos established the NBCAs system in 1993, naming and mapping 18 NBCAs covering nearly 12% of the national area. It is clear that the Lao NBCAs system is significant and of international importance to species conservation. The Lao Government has now established a national system comprising 21 NBCAs (Figure 1); the protected area has expanded to cover almost 14% of the total land area.

Many of these protected areas are inhabited or surrounded by populations that use forest resources in their daily lives. Population growth rates are high in the protected area, estimated in excess of 3% per year and possibly up to 4% in some villages (Alton & Sylavong 1997) compared with 2.2% for Laos as a whole (UNDP 2004). In many cases, the true impact of human disturbances and the results of past forest logging remain unknown in the protected areas.

It is essential to have a clear idea of the species and forest ecology under different situations in order to support forest management and conservation. Phou Khao Khouay National Park, the site of this study, is a good example of the general situation in Laos, having previously undergone logging and degradation and still experiencing disturbances. The intensive logging conducted in the area up till 1993 has been intensified by recent construction of dams. This has not only increased accessibility to the remote forests by opening roads but also resulted in further rigorous forest loggings during the creation of dams. Shifting cultivation and permanent extraction by local and non-local people continue to occur as the great biodiversity of the forest offers a wide range of food, medicinal and tradable products. The forests of Phou Khao Khouay have been unduly affected by human activities, resulting in the creation of patches of differing forest compositions and diversity which remain poorly documented. The objective of this study was to investigate how the remaining forest trees were arranged in relation to environmental conditions (altitude, soil) and human impact. This paper aims to better understand the forest types in Phou Khao Khouay, their biodiversity and their reasons for existence in order to present scientifically sound information to support development of better forest policies and management approaches in this protected area. The main activities of this study were to: (1) characterise different types of forests under different environmental situations, (2) identify existing relationships between forest composition, structure and soil factors in order to understand the environmental and human effects on forest composition and (3) evaluate the diversity of each forest type.

MATERIALS AND METHODS

Study area

Phou Khao Khouay National Park encompasses an area of about 2000 km^2 (Figure 1) where elevation varies from less than 100 m to nearly 1700 m above sea level. The tropical monsoonal climate is similar to the rest of central Laos with rainy season beginning April–May and lasting till October and a distinct dry season from November till March–April. On the lowland of Phou Khao Khouay, the average annual rainfall is about 2049 mm with 92% of rains in May–October. Temperatures are highest just before and during the early part of the rainy season, so April is the hottest month with temperature averaging 39 °C. December is the coldest month with 10 °C at low elevation. Most of the area is covered by typical tropical red to brown soils (orthic acrisols and lithosols), which are sandy to sandy loam in texture and poor in organic matter (Kingston 1987). Richer soils (dystric nitosols, ferratic cambisols) can be found in valleys and river gorges where the moisture level is high. The original vegetation cover of the area consisted primarily of lowland mixed deciduous forest and tropical montane evergreen forest located centrally within the reserve. The forest types correspond approximately to the mixed deciduous forest (mainly Fabaceae), dry evergreen Dipterocarpaceae forest and monospecific coniferous forest (mainly Pinaceae) types. At present, the vegetation cover still comprises mainly closed forest but most of the area is now affected by undocumented human activity including extraction of minor forest products, fire, livestock grazing, shifting cultivation and commercial logging.

Figure 1 Map of the 21 national parks in Lao PDR (ICEM 2003)

Sampling

For this study, we chose three sites located at different elevations that had a mosaic of forests types (Figure 2). The first is to the west, in the Thulakhom district (Vientiane province) and located around the Vang Heua village at elevation 816 m. The second is situated in the north and the third to the east. They are both located in the Thaphabhat district (Bolikhamxay province) named Tad Leuk (elevation 569 m) and Tad Xay (elevation 390 m) respectively. The nearest village to Tad Xay is about 10 km while to Tad Leuk, at least 30 km. Vang Heua and Tad Leuk are close to dams. This means that they are accessible by road.

At each site, we established permanent plots (Figure 3) of 0.25 ha (50 m × 50 m), geolocated and materialised by poles, within different forest types. The plot size was determined by the species–area curve and was driven by the possibility of sampling in homogeneous areas. For each forest type, a minimum of two plots were arranged in order to perform statistical analyses. Each plot was divided into 25 subplots of 10 m × 10 m. In total, we set up 32 plots: 15 plots in the forest of the village of Vang Heua, 11 plots in Tad Xay and 6 plots in Tad Leuk. In each identified plot, we took readings for global positioning system position and elevation.

Data collection

In each plot, the canopy openness percentage was estimated by standing at the corner of each subplot and assigning a zero if the canopy was open or one if the canopy was closed. The canopy openness percentage value for the entire plot was calculated by averaging all 36 marks taken at the subplot corners. All individual trees with diameter at breast height (dbh) ≥ 10 cm were numbered and recorded for dbh, height, position in the subplot and species. If possible, specimens were collected to confirm identification at the herbarium of the Faculty of Forestry (Anonymous 1960–2011, Vidal 1997, Inthakoun & Delang 2002, Min et al. 2006). Plots were sampled from March 2009 till March 2011. Soil samples were collected at two levels: between 0 and 10 cm as well as 10 cm depth from two locations on the

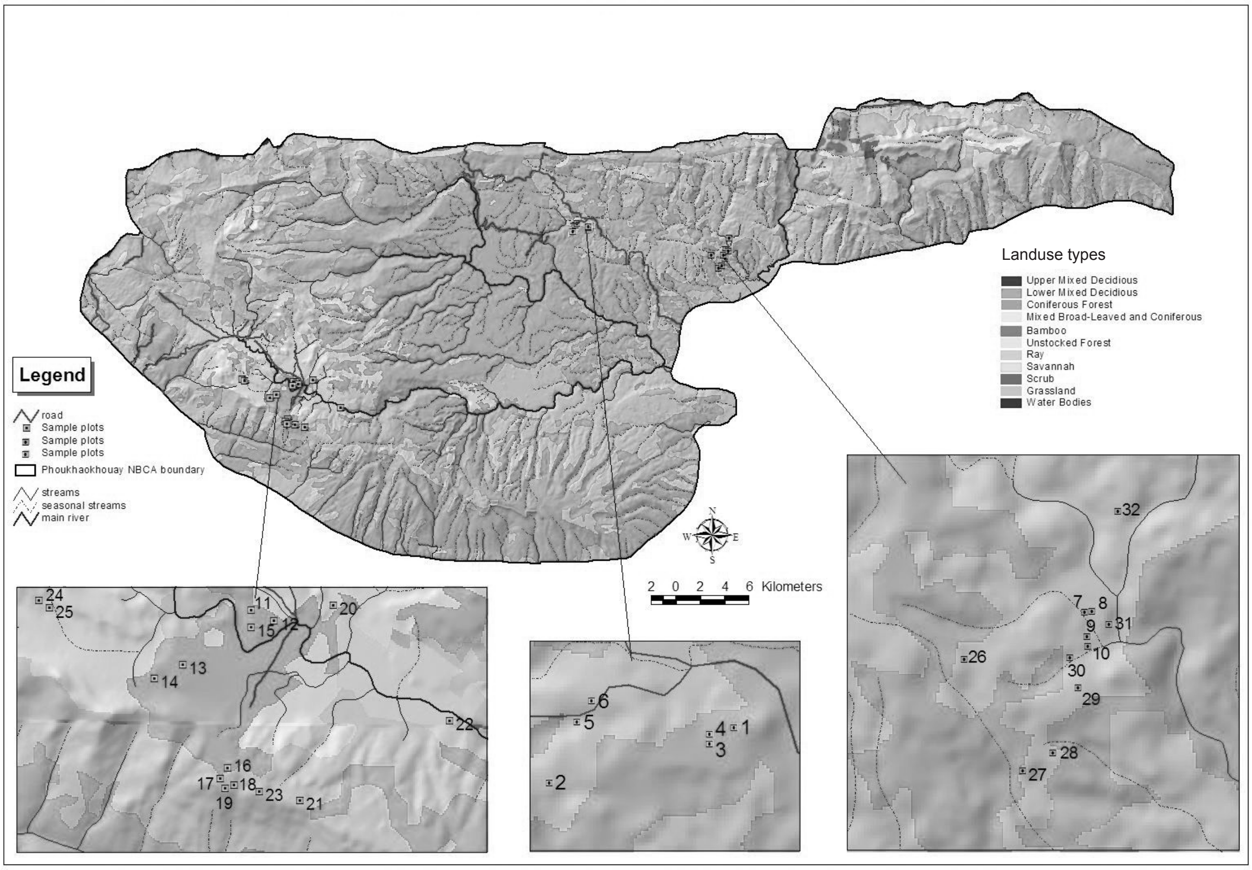

Figure 2 Map of sample plots located in the Phou Khao Khouay protected area

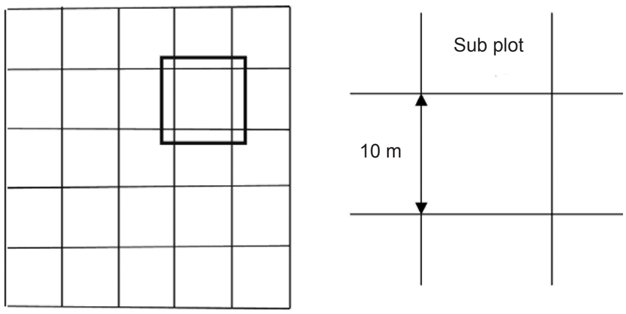

Figure 3 Plot design

diagonal of each plot using an auger. Soils were analysed at the National Agriculture and Forestry Research Institute in Vientiane.

Data analysis

Species composition and typology

The forest composition was first analysed with Sorensen similarity index (based on presence absence of species) to compare the composition of vegetation between each site. The species composition was than analysed by multivariate analyses performed with R software (R 2.5.1). Non-symmetric correspondence analysis (NSCA) which examined the patterns of variation in species composition between plots was complemented by a hierarchical classification made from the factorial coordinates of the 32 plots from the results of the NSCA using the Ward method to identify key types of species assemblages.

Forest group structure and soil preference

Based on the data collected, a set of variables were measured for each plot: forest structure (density, basal area, canopy openness, average height) and soil parameters. In order to analyse the link between species assemblages, their forest structure and soil environment, a co-inertia analysis was performed with ADE-4 package under R.2.5 software. The first step of the co-inertia analysis is to perform a separate analysis of both tables: principal component analysis on forest structure and soil variables and NSCA on the floristic table. The co-inertia was performed to identify a possible co-structure between species abundance, forest structure and soil variables. The co-structure resulting from the co-inertia was tested using Monte Carlo test (permutation test).

Diversity

The total species richness was estimated by ICE (Incidence-based Coverage Estimator) and ACE (Abundance-based Coverage Estimator) species richness estimators. These have been calculated using EstimateS software. Diversity indices (species richness, Shannon, equitability, Simpson) have been calculated using PAST (PAlaeontological STatistics) software. A series of analysis of variance (one-way ANOVA) was used to determine whether diversity indices were significantly different. These analyses were performed using STAGRAPHICS Centurion XV.I software.

RESULTS

Species composition and typology

A total of 4072 individual trees of 395 different species were recorded in the 32 plots. The most frequent species are presented in Table 1. Among the 25 most frequent species, only 3 were present in the three sites: *Alphonsea gaudichaudiana*, *Fagerlindia fasciculata* and *Gironniera nervosa*. The other species were found only in one (16) or two sites (6). The indices of Sorensen similarity (result not shown) showed that the floristic compositions between Tad Xay and Vang Heua were the closest (0.35), followed by Tad Xay and Tad Leuk (0.34) and finally Vang Heua and Tad Leuk (0.31).

Figure 4 shows the distribution of the most abundant species among the 32 plots and provides a typology of the forest types. Six different groups of plant communities occurred in Phou Khao Khouay.

Group I (plots 1, 2, 9, 10, 29, 31 and 32) was composed mainly of Dipterocarpaceae *Hopea* sp. (4.2%), *Hydnocarpus borneensis* (2.95%), *Xerospermum laoticum* (1.5%), *F. fasciculata, A. gaudichaudiana*, *Xanthophyllum ecarinatum* and *G. nervosa*. Group II (plots 13, 18 and 21) was composed of *Dipterocarpus obtusifolius* (1.4%) mixed with monospecific coniferous *Pinus merkusii* (1.08%). *Horsfieldia sucosa* (1.65%) and *Schima wallichii* were often associated with this community. Group III (plots 8, 26, 27, 28 and 30) was composed mainly of *Lagerstroemia calyculata* (1.06%), *Hydnocarpus ilicifolia* (2.95%) and *Hopea ferrea* (1.84%). Group IV (plots 3 and 4) was composed largely of conifers: *P. merkusii* (0.71%) and *Dacrydium elatum* (1.84%). Group V (plots 17, 19, 23, 24 and 25) comprised *Cratoxylum formosum* (3.1%), *Aporosa villosa* (2.48%), *S. wallichii* (3.64%), *Syzygium compongensis*, *Glochidion fagifolium* and *Barringtonia annamica*. Group VI (plots 5, 6, 7, 11, 12, 14, 15, 16, 20, 22) included *A. gaudichaudiana* (3.27%), *G. nervosa* (2.77%), *F. fasciculata* (1.84%), *X. laoticum*, *S. compongensis*, *B. annamica*, *S. wallichii* and *D. obtusifolius*. In addition, *Quercus* sp., *Elaeocarpus robustus*, *Vatica harmandiana* and *Chrysophyllum cainito* could be found.

Description of structure and soil preference of the forest groups

Figure 5 shows the co-inertia analysis which ordinates tree species with forest structure and soil variables (Table 2) in two axes accounting for 79.42% of the total variance. Correlation between forest structure, soil variables and species composition of plots was significant for both axes ($r = 0.93$ and $r = 0.74$ respectively). The Monte Carlo test result was also significant ($RV = 0.57$, $p < 0.001$). Axis 1 (Figure 5a) comprised mainly forest structure variables which were highly correlated with the floristic composition. Axis 2 comprised edaphic factors with minimal discrimination. Axis 1 ranged from forests having high proportion of small trees (10 to 20 cm) and high canopy openings to forests having high basal area and high proportion of over 60 cm diameter trees. Axis 2 dealing with soil variables ranged from sandy soil to silty-clayic-sandy soils.

Based on the co-inertia analysis, co-structures were identified:

Table 1 Relative frequency of the 25 main species in the three sites

Species	Family	Code	Species relative frequency (%)			
			Vang Heua	Tad Leuk	Tad Xay	Total
Hopea sp.	Dipterocarpaceae	Hopsp.		1.25	2.95	4.2
Schima wallichii	Theaceae	Schwal	3.64			3.64
Alphonsea gaudichaudiana	Annonaceae	Alpgau	0.74	1.42	1.11	3.27
Cratoxylum formosum	Hypericaceae	Crafor	3.1			3.1
Hydnocarpus ilicifolia	Flacourtiaceae	Hydili			2.95	2.95
Syzygium compongensis	Myrtaceae	Syzcom	2.58	0.25		2.83
Gironniera nervosa	Ulmaceae	Girner	1.15	0.96	0.66	2.77
Aporosa villosa	Euphorbiaceae	Apovil	2.48			2.48
Dacrydium elatum	Podocarpaceae	Dacela		1.84		1.84
Hopea ferrea	Dipterocarpaceae	Hopfer			1.84	1.84
Fagerlindia fasciculata	Rubiaceae	Fagfas	0.64	0.63	0.57	1.84
Pinus merkusii	Pinaceae	Pinmer	1.08	0.71		1.79
Horsfieldia sucosa	Myristicaceae	Horsuc	1.65			1.65
Xerospermum laoticum	Sapindaceae	Xerlao		0.59	0.91	1.5
Hydnocarpus borneensis	Flacourtiaceae	Hydbor			1.45	1.45
Quercus sp.	Fagaceae	Quesp1	1.2	0.25		1.45
Vatica harmandiana	Dipterocarpaceae	Vathar	1.45			1.45
Dipterocarpus obtusifolius	Dipterocarpaceae	Dipobt	1.4			1.4
Chrysophyllum cainito	Sapotaceae	Chrcai	1.38			1.38
Elaeocarpus robustus	Elaeocarpaceae	Elarob	1.38			1.38
Barringtonia annamica	Lecythidaceae	Barann	1.09			1.09
Glochidion fagifolium	Euphorbiaceae	Glofag	1.06			1.06
Lagerstroemia calyculata	Lythraceae	Lagcal			1.06	1.06
Cinnamomum iners	Lauraceae	Cinine			0.91	0.91
Xanthophyllum ecarinatum	Polygalaceae	Xaneca		0.32	0.37	0.69

Table 2 Soil parameters for each forest group

Group	pH H_2O	OM (%)	Sand (%)	Clay (%)	Silt (%)
I	4.47	2.16	63.8	23.4	12.8
II	4.78	1.06	82.6	7.2	10.2
III	4.55	1.65	76.5	9.4	14.1
IV	5.28	1.61	80.7	14.2	5.1
V	4.75	1.79	62.5	14.3	23.2
VI	4.67	2.16	67.5	14.0	18.5

OM = organic matter

(1) *Hopea* sp. but also *A. gaudichaudiana*, *G.nervosa*, *F. fasciculata*, *X. laoticum* and *H. borneensis* which occurred in forest type I, corresponding to most mature forests (basal area = 38.9 m^2 ha^{-1}, canopy openness = 11%; frequency of trees in the diameter class 60 cm = 6.3%; Table 3), located in Tad Xay and Tad Leuk, up to 600 m altitude.

(2) *Schima wallichii*, *A. villosa* and *Cratoxylum fornosum* were species positively correlated with young forest (88.9% of trees in the diameter class 10–20 cm; Table 3) which were

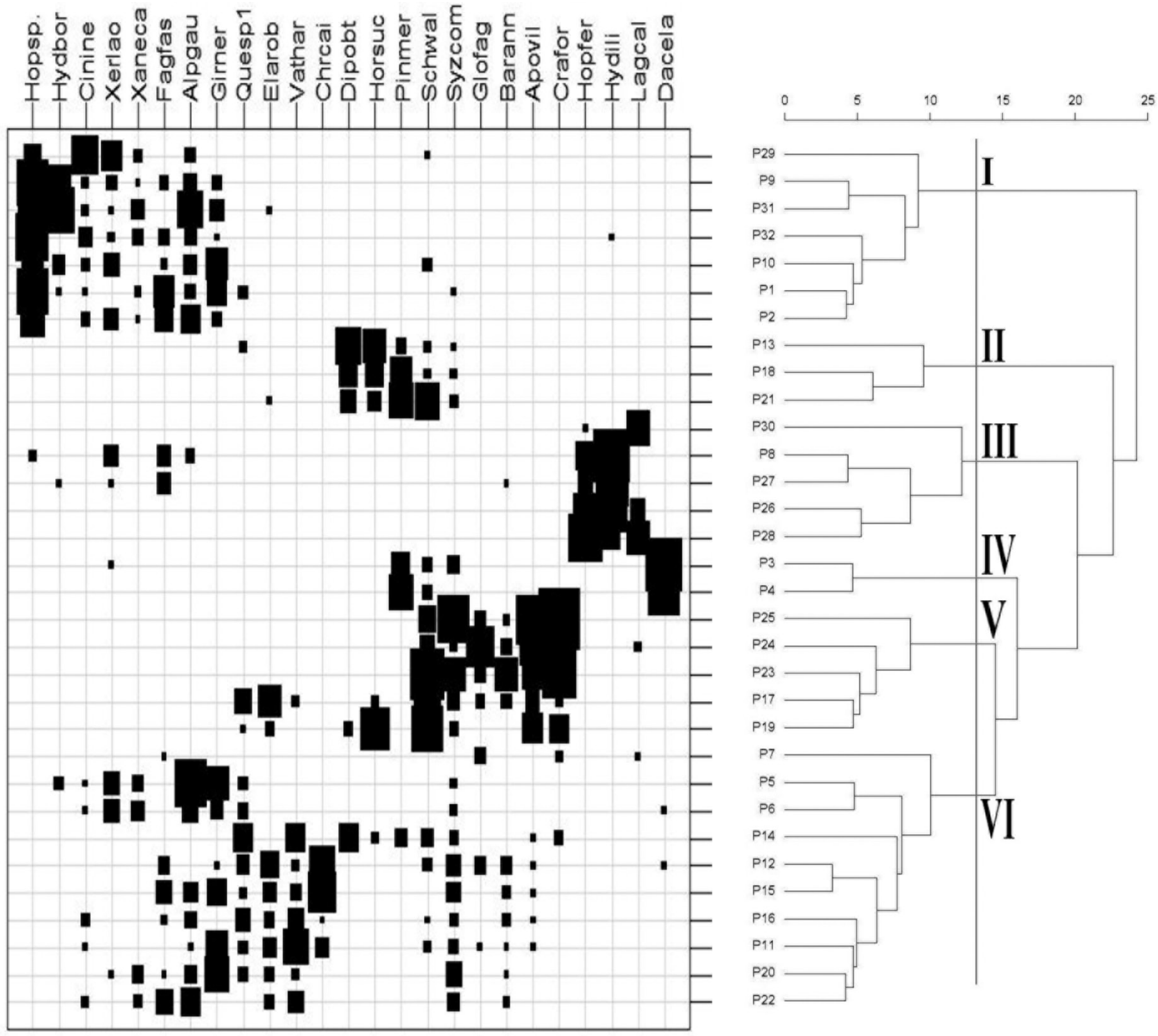

Figure 4 Relationship between the most abundant species and plot clustering based on results of the non-symmetric correspondence analysis (for species codes, see Table 1)

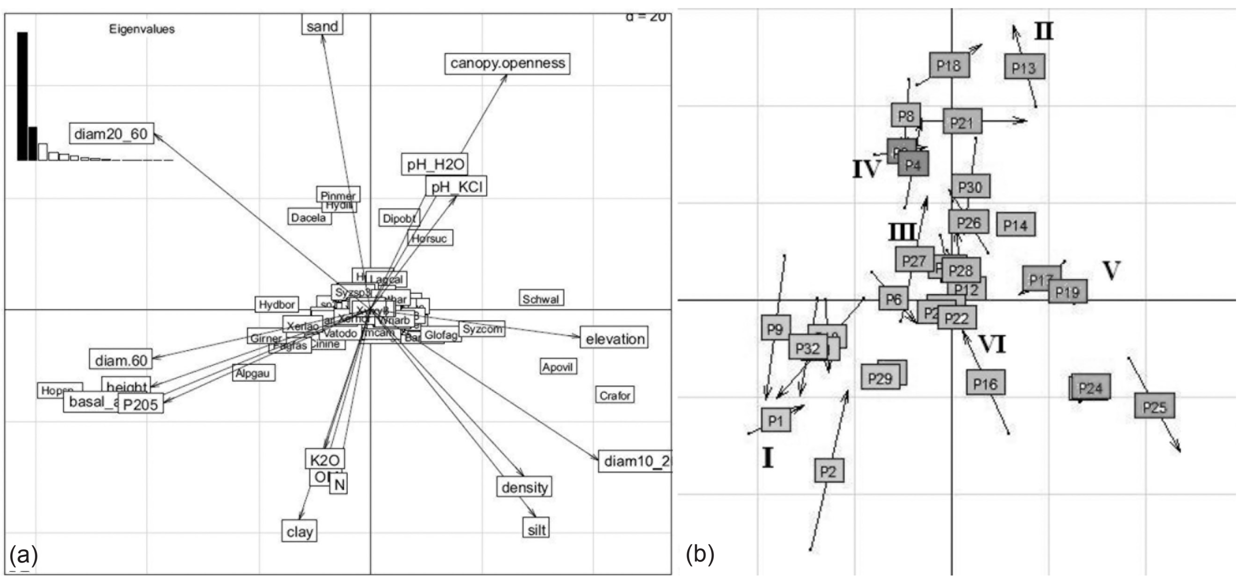

Figure 5 The co-inertia analyses applied on the non-symmetric correspondence analysis and the principal components analysis : (a) scatter of the co-inertia between tree species and environmental variables, (b) match of normed row scores (X and Y) of the plots

identified in forest type V, located in Vang Heua at 800 m altitude.

(3) Forest type II comprising *P. merkusii*, *D. obtusifolius* and *H. sucosa* occurred on sandy soil (82.5% of sand) and associated with a high percentage of canopy openness (48%). This forest type was found in Vang Heua at 800 m altitude.

(4) Forest type IV comprising *P. merkusii* and *D. elatum* was also associated with the previous forest stand structure and soil environment but at 500 m altitude.

(5) Forest type III made up of *L. calyculata*, *H. ilicifolia* and *H. ferrea* was also slightly associated with sandy soil, in particular *H. ilicifolia*. This forest type was found in Tad Xay at low elevation.

(6) Finally, the forest type VI was not clearly associated with any forest structure or soil variable. This corresponded to forests between types I and V.

Diversity indices and estimated species richness

The species richness fluctuated from 7 to 59 in 0.25 ha plots while Shannon indices, from 1.36 to 3.58 and Simpson indices, from 0.67 to 0.96 (Table 4). One-way ANOVA showed that the diversity indices (Shannon, equitability, Simpson) were significantly different between forest groups (< 0.05 at 95% confidence level).

The total number of tree species in the entire study area was estimated to be between 537 and 686 with ACE and ICE estimators respectively.

DISCUSSION

The total number of tree species observed in an area of 8 ha (32 plots of 0.25 ha each) in Phou Khao Khouay was 395. This led to the estimations of a total number of tree species between 537 and 686. At the 0.25-ha plot scale, the species richness was between 7 and 59 with an average of 30 species. This is comparable with the number 18 to 52 species found in 0.25 ha plots of primary and fragmented forest in Xishuangbanna (Zhu et al. 2004). However, it is quite low compared with 76 species found in a primary forest in Indonesia (Kessler et al. 2005) or in central Sulawesi where species richness can reach an average of 51 and 63 in 0.25 ha plots in primary forest (Gradstein et al. 2007). The total number of species found in Phou Khao Khouay is in accordance with the

Table 3 Structural parameters of each forest group

Group	Density (trees ha^{-1})	Height (m)	Basa area (m^2 ha^{-1})	Canopy openness %	% of trees in the diameter class 10–20 cm	% of trees in the diameter class 20–60 cm	% of trees in the diameter class > 60 cm
I	467	15.3	38.9	11	49.9	43.8	6.3
II	236	10.0	17.2	48	42.2	53.1	4.7
III	476	10.6	20.1	40	60.2	38.5	1.4
IV	500	14.3	36.5	44	47.1	49.6	3.4
V	740	9.1	16.4	30	88.9	10.8	0.3
VI	523	13.5	26.8	23	59.7	38.0	2.2

Table 4 Diversity indices for the 0.25 ha plots and for the total area in each forest group

Group	Total area	Species richness	Shannon	Simpson	Equitability
I	1.75	18–49 (125)	2.17–3.32 (3.58)	0.84–0.94 (0.93)	0.75–0.87 (0.74)
II	0.75	7–18 (25)	1.36–2.20 (12.20)	0.67–0.83 (0.84)	0.70–0.78 (0.68)
III	1.25	16–36 (88)	2.23–2.96 (3.44)	0.80–0.92 (0.93)	0.72–0.82 (0.77)
IV	0.5	25–30 (45)	2.45–2.73 (2.88)	0.86–0.88 (0.88)	0.76–0.80 (0.76)
V	1.25	16–59 (116)	1.93–3.55 (3.63)	0.80–0.96 (0.94)	0.70–0.87 (0.76)
VI	2.5	21–54 (235)	2.59–3.58 (4.65)	0.89–0.96 (0.98)	0.81–0.91 (0.85)

Values in parentheses are values for the total area species richness of similar forests located in the mainland of South-East Asia region but less than that in the island region. The indexes of similarity between the three distinctive sites fluctuated between 31 and 35% (results not shown). Most of the frequent species were site-specific such as *A. villosa, C. formosum, D. elatum, H. ferrea, Hydnocarpus ilicifolia* and *S. wallichii.* In terms of diversity, the values presented above could be considered quite low compared with results found in secondary forests, between 0.9 and 0.97 (Tran et al. 2005, Sovu et al. 2009, Millet & Truong 2011).

The analysis of the floristic composition allows for characterisation of six groups of forests types in Phou Khao Khouay: forest type I, Dipterocarpaceae evergreen forest, occurring up to 500 m altitude. The dominant species was *Hopea* sp. which was associated with other species such as *A. gaudichaudiana.* This forest occurred on clayic-sandy soil, with high percentage of clay (23.4%, Table 2). Clay has the capacity to retain large quantity of water (70%) and for a long period. At the same time, the organic matter is important (2.16%) and provides good alimentation for trees. This is generally required for Dipterocarpaceae. The average density (467 stems ha^{-1}) encountered in this forest type was similar to forests found in South China (428 stems ha^{-1}; Lu et al. 2010) or in the Borneo rainforest (422 stems ha^{-1}; Small et al. 2004). The mean basal area of 38.9 m^2 ha^{-1} was greater than the average in forests of Laos which is 35 m^2 ha^{-1} (Sovu et al. 2009) but lower than that of a primary forest in Indonesia (139.7 m^2 ha^{-1}; Kessler et al. 2005) and among the highest values ever recorded in tropical forests. This forest was also characterised by high tree species richness, evenness and diversity. In general, Dipterocarpaceae forests are well structured with few signs of disturbances and are of high value in terms of biodiversity.

Forest type II, mixed Dipterocarpaceae and Pinaceae dry forest, determined by the presence of *D. obtusifolius and P. merkusii.* These species were found in an open environment (48%) on acidic and sandy soil (82.6% of sand) at an elevation of around 800 m. Water retention was only 18%. With regard to diversity, the species richness was very poor (25 on 0.75 ha) because of the dominance of *D. obtusifolius* and *P. merkusii* in the community, which resulted in low evenness. The large proportion of trees belonging to the diameter classes 20–60 cm and over 60 cm indicated quite old forest stands. This forest type could probably have resulted from ancient disturbances which occurred on sandy soil.

Forest type III, mixed Dipterocarpaceae and Lythraceae semi-deciduous forest with typical species such as *L. calyculata, H. ilicifolia* and *H. ferrea.* The canopy seemed open (40%) with considerable presence of bamboo and other undergrowth species. This is probably due to intense logging that creates good conditions for the pioneer species as observed by Blanc et al. (2000) in Vietnam. It is recognised that forest logging promotes a change in floristic composition, favouring the regeneration of pioneer species (Van Gardingen et al. 2006). In the present case, the disturbance was followed by the regeneration of trees of small diameter (60.2% in the diameter class 10–20 cm), belonging mostly to deciduous species such as *L. calyculata and Vitex pinnata.* This forest represented the extreme stage of disturbance of the evergreen Dipterocarpaceae forest (type I). As a result, this forest was characterised by quite low species richness (88 on 1.25 ha). According to Goldsmith et al. (2011), succession in degraded lands appears to be an extremely slow process.

Forest type IV, a coniferous forest with predominance of *P. merkusii* and *D. elatum.* The texture of soil was largely sandy (80.7%). The species richness (45 on 0.5 ha) and diversity were low. The presence of trees of large diameter found in this forest type indicated aged trees characterising a mature forest. This could represent the type of forest that develops naturally on sandy soil at a minimum altitude of 500 m.

Forest type V, a gradient from semi-deciduous to evergreen forests at 800 m altitude. This forest comprised a mixture of evergreen species such as *A. villosa, S. wallichii, S. compongensis* and deciduous ones like *C. formosum.* This forest occurred on silty-sandy soil where sand and silt are 62.5 and 23.2% respectively. Water retention was not high but the high proportion of silt provided rich soil. This forest type was heterogeneous and represented a gradient of degradation of the native forest. The high average density (740 trees ha^{-1}) encountered in this forest type was similar to those encountered in logged forests in Vietnam, where it could reach 706 stems ha^{-1} (Millet et al. 2010). In this case (plots 24, 25), the forest was made up of a large proportion of small diameter trees and it could be assumed that this was the result of recent logging or fallow. The disturbance was followed by the regeneration of pioneer species which could be deciduous or evergreen. As a result, species richness and evenness were high. This disturbed forest had high diversity value.

Forest type VI corresponds to an intermediate degradation of the forest type I named Dipterocarpaceae evergreen forest. It shared some species with this group but *Hopea* was no more frequent. Due to disturbance, the diversity here was most remarkable—an average of 44 species in 0.25 ha plot or a total of 235 species on 2.5 ha. The density of trees was quite low (523 trees ha^{-1}). The three classes of diameter were equally represented and the basal area (26.8 m^2 ha^{-1}) was among the highest. It could be assumed that this forest type corresponded to moderate disturbance of Dipterocarpaceae forests.

CONCLUSIONS

Overall, forests of Phou Khao Khouay were disturbed. The proportion of trees larger than 60 cm diameter was less than 3.1%. The less disturbed forest stands were found at low elevation, 300 to 600 m, where *Hopea* sp. was dominant and associated with *H. borneensis*, *X. laoticum*, *F. fasciculata*, *A. gaudichaudiana*, *Xanthophyllum ecarinatum* and *G. nervosa* (forest type I). This forest type was sometimes modified by more extensive disturbance, leading to the rarefaction of *Hopea* sp. compensated by the development of *A. gaudichaudiana* and *G. nervosa* (forest type VI) or by replacement with deciduous species such as *L. calyculata* (forest type III). At higher elevation, 750 to 900 m, the disturbance of native forests led to the existence of both pioneer deciduous species (*Cratoxylon formosum*) and pioneer evergreen species (*A. villosa, S. compongensis*) found in forest type V. On the plateau associated with sandy soils, from 500 m altitude, nearly pure coniferous forests (forest type IV) composed of *P. merkusii* and *D. elatum* or mixed Dipterocarpaceae and Pinaceae forests (type II) consisting of *D. obtusifolius* and *P. merkusii* could be found.

The improvement of knowledge on forest biodiversity, past evolution, species composition and species arrangement in Phou Khao Khouay National Park should lead to better forest management. In particular, Phou Khao Khouay National Biodiversity Conservation Area retains mature forests of Dipterocarpaceae (forest type I) with high biodiversity value which need care and attention to avoid possible disturbances. In the long term, permanent plots would allow for evaluation of the evolution of biodiversity by following the changes in floristic composition and diversity. This could provide additional information to the management. This study allows for better identification of habitats and future identification of threatened species. This in turn can lead to the development of more comprehensive conservation measures based on the relationship existing between forest types and their compositions.

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