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# Composition and structure of mountain forests containing two tropical pines, *Pinus krempfii* and *Pinus dalatensis*, on the Da Lat Plateau, southern Vietnam

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## Abstract

We examined the floristic composition and stand structure of tropical mountain forests containing two pine species, *Pinus krempfii* Lecomte and *Pinus dalatensis* Ferré, on the Da Lat Plateau in southern Vietnam. A total of 92 tree species were identified, and the greatest species richness at the family level was found in Lauraceae and Fagaceae. Both pine species grew to more than 25 m in height and spread their crowns over the continuous canopy layer. Under crowns of *P. krempfii*, *Castanopsis chinensis*, *Trigonobalanus verticillata*, *Engelhardia roxburghiana*, and *Dendropanax hainanensis* constituted the continuous canopy layer. Under crowns of *P. dalatensis*, pioneer species such as *Schima wallichii*, *Exbucklandia populnea*, and *Pentaphylax euryoides* along with gymnosperms such as *Dacrycarpus imbricatus* and *Dacrydium elatum* constituted the continuous canopy layer. Juveniles of *P. krempfii* were prevalent on the forest floor, but juveniles of *P. dalatensis* were scarce. We suggest that two pine species have different regeneration requirements related to disturbance and soil condition.

#### Introduction

*Pinus* is the largest genus in family Pinaceae. Over 100 species are known, mostly from the northern hemisphere (Price et al. 1998). The genus is widespread in boreal, temperate, and sub-tropical regions, but its distribution is rather limited in the tropics.

Two pine species, *Pinus merkusii* Jung et de Vriese and *Pinus kesiya* Royle ex Gordon, are known widely from tropical Asia (Whitmore 1984; Ashton 2014). In the continental part of the Asian tropics, where the climate is seasonal with distinct dry seasons, pine-deciduous dipterocarp forests often develop in mountainous areas where forest fires occur periodically (Santisuk 1988). *P. merkusii* has a so-called grass stage of seedlings, that is considered to be fire-resistant during the initial period of regeneration (Keeley & Zedler 1998). In the humid tropics of the Malaysian region, where the climate is aseasonal, the distribution of pine species is limited to xeric, poorly vegetated sites where frequent fires occur in Philippines and Sumatra (only *P. merkusii*).

Other tropical pines, *Pinus krempfii* Lecomte and *Pinus dalatensis* Ferré, can be found along the southern part of the Annamite Range, Vietnam, where the climate is orographically very humid. In contrast to the distribution of *P. merkusii* and *P. kesiya*, these pine species are limited to quite small areas (Hiep et al. 2005). *P. krempfii* is endemic to the Da Lat Plateau, the southernmost part of Annamite Range. *P. dalatensis* also grows only on the Da Lat Plateau and several nearby areas to the north. Both species are known from fewer than 10 locations and are listed as vulnerable on both global and national red lists (Hiep et al. 2005).

Population genetics studies (Phong et al. 2015; Wang et al. 2014) have been performed for *P. krempfii*. Genetic differentiation among populations at nuclear loci was extremely low in comparison with other pine species. Its small population sizes and low genetic diversity suggest that the extinction risk of *P. krempfii* is very high. For *P. dalatensis*, small population size and scarce regeneration are becoming a major threat to the survival of this species through the loss of genetic diversity (Truong et al. 2019), but further genetic studies are necessary.

Ecological information on *P. krempfii* and *P. dalatensis* is scarce. Neither pine species grow in xeric deciduous forests; both grow in moist evergreen broad-leaved forests where forest fires are rare. Thus, the regeneration processes of *P. krempfii* and *P. dalatensis* are

expected to be quite different from those of *P. merkusii* and *P. kesiya*. *P. krempfii* is a unique pine having flat needles like Podocarpaceae, and its juveniles appear to be shade-tolerant, based on the physiological features of the leaves (Brodribb & Field 2007).

To conserve these endangered pine species in situ, it is important to understand the regeneration process of their natural populations. To elucidate these regeneration processes, vegetation studies are important. Such studies can help us to understand the habitat and community dynamics of these pine forests. However, to date, there have been few studies on mountain vegetation in Vietnam, including on these pine species. Averyanov et al. (2003) described the floristic composition of mountain vegetation in Vietnam at the macroscale. *P. krempfii* and *P. dalatensis* are seen in the same geographical area, but information on vegetation at the forest stand level is lacking. Therefore, we aimed to determine whether there are differences in stand structure and floristic composition between *P. krempfii* forests and *P. dalatensis* forests.

In the present study, in order to clarify the regeneration process of these tropical pine species, we examined the floristic composition and stand structure of tropical pine forests containing *P. krempfii* and *P. dalatensis*. Juvenile occurrence of these pines on the forest floor was also examined. We asked the following questions: (1) What are the structural and floristic differences between these two types of pine forests; and (2) Does the regeneration process of these pine species differ?

## Methods

#### Study area

Field surveys were conducted at Bidoup Nui Ba National Park in Lam Dong District, Vietnam. Bidoup Nui Ba National Park was established in 2004 and is one of the five largest national parks in Vietnam. The park area is mostly covered with mountain evergreen broad-leaved forests with coniferous species (Figure 1, upper). The park is located on the Da Lat Plateau, in the southern part of the Central Highlands (Figure 2).

The Da Lat Plateau is a hilly region, lying mostly at elevations from 1,200 m to 2,200 m, the highest peaks of the Nation Park being Bi Doup (2,287 m) and Nui Ba (2,167 m). The geology of the plateau is rather complex with a mixture of granites, dacites, and sedimentary rocks.

In Da Lat City (1513 m a.s.l.), the mean annual temperature is 18.2°C and the mean annual rainfall is 1865 mm, with a summer rain peak and several months of a dry winter period with <50 mm rainfall (Averyanov 2003). However, in the mountainous area, morning condensation as dew and frequent heavy, foggy mists are very common and the amount of rainfall increases with altitude.

The Da Lat Plateau has been recognised as a core area of biodiversity conservation in tropical Asia (Davis et al. 1998). The area also harbours rich coniferous flora, including relict, endangered species such as *Fokienia hodginsii* (Dunn) A. Henry and H. H. Thomas, *Glyptostrobus pensilis* (Staunt.) K. Koch, and *Keteleeria evelyniana* Mast (Hiep et al. 2005).

## Study species

*P. krempfii* is a two-needle pine, morphologically quite unique in having two flat, podocarp-like needles (Figure 3 left). There have

been discussions on the taxonomic position of the species, but it is broadly recognised as being included in the genus *Pinus*, subgenus *Strobus*, subsection *Krempfianae* based on analyses of chloroplast DNA (Gernandt et al. 2005). It is thought to be an ancient relict and is the only extant species in subsection *Krempfianae*.

*P. dalatensis* is a five-needle pine (Figure 3, right) that also belongs to subgenus *Strobus*. This species was previously known only from several locations in the Central Highlands, Vietnam, but was recently discovered on the Lao side of the Annamite range (Thomas et al. 2007). Several infraspecific taxa are distinguished, var. *bidoupensis* (in the study area), var. *dalatensis*, and subsp. *procea* (Businsky 1999).

## Field methods and data analysis

In March 2018, four vegetation plots of 20 m by 20 m were established in an evergreen forest at approximately 1500 m above sea level, two for *P. krempfii*-dominant stand and two for *P. dalatensis*-dominant stand. The plots were situated within a small area, and the distances between plots were <1.5 km. The topography of the study area was gentle. Elevations of the plot were similar for all plots (Table 1). In terms of topography, Plots 1 and 2 were located on gentle convex slopes and Plots 3 and 4 were on gentle concave slopes.

Each plot was divided into four subplots of 10 m by 10 m, and trunk diameter and tree height were measured for every tree >1.3 m in height in one subplot. In the remaining three subplots, the same measurements were made for trees >5 cm in trunk diameter. Species identification was performed for every tree measured. When species identification in the field was difficult, branch samples were taken to the laboratory and the species was confirmed there. Species identification was made primarily by Trường Thanh Hoàng. Furthermore, the height of every pine seedling in the whole plot was measured.

Coefficients of floristic similarity C by Jaccard (1901) and CC by Sørensen (1948) were calculated among plots.

Nomenclature follows the Angiosperm Phylogeny Group (APG IV 2016).

## Results

## Floristic composition of plots

In total, 92 species were found in the plots (Appendix). Species richness in each plot was relatively high; 20–25 families and 41–52 tree species were identified in each plot. The highest species richness at the family level was shown by Lauraceae (12 spp.), followed by Fagaceae (9 spp.), Symplocaceae (6 spp.), Elaeocarpaceae (5 spp.), Ericaceae (5 spp.), and Rubiaceae (5 spp.). The most common species occurring in every plot were *Castanopsis chinensis, Engelhardia roxburghiana, Neolitsea cambodiana, Magnolia annamensis, Ardisia crenata, Syzygium zeylanicum, Lasianthus condorensis, Euodia lepta, Symplocos adenophylla, Pyrenaria jonqueriana, and Ternstroemia japonica.* 

Floristic similarities among plots were rather low (Table 2), indicating that  $\beta$  diversity was high among plots. Distinguishing between *P. krempfii* forest (Plots 1 and 2) and *P. dalatensis* forest (Plots 3 and 4) was difficult in terms of overall floristic composition based on the presence/absence of species.



**Figure 1.** Upper, forests in Bidoup Nui Ba National Park. Note emergent pine trees of which crowns spread over continuous forest canopy of evergreen broad-leaved trees; Lower, tree form of *Pinus krempfii*.

## Relative basal area

The sum of the basal area was  $>70 \text{ m}^2/\text{ha}$  in each plot because of the large pine trees included in the plots (Table 1). In terms of relative basal area (RBA), pine species were dominant in every plot: *P. krempfii* in Plot 1 and Plot 2 and *P. dalatensis* in Plot 3 and

Plot 4 (Figure 4). In *P. krempfii* forest, the RBA of Fagaceae species such as *C. chinensis* and *Trigonobalanus verticillata* was relatively high and Fagaceae showed the second largest share of basal area at the family level: 10.3% in Plot 1 and 22.5% in Plot 2. On the other hand, in *P. dalatensis* forest, the share of Fagaceae species was very

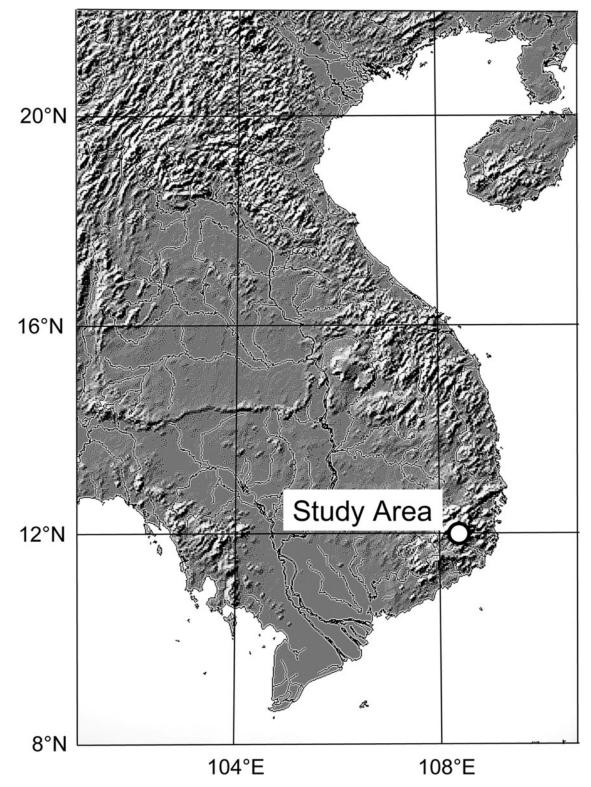


Figure 2. Location of the study area. Base map is modified from Topographic30deg N0E90.png (https://commons.wikimedia.org/w/index.php?curid=166887).

low, <3.0%, and the share of pioneer/seral species, such as *Pentaphylax euoryoides* and *Schima wallichii*, was higher. Although the species richness of Lauraceae was highest at the family level, the RBA of Lauraceae species was low in every plot (<2.5%).

## Stand structure and floristic composition

Both pine species grew as emergent trees in the evergreen broadleaved forest. The stem of both pine species is straight and tall, with a broad, umbrella-like crown (Figure 1, lower). The lowest branches of a crown originate from the upper part of the main

#### Table 1. General features of plots.

Plot No.	1	2	3	4
Size	20m×20m	20m×20m	20m×20m	20m×20m
Topography	flat ridge	flat ridge	gentle lower slope	undulating slope
Inclination	15°	10°	5°	5°
Slope direction	W-S	NNW 335	W 256	SWW 245
Altitude (m)	1490	1493	1494	1490
Latitude	N 12° 10' 30"	N 12° 10' 36.5"	N12° 11'02"5	N 12° 11' 1"
Longitude	E 108° 42'2"	E 108° 40'57"	E 108° 41' 29,1"	E 108° 41'26''
Total BA (m³/ha)	79.2	73.9	75.1	76.9
Dominant spp.	Pinus krempfii	Pinus krempfii	Pinus dalatensis	Pinus dalatensis , Pentaphylax euryoides
Familyrichness (H>1.3m)	20	25	22	22
Species richness (H>1.3m)	41	48	52	44





Figure 3. Branches of target pine species. Left, Pinus krempfii; Right, P. dalatensis.

stem, usually around 15 m above the ground. In the plots, both species reached heights >25 m and spread their crowns over the main canopy layer (Figure 5). The stem diameters of the pine species also exceeded those of most other trees.

The floristic composition of the main canopy layer clearly differed between *P. krempfii* forest (Plots 1 and 2) and *P. dalatensis* forest (Plots 3 and 4), as shown in Table 3. In *P. krempfii* forest, Fagaceae species (*C. chinensis* and *T. verticillata*), *E. roxburghiana*, and *Dendropanax hainanensis* constituted main canopy layer. In contrast, in *P. dalatensis* forest, *Pentaphylax euryoides* was common in main canopy layer. Pioneer species such as *S. wallichii* and *Exbucklandia populnea* and gymnosperms such as *Dacrycarpus imbricatus* and *Dacrydium elatum* were also found. Although two Fagaceae trees (*Lithocarpus echinotolus, L. microbalanus*) were also found in plots of *P. dalatensis* forest, those were confined to the lowest part of the main canopy layer. Broad-leaved species bearing small, winged seeds dispersed by wind (anemochory) were prevalent in *P. dalatensis* forest, while broad-leaved species bearing fruits dispersed by animals (endozoochory and hoarding dispersal) were prevalent in *P. krempfii* forest.

In the understory, a variety of shrub and small tree species were found, in addition to saplings and sprouts of various tree species (Appendix). *L. condorensis* (Rubiaceae), *Polyosma annamensis* (Escalloniaceae), and *N. cambodiana* (Lauraceae) were found in every plot and were the most abundant.

## Juveniles of pine species

Juveniles of *P. krempfii* occurred in every plot. In Plot 1, in particular, many juveniles were observed and some reached heights >50 cm (Figure 6). There was a small canopy gap formed by an uprooted tree, just near Plot 1. Few juveniles of *P. dalatensis* were found, and these were confined to the smallest height class.

<sup>55</sup> 

 Table 2.
 Coefficients of floristic similarities among plots. C, index by Jaccard (1901);

 (CC, index by Sørensen (1948).

	P1	P2	P3	$\mathbf{P4}$	
P1		0.49	0.50	0.55	
P2	0.33		0.50	0.55	$\mathbf{C}\mathbf{C}$
$\mathbf{P3}$	0.33	0.34		0.55	
P4	0.38	0.38	0.38		
		С			

## Discussion

## Phytogeography of the forests

From a phytogeographical viewpoint, forest vegetation in Vietnam has a close affinity with forests in several adjacent areas (Averyanov et al. 2003). In lowlands with humid climates, forests have many floristic affinities with wet evergreen forests in Malaysian region, which is characterised by the presence of many tropical families such as *Dipterocarpaceae, Apocynaceae*, *Burseraceae* etc. In southwestern Vietnam with tropical monsoonal climates, forests have many floristic affinities with semievergreen, semi-deciduous, or deciduous forests in Myanmar, Thailand, Cambodia, and Laos, which are characterised by deciduous *Dipterocarpaceae, Lithraceae (Lagerstroemia), Fabaceae*, etc. (Rundel 1999; Schmid 1974).

However, the change in flora and vegetation from lowland to mountain areas is marked in Vietnam. Tropical families such as Dipterocarpaceae, Anacardiaceae, Euphorbiaceae, etc. rapidly decrease above 1,200 m in altitude, and plant families dominant in subtropical regions, such as Fagaceae, Lauraceae, Theaceae (in broad sense; Pentaphylaceae and Theaceae in narrow sense), etc., increase in species richness and dominance. Mountain forests in Vietnam are a type of Lauro-Fagaceous forest that is distributed broadly in the subtropical and warm-temperate regions of East Asia, from Himalaya to Japan through southern China. The Da Lat Plateau, which is located in the southernmost part of the Annamite Range, is actually a southern range limit of this type of forest. Mountain flora in Vietnam has a close affinity with that of Yunnan and Guangxi in southwestern China. For example, among nine species of Fagaceae in the plots, six are common to Yunnan and two, Lithocarpus microbalanus and Lithocarpus stenopus, are endemic to Vietnam. The flora of P. krempfii and P. dalatensis forests in this study (Appendix) probably fall within the floral range of Lauro-Fagaceous forests in the area, although pine species are dominant in the overstory.

Another feature of mountain forests in Vietnam is that they harbour many relict, primitive taxa. For example, *T. verticillata*, which was recently found in Vietnam and in southern China (Ng & Lin 2008; Zhu & Zhou 2017), is a basal, extant species of Fagaceae that was previously known only from tropical mountains in Malaysia. For Hamamelidaceae, two genera found in the plots, *Exbucklandia* and *Rhodoleia*, form the most basal clade in the family (Li et al. 1999; Magallón. 2007). Among the conifers, 6–9 species are endemic to Vietnam and ancient relictual genera such as *Xanthocyparis, Glyptostrobus, Pseudotsuga*, etc. occur.

# *Structural and floristic differences between* P. krempfii *and* P. dalatensis *forests*

In both *P. krempfii* and *P. dalatensis* forests, pine species grow as emergent trees, spreading their crowns over the continuous canopy formed by evergreen broad-leaved species. Straight, massive trunks and long, laterally spreading crowns characterise the tree forms of these pine species. This growth form is a very important trait that allows pine species to coexist with surrounding evergreen broad-leaved trees in the forest overstory. However, the growth process that produces this tree form is not obvious. A rapid initial growth capable of outcompeting the surrounding broad-leaved trees and the subsequent, rapid development of a large spreading crown can be predicted; however, further study is necessary on this point.

Notably, the floristic composition of the main canopy layer just below the pine crowns clearly differed between *P. krempfii* and *P. dalatensis* forests. This might reflect the difference in regeneration processes of the two forest types as below.

In the main canopy layer of *P. krempfii* forest, shade-tolerant species such as Fagaceae, *C. chinensis, T. verticillata*, and *D. hainanensis* were abundant. These broad-leaved species are major components of the canopy of Lauro-Fagaceous forests, which are climax forests in the study area (Schmid 1974). *C. chinensis* and *Dendropanax* species were also abundant in the understory. Thus, forest stands with *P. krempfii* in the canopy can be expected to reach the mature stage, from the viewpoint of successional development of a forest stand.

Conversely, the main canopy of the *P. dalatensis* forest was mostly composed of pioneer species having small winged seeds, including *S. wallichii, E. populnea, P. euryoides,* and *Rhodoleia championii,* or was composed of conifers, *D. imbricatus* and *D. elatum.* Pioneer species with small seeds usually cannot regenerate in mature forests, but require disturbed sites. Thus, it is suggested that *P. dalatensis* forest is generally established after a larger disturbance and is a successional stage to a mature forest stand.

Among the pioneer/seral species occurring in *P. dalatensis* forest, *S. wallichii* and *E. populnea* are known widely as pioneer species in Asian lower mountain forests of tropical and subtropical regions (Khan et al. 1987; Rao et al. 1990). Both species regenerate well at disturbed sites and grow rapidly in open conditions (Zhang & Xu 2004; Bhat et al. 2010), but are often seen in mature forests as large remnant trees.

Ecological information on *P. euryoides* is limited. This species is a shrub or small tree that occurs widely in lower to upper montane forests in southern China, Indochina, the Malay Peninsula, and northern Sumatra. In Malaysia, it is abundant on rocky ridges near the summit of Gunung Ulu Kali at 1758 m a.s.l. (Chua & Saw 2001) and in upper montane forests with a thick layer of dry peat on Gunung Kob, 1266 m a.s.l. (Yao et al. 2009). This species has primitive, xeromorphic to mesomorphic wood anatomy features and can grow in a wide range of habitats (Carquist 1984). Interestingly, *P. euryoides* and *Schima remotiserrata* are codominant in forests of another endangered pine, *P. kwangtungensis*, which occurs from northern Vietnam to Southern China (Wang et al. 2008).

Ecological information on *R. championii* is also limited. This species is a shrub or small tree belonging to the Hammamelidaceae and occurs widely in lower to upper montane forests in southern China, Indochina, the Malay Peninsula, and Indonesia. Regeneration is evident along roads and in open places, but it often becomes a

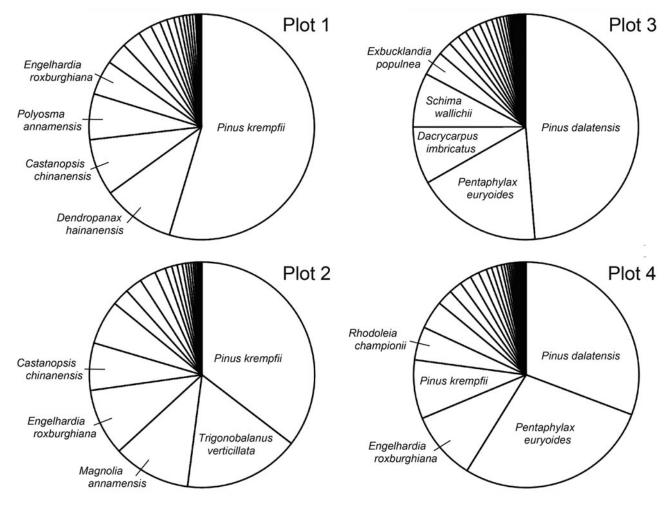


Figure 4. Relative basal area of component species in each plot. Species names of upper five rank in each plot are indicated.

codominant species in tropical lower montane forests (Averyanov et al. 2003).

There have been a few studies on the regeneration of *D. imbricatus* and *D. elatum*. Kitayama et al. (2011) found that in Borneo, Podocarpaceae trees (*D. imbricatus* and *Dacrydium gracile*) regenerate under well-lit conditions in nutrient-limited soils where nutrient-demanding pioneer species (e.g. *Macaranga* and *Ficus* species) cannot grow well. Another study (Akkarasedthanon et al. 2017) examined factors affecting the size structure and sapling occurrence of Podocarpaceae species in tropical montane forests of central Thailand. They reported that small seedlings of *D. elatum* were prevalent in the forest, but saplings were few and were seen only on top ridges and cliffs with plenty of light because seeds of this species need well-lit conditions to germinate.

### Regeneration of pine species

Two pine species, *P. krempfii* and *P. dalatensis*, were found in the same area, both as emergent trees in evergreen broad-leaved forests. However, the regeneration process was quite different between the two species, as described below.

Juveniles of *P. krempfii* were prevalent on the forest floor. As shown in Plot 1, juveniles sometimes reached heights >50 cm near small canopy gaps. Brodribb & Field (2007) examined

the photosynthetic and hydraulic physiology of *P. krempfii* leaves and clarified that this species shows relatively high shade tolerance. They suggest that this species can grow in tropical evergreen forests by acquiring the ability to compete with evergreen species.

The floristic composition of the main canopy layer of *P. krempfii* forest suggests that the forest stand had reached a late successional stage in which Fagaceae species are dominant. It is thought that *P. krempfii* can regenerate in small canopy gaps created by death of a single or a few canopy trees because it has seedling banks on the forest floor.

Conversely, few juveniles of *P. dalatensis* were found in the forest interior, and the main canopy layer of *P. dalatensis* forest was mostly composed of pioneer/seral species and conifers. Fagaceae species that are common in mature forests were scarce in this type of forest. This suggests that *P. dalatensis* requires the open conditions created by large disturbances coupled with the death of multiple canopy trees. Factors causing large disturbances are unknown, but strong winds brought by typhoons might be responsible.

Another possible explanation for the different regeneration patterns of the two pine species is different requirements of soil conditions. Although no soil surveys were performed in this study, we have some preliminary field observations. We observed brown forest soil in *P. krempfii* forest, but white, strongly leached soil, a kind

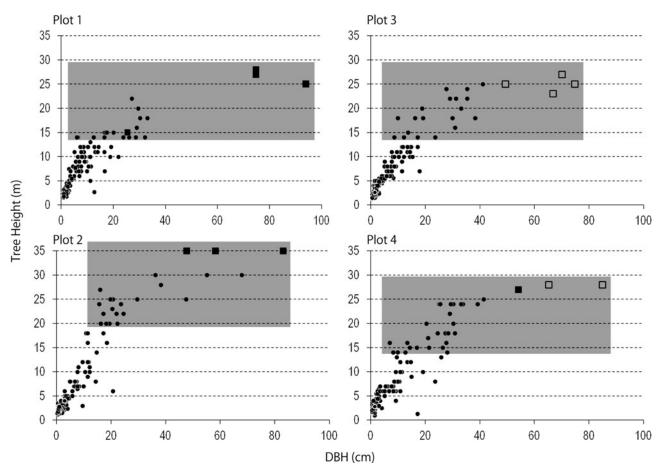


Figure 5. Relationships between stem diameter and tree height in each plot. Filled square, *Pinus krempfii*; open square, *Pinus dalatensis*. Shaded areas indicate the range of which floristic composition was presented in Table 3.

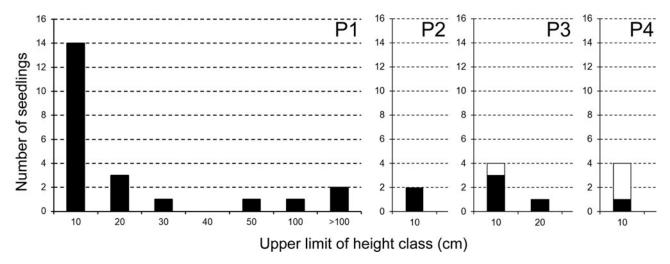


Figure 6. Juveniles of pine species in each plot. Solid bar indicates juveniles of P. krempfii and open bar those of P. dalatensis.

of Podozol, in the *P. dalatensis* forest. *P. dalatensis* forest might be a kind of tropical heath forest, or Kerangas. Stunted heath forest in which *D. elatum* and *D. imbricatus* dominate is reported from the Bokor Plateau (ca. 1,000m a.s.l.) in the Elephant Mountains of Cambodia, where the shallow soils and water-logged

depressions are common (Rundel & Middletown 2017). On Mt. Kinabalu in Malaysia, lower montane kerangas in which *D. elatum, D. imbricatus*, and *S. wallichii* are included develop on podzolised soil of sedimentary rock origin (Aiba & Kitayama 1999; Ashton 2014; Kitayama et al. 2004). This forest

Table 3. Floristic composition of the canopy layer in each plot. Refer Fig. 5 for size of trees included in the calculation; Plot 1, Plot 3 and Plot 4, H>=14m; Plot 2, H>=
20m. A, Anemochory; E, Endozoochory; H, Hoarding dispersal.

Species	Plot 1	Plot 2	Plot 3	Plot 4	Total	Seed dispersal typ
Pinus krempfii	4	3		1	8	А
Engelhardia roxburghiana	2	9		4	15	А
Dendropanax hainanensis	5	1	1		7	E
Castanopsis chinensis	3	1			4	Н
Trigonobalanus verticiliata		2			2	Н
Lithocarpus stenopus	1			1	2	Н
Adinandra sp.	1			1	2	E
Helicia sp.	1			1	2	Н
Magnolia annamensis		2			2	E
Syzygium zeylanicum	2				2	E
Craibiodendron henryi var. bidoupensis	1				1	А
Illicium cambodianum	1				1	E
Phoebe lanceolata		1			1	E
Syzygium wightianum		1			1	E
Vaccinium sprengelii		1			1	E
Pinus dalatensis			4	2	6	А
Pentaphylax euryoides			10	14	24	А
Schima wallichii			3		3	А
Dacrycarpus imbricatus			2		2	E
Dacrydium elatum				2	2	E
Rhodleia championii		1		1	2	А
Ternstroemia japonica				2	2	E
Exbucklandia populnea			1		1	А
Lithocarpus echinotholus			1		1	Н
Lithocarpus microbalanus				1	1	Н
Syzygium sp.			1		1	E
Unidentified sp.			1	1	2	-
Total	21	22	24	31	98	

resembles to *P. dalatensis* forest viewed from soil condition and floristic composition of stand. The study area is geologically composed of complexes of granites, dacites, and sedimentary rocks. Different soil conditions related to the underlying geology might increase the vegetation diversity of the area.

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## References

- Aiba S and Kitayama K (1999) Structure, composition and species diversity in an altitude-substrate matrix of rain forest tree communities on Mount Kinabalu, Borneo. *Plant Ecology* 140, 139–157.
- Akkarasedthanon J, Chuea-Nongthon C and Grote PJ (2017) Factors affecting size distribution and sapling occurrence of Podocarpaceae at Khao Yai National Park, Thailand. *Tropical Natural History* 17, 94–110.

- APG IV Angiosperma Phylogeny Group (2016) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Botanical Journal of the Linnean Society* 181, 1–20.
   Ashton P (2014) On the Forests of Tropical Asia: Lest the Memory of Fade. Kew:
- Royal Botanic Gardens. Averyanov LV, Loc PK, Heap NT and Harder DK (2003) Phytogeo-
- graphic review of Vietnam and adjacent areas of eastern Indochina. *KOMAROVIA* **3**, 1–83.
- Bhat BP, Singha LB, Satapathy KK, Sharma YP and Bujarbaruah KM (2010) Rehabilitation of shifting cultivation areas through agroforestry – a case study in eastern Himalaya, India. *Journal of Tropical Forest Science* 22, 13–20.
- Brodribb TJ and Field TS (2007) Evolutionary significance of a flat needle *Pinus* in Vietnamese rainforest. *New Phytologist* **178**, 201–209.
- Businsky R (1999) Study of Pinus dalatensis Ferré and of the enigmatic "Pin du Moyen Annam." Candollea 54, 125–143.
- Carlquist S (1984) Wood anatomy and relationships of Pentaphylaceae: significance of vessel features. *Phytomorphology* 34, 1–4.
- Chua LSL and Saw LG (2001) A reassessment of the flora of Gunugn Ulu Kali, Genting Highland, Malaysia – preliminary findings and trends. *Malaysian Nature Journal* 55, 65–76.

- Davis SD, Heywood VH and Hamilton AC (eds.) (1998) Centers of Plant Diversity, volume 2. Asia, Australia and the Pacific. Cambridge: IUCN Publications Unit.
- Gernandt DS, López GG, Garcia, SO and Liston A (2005) Phylogeny and classification of *Pinus. Taxon* 54, 29–42.
- Hiep NT, Loc PK, Luu NDT, Thomas PI, Farjon A, Averyanov L and Regalado JJ (2005) Vietnam Conifers: Conservation Status Review 2004. Hanoi: Fauna and Flora International, Vietnam Programme.
- Jaccard P (1901) Etude comparative de la distribution florale dans une portion des Alpes et du Jura. Bulletin de la Société vaudoise des sciences naturelles 37, 547–579.
- Keeley JE and Zedler H (1998) Evolution of life histories in Pinus. In Richardson DM (ed.), Ecology and Biogeography of Pinus, Cambridge: Cambridge University Press, pp. 219–250.
- Khan ML, Rai JPN and Tripathi RS (1987) Population structure of some tree species in disturbed and protected subtropical forests of north-east India. *Acta Oecologia* 8, 247–255.
- Kitayama K, Aiba S, Takyu M, Majalap N and Wagai R (2004) Soil phosphorus fractionation and phosphorus-use efficiency of a Bornean tropical montane rain forest during soil aging with podozolization. *Ecosystems* 7, 259–274.
- Kitayama K, Aiba S, Ushio M, Seino T and Fujiki Y (2011) The ecology of podocarps in tropical montane forests of Borneo: distribution, population dynamics, and soil nutrient acquisition. *Smithsonian Contributions to Botany* 95, 101–117.
- Li J, Bogle AL and Klein S (1999) Phylogenetic relationships in the Hammamelidaceae: evidence from the nucleotide sequences of the plastid gene matK. *Plant Systematics and Evolution* **218**, 205–219.
- Magallón S (2007) From fossils to molecules: phylogeny and the core Eudicot floral groundplan in Hamamelidoideae (Hamamelidaceae, Saxifragales). Systematic Botany 32, 317–347.
- Ng SC and Lin JY (2008) A new distribution record of *Trigonobalanus* verticillata (Fagaceae) from Hainan Island, South China. *Kew Bulletin* 63, 341–344.
- Phong DT, Lieu TT, Hien VT and Hiep N (2015) Genetic diversity of the endemic flat-needle pine *Pinus krempfii* (Pinaceae) from Vietnam revealed by SSR markers. *Genetics and Molecular Research* 14, 7727–7739.
- Price RA, Liston A and Strauss SH (1998) Phylogeny and systematics of Pinus. In Richardson DM (ed.), Ecology and Biogeography of Pinus, Cambridge: Cambridge University Press, pp. 3–46.

- **Rao P, Barik SK, Pandey HN and Tripathi RS** (1990) Community composition and tree population structure in a sub-tropical broad-leaved forest along a disturbance gradient. *Vegetatio* **88**, 151–162.
- Rundel PW (1999) Forest Habitats and Flora in Laos PDR, Cambodia and Vietnam. Conservation Priorities In Indochina - WWF Desk Study. Prepared for World Wide Fund for Nature. Hanoi: Indochina Programme Office.
- Rundel, PW and Middleton, DJ (2017) The flora of the Bokor Plateau, southeastern Cambodia: a homage to Pauline Dy Phon. *Cambodian Journal of Natural History* 1, 17–37.
- Santisuk T (1988) An Account of the Vegetation of Northern Thailand. Stuttgart: Franz Steiner Verlag Wiesbaden GMBH.
- Schmid M (1974) Végétation du Viet-Nam: Le Massif Sud-Annamitigue et les Régions Limitrophes. Paris: Orstom.
- Sørensen T (1948) A method of establishing groups of equal amplitude in plant sociology based on similarity of species content and its application to analysis of the vegetation on Danish commons. *Biologiske skrifter* 5, 1–34.
- Thomas P, Sengdala K, Lamxay V and Khou E (2007) New records of conifers in Cambodia and Laos. *Edinburgh Journal of Botany* 64, 1–9.
- Truong NK, Tien TV, Trieu LN, Giang, NV, Anh TTL, Nghia NH and Truong HT (2019) Geographical variation in vegetative growth, sexual reproduction and genetic diversity of *Pinus krempfii* H. Lec. and *Pinus dalatensis* Ferré in Tay Nguyen Plateau, Vietnam. Annual Report of Pro Natura Foundation Japan 28, 211–223.
- Wang B, Mahani MK, Ng WL, Kasumi J, Phi HH, Inomata N, Wang XR and Szmidt AE (2014) Extremely low nucleotide polymorphism in *Pinus krempfii* Locomte, a unique flat needle pine endemic to Vietnam. *Ecology and Evolution* 4, 2228–2238.
- Wang HL, Miao SY, Wu WD, Xue XT and Jin JH (2008) Characteristics of *Pinus kwantongensis* community in Luokeng Nature Reserve, Guangdong Province. *Journal of Wuhan Botanical Research* 26, 53–58. In Chinese with English abstract.
- Whitmore TC (1984) *Tropical Rain Forests of the Far East.* 2nd ed., Oxford: Oxford University Press.
- Yao TL, Kamarudin S, Chew MY and Kiew R (2009) Sphagnum bogs of Kelantan, Peninsular Malaysia. Blumea 54, 139–141.
- Zhang D and Xu Y (2004) A preliminary study on the growth of 5 native broadleaf tree species. *Guangdong Forestry and Science Technology* 3, 39–41. In Chinese with English abstract.
- Zhu H and Zhou SS (2017) A primitive Cupuliferae plant (*Trigonobalanus verticillata*) found in Xishuangbanna, Yunnnan, and its biogeographical significance. *Plant Science Journal* 35, 205–206. In Chinese with English abstract.

# Appendix

Floristic composition of plots.

Family and Specie	25	P1	P2	P3	P4
Annonaceae					
	Miliusa aff. campanulata			+	+
	, Polyalthia parviflora				+
	Polyalthia sp.		+		
Aquifoliaceae			· ·		
	Ilex rotunda		+		
Araliaceae					
/	Dendropanax chevalieri	+	+		
	Dendropanax hainanensis	+	1		
	Dendropanax sp1.	+	+	+	+
	Dendropanax sp1.				
Chusiasaaa	Denaropanax spz.	+	+	+	+
Clusiaceae	College bulling management				
	Callophyllum rugosum		+		+
	Callophyllum sp.	+	+	+	
	Garcinia sp.		+	+	+
Ebenaceae					
	Diospyros lotus		+	+	+
Elaeocarpaceae					
	Elaeocarpus bidoupensis	+		+	
	Elaeocarpus poilanei	+			
	Elaeocarpus stipularis var. longipetiolatus			+	+
	Elaeocarpus sylvestris		+		
	Sloanea sp.	+			+
Ericaceae					
	Craibiodendron henryi var. bidoupensis	+	+		+
	Craibiodendron vietnamense				+
	Rhododendron moulmainense				+
	Vaccinium sprengelii	+			
	Vaccinium sp.	+	+	+	
Escalloniaceae					
	Polyosma annamensis	+	+	+	+
Fabaceae					
	Archidendron robinsonii		+		
Fagaceae					
	Castanopsis chinensis	+	+	+	+
	Lithocarpus annamensis		+		+
	Lithocarpus echidnocarpa		,	+	
	Lithocarpus echinotholus			+	+
	Lithocarpus ecimotions Lithocarpus microbalanus			+	+
	Lithocarpus stenopus			т	
		+	+		+
	Lithocarpus truncatus		+		
	Quercus sp.			+	
	Trigonobalanus verticiliata		+		

(Continued)

continucu j					
Family and Species		P1	P2	P3	P
Hammamelidaceae					
	Exbucklandia populnea			+	
	Rhodleia championii		+		+
Illiciaceae					
	Illicium cambodianum	+			
Juglandaceae					
	Engelhardtia roxburghiana	+	+	+	+
Lauraceae	5 5	<u> </u>			
	Ciinamomum burmannii			+	
	Cinnamomum kunstleri		+	+	
	Cinnamomum loureirii	+	+	+	
	Cinnamomum mairei	1	+	+	
	Cryptocarya sp.		+		
	Litsea samolnea			+	
				+	+
	Litsea verticillata		+	+	
	Litsea sp1.		+	+	+
	Litsea sp2.			+	
	Litsea sp3.				+
	Neolitsea cambodiana	+	+	+	-
	Phoebe lanceolata		+	+	
Magnoliaceae					
	Magnolia annamensis	+	+	+	+
	Magnolia sp.	+			
Meliaceae					
	Dysoxylon sp.			+	
Moraceae					
	Ficus sp.	+	+		-
Myrtaceae					
	Syzygium lineatum	+		+	+
	Syzygium wightianum		+		
	Syzygium zeylanicum	+	+	+	
	Syzygium sp.	+		+	
Opiliaceae					
	Urobotrya siamensis	+			
	Unidentified	+			
Pentaphylacaceae		1			
rentaphylacaceae	Adinandra sp.				
		+			-
	Eurya japonica	+			
	Pentaphylax euryoides	+		+	-
	Ternstroemia japonica	+	+	+	-
Pinaceae					
	Pinus dalatensis			+	+
	Pinus krempfii	+	+		+

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(Continued)

Family and Species		P1	P2	P3	P4
Podocarpaceae					
	Dacrycarpus imbricatus		+	+	
	Dacrydium elatum			+	+
Primulaceae					
	Ardisia crenata	+	+	+	-
	Ardisia sp.		+	+	-
	Maesa acuminatissima		+		
	Maesa sp.	+			
Proteaceae					
	Helicia sp.	+		+	-
Rosaceae					
	Eriobotrya poilanei		+		
	Sorbus corymbifera		+		
Rubiaceae					
	Alleizettella rubra			+	-
	Lasianthus chevalierii			+	
	Lasianthus condorensis	+	+	+	
	Lasiantus poilanei	+			
	Lasianthus sp.		+		
Rutaceae					
	Euodia lepta	+	+	+	-
	Euodia sp.			+	
Sabiaceae					
	Meliosma sp.		+		
Symplocaceae					
	Symplocos adenophylla	+	+	+	-
	Symplocos aff. lucida			+	
	Symplocos cochinchinensis			+	-
	Symplocos racemosa		+	+	
	Symplocos lancifolia	+			
	Symplocos sp.	+			
Theaceae					
	Gordonia bidoupensis		+		-
	Pyrenaria jonqueriana	+	+	+	-
	Schima wallichii			+	
Unidentified		+	+	+	-