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# Ecological species groups and interspecific associations of dominant woody species in a seasonal tropical forest of Laos

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**Abstract** The study of ecological species groups (ESGs) and interspecific interactions offers important insights into the mechanisms that drive tree species coexistence and enhances our understanding of plant community structure, function, and taxonomy. This study aimed to identify ESGs within a seasonal tropical forest in Phou Khao Khouay National Park, located in central Laos, and to investigate the key environmental factors influencing their distribution. Additionally, the study analysed community stability and interspecific associations among woody species using various statistical techniques, including Variance Ratio (VR), chi-squared tests, Association Coefficients (AC), and percentage of Co-occurrence (PC). To collect data, thirty-two permanent plots, each covering an area of 2500 m² (50 × 50 m), were established. In each plot, floristic data and species abundance were recorded, along with soil samples from two depths (0–10 cm and 10–20 cm) for physicochemical analysis. Vegetation data were classified using Two-Way Indicator Species Analysis (TWINSPAN), and differences between ESGs were evaluated using Analysis of Variance (ANOVA). Indicator Species Analysis (ISA) was applied to identify key species for each ESG, while Canonical Correspondence Analysis (CCA) was employed to explore the relationships between ESGs and environmental variables. The results revealed that the woody plant communities in the study area were relatively stable, exhibiting predominantly positive interspecific associations. Additionally, the distribution of the fosur identified ESGs showed a strong correlation with topographical factors – such as elevation, aspect, and slope – and soil properties, including pH, organic matter content, cation exchange capacity, total nitrogen, phosphorus, potassium, and soil texture. These findings underscore the importance of recognizing microhabitats that support the growth and conservation of woody plant species in Phou Khao Khouay National Park, offering valuable insights for future ecological research and conservation initiatives.

**Keywords:** environmental factors, multivariate analysis, permanent plot, indicator species, similar habitats.

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## Introduction

The study of ecological species groups (ESGs) and interspecific interactions has garnered increasing attention due to their pivotal role in elucidating ecological processes across various scientific domains, including ecology, botany, and zoology (Bergeron & Bouchard 1984, Wiegand et al. 2007, Kunwar et al. 2012, Su et al. 2015). ESGs are characterized by the composition and spatial arrangement of species within a defined area (Li et al. 2008). Their identification is based on recognizing species that exhibit similar environmental preferences and occupy comparable ecological niches, thereby forming distinct patterns across landscapes (Archambault et al. 1989). These species groups serve as important indicators of ecosystem health, often consisting of species with a high degree of fidelity to specific niches, and thus are valuable tools for assessing forest ecosystem conditions (Li et al. 2008, Su et al. 2015).

In applied ecology, ESGs are essential for delineating and mapping ecosystem types based on species composition and coverage, providing key insights into ecological classification and habitat management (Abella & Covington 2006, Rad & Shafiei 2010). A more comprehensive understanding of ESGs not only enhances biodiversity monitoring and conservation but also strengthens our grasp of ecosystem resilience and sustainability in the face of environmental change (Daubenmire 1952, Robertson et al. 1988, Burke 2001, Adel et al. 2014).

In ecological communities, species distributions are often uneven, with dominant species being more abundant and conspicuous, while rarer species are less numerous and harder to detect (Grime 1998, Hou et al. 2023). Dominant species typically occupy broader ecological niches, leading to greater overlap with other species and more extensive resource utilization compared to rarer species, which tend to be restricted to specialized niches with limited resources (Song & Zhang 2018, Jiang et al. 2024). Dominant species also exhibit higher resource acquisition efficiency and greater resilience to extreme environmental conditions, whereas rare species are more likely to be confined to resource-rich habitats (Nguyen et al. 2022, Xue et al. 2023).

Understanding the dynamics among dominant species is crucial for vegetation restoration, particularly in degraded ecosystems such as barren hillsides or disturbed environments (Nguyen et al. 2023c). These species play a key role in enhancing ecosystem resilience and supporting ecological restoration, making them central to efforts aimed at restoring ecological balance in disturbed habitats (Wang & Cui 2023). To ensure the reliability of ecological assessments, it is critical to consider not only the status of dominant tree species but also key environmental factors, such as topography, soil properties, and microclimatic conditions (Adel et al. 2014). Soil structure and nutrient availability are particularly significant, as they directly influence plant growth and community dynamics (Ball et al. 2005, Robertson et al. 1988).

In tropical forests, where soil properties are often heterogeneous, understanding the complex interactions between plant species and their environment is vital for effective ecosystem management and restoration (Crouzeilles et al. 2017, Gatica-Saavedra et al. 2017). Therefore, a comprehensive understanding of dominant species and their interactions with environmental factors is essential for advancing ecological research and implementing successful restoration strategies (Liu et al. 2022).

Interspecific interactions, ranging from facilitation to competition, are fundamental to the stability and dynamics of forest communities, especially across different stages of ecological succession (Fichtner et al. 2017, Pretzsch 2022). These interactions offer critical insights into species relationships and their spatial distribution, thereby improving our understanding of species assembly and community structure evolution (Cavard et al. 2011). By analysing species' habitat preferences and their interspecific interactions, associations can be classified into positive, negative, or neutral categories (Liu et al. 2014, Nguyen et al. 2023b). Investigating these associations alongside ESG identification is essential for developing effective strategies for vegetation restoration and biodiversity conservation (Adel et al. 2014, Su et al. 2015).

In regions like Laos and the broader Indochinese Peninsula, afforestation efforts have historically focused on monoculture plantations, which often result in simplified stand structures, reduced productivity, and ecological instability (McElwee 2003). Recognizing the limitations of monoculture systems, there has been a shift toward establishing mixed-species forests (McElwee 2016). This transition requires careful selection of appropriate ESGs, a process that is both complex and resource-intensive (Yang et al. 2016). Identifying viable ESGs involves long-term monitoring, making it a time-consuming and costly endeavour (Li et al. 2008). However, recent studies have highlighted the resilience of certain species guilds - particularly stable species pairs - under natural selection, suggesting promising avenues for identifying sustainable ESGs that could enhance afforestation practices and promote integrated forest ecosystem management (Li et al. 2008, Su et al. 2015, Yang et al. 2016).

To effectively classify ESGs across diverse ecosystems, including forests, wetlands, and phytoplankton communities, a combination of traditional and advanced methodologies is essential (Meyer 2006). For example, Abella & Shelburne (2004) employed discriminant analysis and R-mode factor analysis to classify plant species into distinct ESGs, providing a robust framework for ecological classification. Similarly, Li et al. (2008) utilized statistical methods, such as chi-square tests, co-occurrence analysis, and clustering techniques, to study plant associations in the tropical rainforest of Hainan Island, China. Although these approaches have proven effective in various contexts (Su et al. 2015), ESG research in Laos remains underdeveloped due to logistical challenges and the nascent stage of regional forestry practices. The lack of standardized methodologies for studying interspecific interactions and ESG categorization in Southeast Asia further exacerbates these challenges. Therefore, region-specific research and the application of advanced analytical techniques are urgently needed to address these gaps and deepen our understanding of local ecosystems.

This study, conducted in Phou Khao Khouay (PKK) National Park in central Laos, aims to bridge these gaps by classifying ESGs using multivariate analytical techniques. Specifically, cluster analysis was employed for ESG classification, while ordination methods - such as Indicator Species Analysis (ISA) and Canonical Correspondence Analysis (CCA) - were used to explore species-environment relationships. The study also examined interspecific associations by focusing on dominant tree species across thirty-two permanent plots within the park. Statistical methods, including variance ratio, chi-square tests, association coefficients, and species co-occurrence percentages, were applied to analyse these interactions.

The study addresses five key research questions: (Q1) What are the dominant tree species in the seasonal tropical forest of PKK National Park? (Q2) Are the woody plant communities in the study area stable? (Q3) What interspecific associations exist among the dominant tree species? (Q4) Can the tree species in the study area be classified into distinct ESGs? (Q5) Are there significant variations in environmental factors, such as elevation and soil properties, across the identified ESGs?

The findings from this research provide valuable insights that can inform decision-making in afforestation and forest restoration efforts. Specifically, the study offers a scientific framework for selecting optimal mixed-species compositions in plantations, facilitating the transition from monoculture to diverse, mixed-species stands. Additionally, the results support enrichment planting in degraded secondary forests and contribute to the development of more effective tropical forest management strategies. By enhancing our understanding of community composition and interspecific interactions, this study provides crucial guidance for habitat conservation and promotes the sustainable management of plant species in the region. Furthermore, it serves as a valuable reference for future research on tropical forest dynamics.

## Materials and Methods

### Study area

Laos, a landlocked nation in the heart of the Indo-Chinese peninsula, is home to Phou Khao Khouay (PKK) National Park, a protected area since 1993 (Manichanh et al. 2015). Located approximately 40 km northeast of Vientiane, the park covers an area of about 2,000 km² and is situated in a predominantly mountainous region (Lucas et al. 2013). Its geographical coordinates range from 18°14’ to 18°32’ N and 102°38'' to 102°59’ E (Fig. 1). To the northwest, PKK National Park is bordered by the Ang Nam Ngum Reservoir, the largest artificial lake in southeast Asia, which marks the park's boundary in that direction.

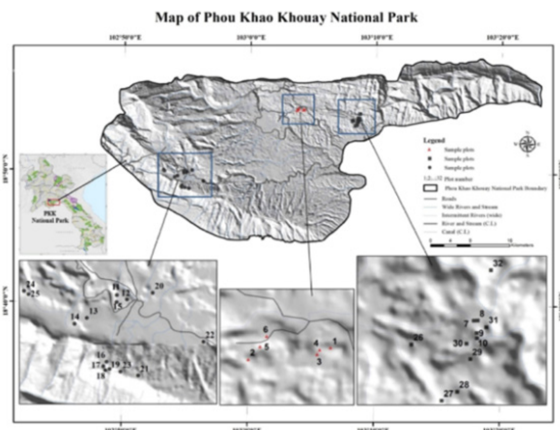


**Figure 1** Maps of study region and locations of the study plots.

PKK National Park is home to a variety of forest types, including mixed deciduous forests dominated by Fabaceae, dry evergreen Dipterocarp forests, and monodominant coniferous forests, primarily composed of Pinaceae, at higher elevations (Nguyen et al. 2023a). The park’s elevation ranges from 100 m to nearly 1,700 m a.s.l., supporting a variety of ecosystems at different altitudes.

The climate in PKK National Park is characterized by a distinct rainy season from May to October, with an average annual rainfall of approximately 1,769 mm (Chanthalaphone et al. 2020). Precipitation peaks in August, with an average of 494.2 mm. In contrast, the dry season, from November to March, experiences significantly lower rainfall, with February typically recording the lowest monthly average of about 2.5 mm. Temperature fluctuations are also notable: April, the hottest month, sees average temperatures reaching 39°C, while December, the coldest month, averages 10°C. Throughout the year, temperatures range from 16.6°C to 31.8°C during the rainy season and from 16.8°C to 24.6°C during the dry season (Phomphoumy et al. 2023).

The soils in PKK National Park are primarily tropical red to brown soils, including organic acrisols and lithosols, with textures ranging from sandy to sandy-loam and generally low organic matter content (Soukhavong et al. 2013). The combination of diverse ecosystems, varying climatic conditions, and distinct soil types makes PKK National Park an important area for biodiversity conservation and ecological research.

### Data collection

This study is based on permanent plots established in 2009 by the Institut de Recherche pour le Développement (IRD), France, in collaboration with the Faculty of Forestry Science at the National University of Laos. A total of thirty-two 50 × 50 m plots were geographically mapped, with each plot subdivided into 25 subplots of 10 × 10 m. The plots were randomly allocated after stratification by forest type to ensure representativeness across different ecosystems. Within each subplot, all woody tree individuals with a diameter at breast height (DBH) ≥ 5 cm were surveyed. The DBH of each tree was measured, and species were identified by taxonomists from the herbarium of the Faculty of Forestry Science.

In addition to the botanical data, key topographical variables - such as latitude, longitude, aspect, slope, and elevation - were recorded for each plot. These measurements were collected using a compass and a Garmin GPS 60s device.

Five soil pits were excavated to a depth of 20 cm at the four corners and the centre of each plot. Soil samples were then collected from two depth intervals (0–10 cm and 10–20 cm) using a soil drilling sampler with a 5 cm diameter. For each plot, soil samples from the same depth layer were combined in equal volume proportions, air-dried naturally, and stored at room temperature. In total, 64 soil samples were collected (32 plots × 2 depths). Before analysis, all samples were sieved through a 2-mm screen to remove soil fauna, plant roots, and other debris. The samples were then analysed at the soil laboratory of the National Agriculture and Forestry Research Institute (NAFRI) in Laos. A range of soil properties was assessed, including pH, organic matter content (OM), cation exchange capacity (CEC), total nitrogen (TN), total phosphorus (TP), total potassium (TK), and the particle size distribution of sand, clay, and silt.

## Data analysis

### *Importance value index*

The importance value index (IVI) functions as a comprehensive metric employed to assess the relative significance of species within a forest community, reflecting their dominance in a specific plot. The magnitude of a species' IVI is directly correlated with its dominance within the plot. The calculation of IVI followed the formula (Chai et al. 2016, Nguyen et al. 2023b):

$$IVI = (Rd + Ra + Rf) \times 100/ 3 \quad (1)$$

$$\text{Relative dominance (Rd)} = a_i / \sum^{S}_{i=1} a_i \quad (2)$$

$$\text{Relative abundance (Ra)} = n_i / \sum^{S}_{i=1} n_i \quad (3)$$

$$\text{Relative frequency (Rf)} = f_i / \sum^{S}_{i=1} f_i \quad (4)$$

where, S represents the total number of species, $a_i$ corresponds to the basal area of the ith species, $n_i$ signifies the number of individuals of the ith species, and $f_i$ denotes the number of subplots in which the $i^{th}$ species occurred.

Tree species exerting significant ecological influence were identified as those with an IVI ≥2% within the study plot (Nguyen et al. 2023c). The collective IVI of tree species surpassing 50% was designated as the dominant species group within the forest communities (Nguyen et al. 2021).

### *Interspecific association quantification*

This study focused on the interspecific associations among dominant woody species in thirty-two study plots. The dominant species were sorted by IVI, and various indices were calculated, including chi-square tests, association coefficients, and the percentage co-occurrence (Jin et al. 2022). The approach involved transforming the original data matrix of S×N (where S represents tree species and N denotes the number of plots) into a binary data matrix in 0-1 format. Subsequently, 2×2 contingency tables were constructed for each species pair, and the values of a, b, c, and d were calculated. Specifically, a represented the number of sample plots containing both species A and B, b signified the number of sample plots with only species B, c denoted the number of plots with only species A, and d accounted for the plots where neither species A nor B was present. The parameter n represented the total number of plots.

In this study, we utilized the variance ratio (VR), introduced by Schluter (1984), to assess the overall association among different species based on their presence or absence in the plots (Chai et al. 2016). The VR equals 1 when assuming independence, with a VR greater than 1 indicating a positive association among species. Conversely, a VR less than 1 suggests a negative association for the species involved.

The interspecific association between species pairs was assessed using the chi-squared test. Given the non-continuous nature of the samples, the chi-squared value for the study data was determined using Yates' continuity correction formula as follows (Shao & Zhang 2021):

$$\chi^2 = \frac{n\,(|ad - bc| - 0.5n)^2}{(a+b)\,(a+c)\,(b+d)\,(c+d)} \qquad (5)$$

A positive association is observed when the product of ad exceeds that of bc, whereas a negative association is evident when the product of ad is less than that of bc. If the calculated chi-squared value surpasses 3.841, it implies a significant association between the species ($0.01 < p < 0.05$). Similarly, a chi-squared value exceeding 6.635 indicates an extremely significant association between pairs of species ($p < 0.01$).

The $\chi^2$ statistic provides only a qualitative assessment of whether the association between species is significant, but it does not offer insight into the strength of these interspecific associations (Liu et al. 2019b). To quantify the strength of the association, the association coefficient (AC) and percentage co-occurrence (PC) are commonly employed. Among these, PC is generally considered more reliable than AC in reflecting the strength of positive associations, as it mitigates the influence of high AC values resulting from large d values or low AC values due to small values. Consequently, a combined analysis of both PC and AC is often conducted to enhance the accuracy and robustness of the results (Liu et al. 2019a).

Association coefficient: the AC is employed to further scrutinize the results obtained through $\chi^2$ and to clarify the strength of interspecies association. Its formula is as follows (Liu et al. 2019a):

$$\text{when } ad \geq bc,\ AC = \frac{(ad - bc)}{(a+b)(b+d)} \qquad (6)$$

$$\text{when } ad < bc \text{ and } d \geq a,\ AC = \frac{(ad - bc)}{(a+b)(a+c)} \qquad (7)$$

$$\text{when } ad < bc \text{ and } d < a,\ AC = \frac{(ad - bc)}{(a+b)(a+c)} \qquad (8)$$

The range of AC values is [-1, 1]. As the AC value approaches 1, it indicates a more robust positive association among species pairs; as the AC value approaches -1, it signifies a more pronounced negative association between species; when the AC value is 0, it denotes complete independence among species.

Percentage of co-occurrence: The PC is used to evaluate the degree of positive association between species. Its formula is as follows (Bosun & Shaolin 1985):

$$PC = \frac{a}{(a+b+c)} \qquad (9)$$

The range of PC values is [0, 1], with values approaching 1 indicating a stronger positive association between the species.

Data processing was carried out using Excel 2016 software to generate a half-matrix plot based on the calculated $\chi^2$ test values for the associations between various woody species. The AC and PC values obtained were then analysed using R 4.1.3 software and the vegan package to generate half-matrix plots (Nguyen et al. 2023c).

### *Clustering analysis and determination of indicator species*

This study utilized the Two-Way Indicator Species Analysis (TWINSPAN) method to classify forest plant communities in PKK National Park, based on species presence/absence data from study plots. TWINSPAN was chosen for its effectiveness in grouping communities with similar species abundance patterns (Adel et al. 2014). The cut-off level for defining 'pseudo-species' followed the default setting of the software. Subsequently, Indicator Species Analysis (ISA) was applied to identify species that were significantly associated with each group. Both TWINSPAN and ISA analyses were conducted using the PC-ORD 5.10 software (McCune & Mefford 2006).

To evaluate the completeness of the sampling and visualize variations in species richness across ESGs, we calculated and plotted sampling coverage using the iNEXT package (Hsieh et al. 2016). For each ESG, sampling coverage was estimated by performing 50 bootstrap replicates, with a 95% confidence interval. This method allows for an assessment of how well the sample reflects the total species richness of ESGs, providing valuable insights into the reliability and stability of the sampling effort (Dar & Parthasarathy 2023).

CANOCO 5 software was used for multivariate analysis to examine the relationship between environmental factors (topographic and soil variables) and the plant community in PKK National Park (Šmilauer & Lepš 2014). Canonical correspondence analysis (CCA), with detrending by segments, was initially performed to assess the gradient length of the first axis and to determine whether linear or unimodal-based numerical methods should be applied (Liu et al. 2012). The significance of the eigenvalues for the first canonical axis was tested using a Monte Carlo permutation test with 499 random permutations. Inter-set correlations from the ordination analysis were used to evaluate the importance of the environmental variables. The environmental variables considered in the CCA analysis included elevation, slope, slope aspect, soil pH, TN, TP, TK, OM, soil texture (clay, sand, silt), and CEC. Aspect data were transformed using the equation B' = cos (45 − B') + 1 (Beers et al. 1966). The normality of all parameters was assessed using Kolmogorov–Smirnov tests. Differences in the means of environmental variables among groups were analysed using one-way ANOVA, followed by the Duncan test at the 95% level. All statistical analyses were performed using R 4.1.3 software with the 'vegan' and 'agricolae' packages. Scientific names of species were recalibrated according to Plants of the World Online (https://powo.science.kew.org) and World Flora Online (https://www.worldfloraonline.org).

## Results

### Composition of trees species

A total of 5,477 individual trees were recorded across thirty-two permanent plots, representing 194 woody species from sixty-seven plant families (Supplementary materials are available at: https://github.com/quyforest/data-PKK). Among these species, ten were identified as dominant, each with an IVI exceeding 2% (Table 1). These ten species collectively comprised 33.2% of the total individuals in the entire species pool. Notably, *H. pierrei* emerged as the most dominant species, with an IVI of 6.53%, while *L. fenestratus* exhibited the lowest IVI among the dominant species, at 2.38%. Despite their prominence in terms of IVI, the individual density of these dominant species remained relatively low, with none exceeding 50 individuals per hectare.

**Table 1** Trees species composition, acronyms, and importance values[1].

| No. | Species | Acronym | N | D | IVI |
|---|---|---|---|---|---|
| 1 | *Hopea pierrei* Hance | HOPI | 278 | 35 | 6.53 |
| 2 | *Schima wallichii* (DC.) Korth. | SCWA | 266 | 33 | 3.51 |
| 3 | *Pinus merkusii* Jungh. & de Vriese | PIME | 123 | 15 | 3.09 |
| 4 | *Alphonsea gaudichaudiana* (Baill.) Finet & Gagnep. | ALGA | 227 | 28 | 2.97 |
| 5 | *Hydnocarpus ilicifolia* King | HYIL | 224 | 28 | 2.87 |
| 6 | *Syzygium cinereum* (Kurz) Chantar. & J.Parn. | SYCI | 187 | 23 | 2.75 |
| 7 | *Gironniera nervosa* Planch. | GINE | 162 | 20 | 2.56 |
| 8 | *Xanthophyllum lanceatum* J.J.Sm. | XALA | 74 | 9 | 2.46 |
| 9 | *Syzygium syzygioides* (Miq.) Merr. & L.M.Perry | SYSY | 124 | 16 | 2.45 |
| 10 | *Lithocarpus fenestratus* Rehder | LIFE | 154 | 19 | 2.38 |
| 11 | Ten dominant species | ---- | 1,819 | 227 | 31.57 |
| 12 | Others (184 species) | ---- | 3,658 | 457 | 68.43 |
| 13 | All (194 species) | ---- | 5,477 | 685 | 100 |

[1]N represents the number of individuals, D signifies individual density per hectare (individuals ha-1), and IVI stands for Importance Value Index, expressed as a percentage (%).

### Interspecific associations among species

#### *Overall interspecific association*

The calculated VR value of 4.68 for the 194 woody species observed across thirty-two study plots significantly exceeded the threshold of 1.0 established by Schluter (1984), indicating a strong positive co-variation among species within the study area. Additionally, with a W value of 149.8, surpassing the $\chi^2(0.05, 32)$ value, there was a marked deviation from the expected VR of 1.0. This further reinforced the substantial positive association among the 194 species. Together, these results provided robust evidence of stable species interactions within the study area, suggesting a symbiotic relationship among tree populations, characterized by mutualistic benefits.

### *Interspecific associations between dominant species*

The $\chi^2$ test was conducted to assess the significance of associations between dominant species pairs, utilizing a 2×2 contingency table. The analysis included forty-five pairs formed by ten dominant tree species. Of these, twenty-one pairs showed positive associations, while another twenty-one pairs showed negative associations. Three pairs showed no significant association (Fig. 2).

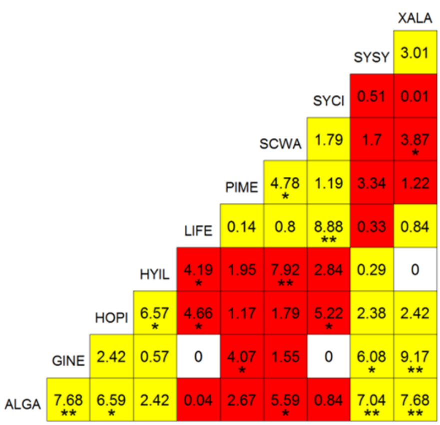


**Figure 2** Half matrix diagrams of $\chi^2$ tests for the association of dominant tree species.

Notably, nine pairs showed significant positive associations, including *P. merkusii* and *S. wallichii*, *L. fenestratus* and *S. cinereum*, *H. pierrei* and *H. ilicifolia*, *G. nervosa* and *S. syzygioides*, *G. nervosa* and *X. lanceatum*, *A. gaudichaudiana* and *G. nervosa*, *A. gaudichaudiana* and *H. pierrei*, *A. gaudichaudiana* and *S. syzygioides*, and *A. gaudichaudiana* and *X. lanceatum*. In contrast, seven pairs showed significant negative associations, including *S. wallichii* and *X. lanceatum*, *H. ilicifolia* and *L. fenestratus*, *H. ilicifolia* and *S. wallichii*, *H. pierrei* and *L. fenestratus*, *H. pierrei* and *S. cinereum*, *G. nervosa* and *P. merkusii*, and *A. gaudichaudiana* and *S. wallichii*. These findings highlighted the complex interactions between the dominant tree species in the study area.

The associations between species are depicted using colors: positive associations (VR > 0) are shown in yellow, negative associations (VR < 0) are depicted in red, and no associations (VR = 0) are shown in grey. Species acronyms match those found in Table 1. Significance levels are denoted as follows: * indicates $p < 0.05$, and ** indicates $p < 0.01$.

### *Measures of dominant species pair associations*

The results from both AC and PC analyses for the dominant species provided a clearer delineation of the strength of association between species pairs (Fig. 3). Regarding the AC values (Fig. 3a), the analysis identified twenty-two pairs with positive associations (AC > 0), twenty-one pairs with negative associations (AC < 0), and only two pairs showed no association (AC = 0). In contrast, the PC values for forty-five species pairs, involving ten dominant species (Fig. 3b), revealed that twenty-two pairs had positive associations (PC > 0), four pairs showed no association (PC = 0), and nineteen pairs demonstrated negative associations (PC < 0).

Importantly, the AC and PC analyses together highlighted that the nine positively associated pairs and the seven negatively associated pairs identified through the chi-square test all exhibited absolute AC values greater than 0.5 and absolute PC values greater than 0.002. Thus, the sixteen species pairs demonstrating significant associations in the chi-square test also satisfied the criteria set by the AC and PC tests, reinforcing the robustness of these associations.

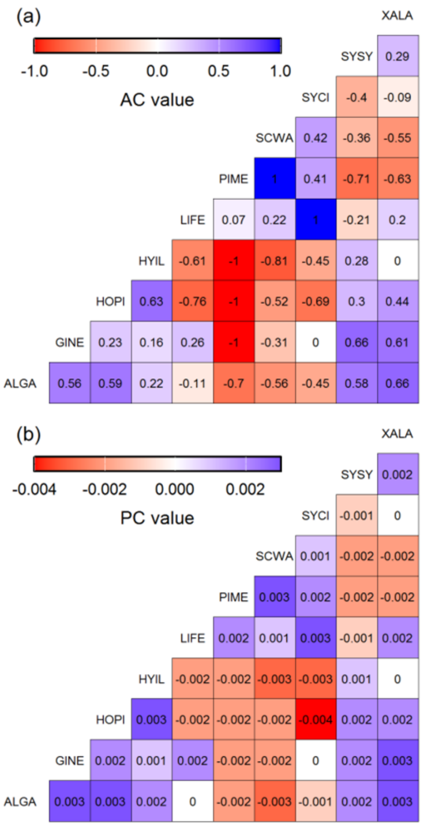


**Figure 3** AC and PC results of dominant species in the study area.

Positive associations are indicated in blue, while negative associations are shown in red. Species acronyms correspond to those in Table 1.

## *Division of ecological species groups*

The TWINSPAN analysis identified four distinct ESGs based on indicator species (Fig. 4). The first group, which included seven plots (01, 02, 09, 10, 29, 31, 32), was characterized by the presence of three indicator species: *A. gaudichaudiana*, *A. polystachya*, and *C. iners*. The second group, consisting of eight plots (05, 06, 11, 12, 15, 16, 20, 22), was defined by the presence of three species: *L. fenestratus*, *S. cinereum*, and *S. wallichii*. The third group,

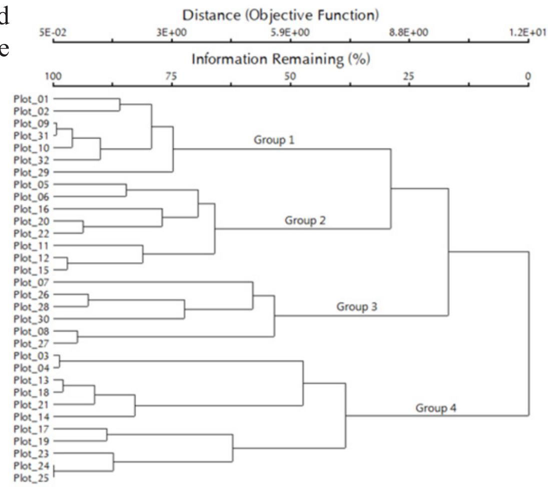


**Figure 4** Diagram of TWINSPAN analyses on thirty-two plots in the study area.

which included six plots (07, 08, 26, 27, 28, 30), was associated with three indicator species: *H. ilicifolia*, *S. siamensis*, and *C. glabrum*. Finally, the fourth group, comprising 11 plots (03, 04, 13, 14, 17, 18, 19, 21, 23, 24, 25), was characterized by three indicator species: G. *nervosa*, *A. gomezianus*, and *B. macrostachya*.

The sample coverage across the four ESGs was nearly identical: Group 1 = 98.25%, Group 2 = 97.88%, Group 3 = 98.88%, and Group 4 = 99.34%, demonstrating that the samples were almost equally complete (Fig. 5). Extrapolation

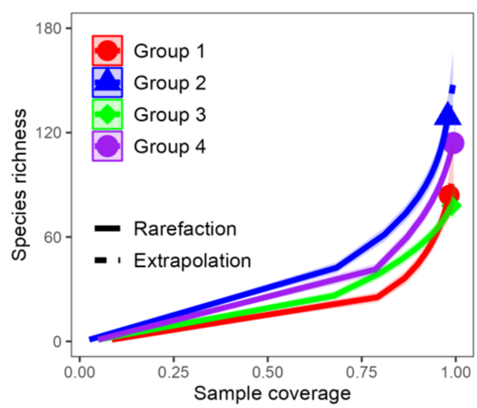


**Figure 5** Coverage-based rarefaction and extrapolation curves with 95% confidence intervals, comparing plant species richness across four ecological groups in the seasonal tropical forest of PKK National Park. The solid lines represent the reference samples, while the extrapolation phase is indicated by the dashed lines.

across the communities resulted in negligible increases in sample coverage—specifically, 0.00197%, 0.00196%, 0.00198%, and 0.00199% for Groups 1, 2, 3, and 4, respectively. These findings from coverage estimation indicated that the samples for each ESG had been almost complete, and further sampling would not significantly alter these results.

The results obtained from the CCA showed the impact of soil and topography variables on the ESGs. Particularly, the first and second axes, possessing eigenvalues of 0.529 and 0.397 respectively, collectively explained 92.6% of the total variance (Fig. 6). This finding indicated that TK, OM, and pH were pivotal determinants within the first group, while TP and clay played significant roles in the second group. Additionally, aspect and slope emerged as influential factors in the third group, whereas elevation, sand, TN, CEC, and silt contributed to distinguishing the fourth group.

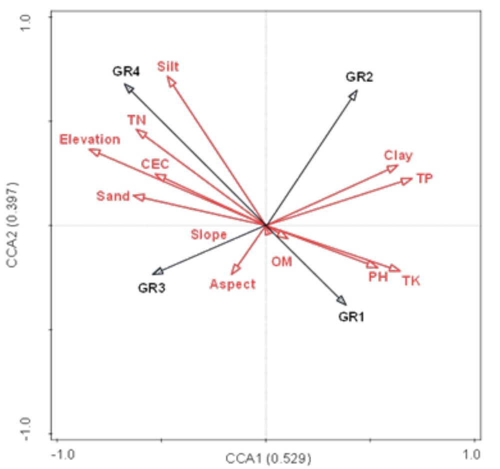


**Figure 6** The diagram illustrates the results of a CCA examining the correlation between species groups and environmental factors in the studied area. Abbreviations are employed for ecological species groups, with GR denoting a specific group.

The ANOVA analysis revealed significant differences in the associations of ESGs with soil and topographic variables (Fig. 7). Specifically, Group 1 was characterized by significantly higher levels of soil pH, OM, TK, and sand content (Fig. 7d, e, i, j). These findings

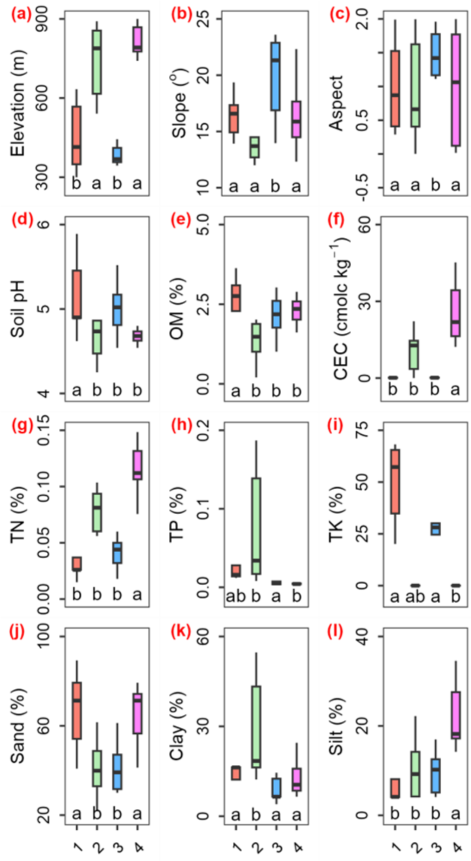


**Figure 7** Differences in environmental variables across ecological species groups.

suggest that the species in Group 1 are adapted to, or preferentially inhabit, environments with more alkaline soils, higher nutrient availability, and coarser-textured soils, which are typically associated with better drainage.

In contrast, Group 2 exhibited significantly higher clay content and TP, indicating a preference for soils with finer textures and higher phosphorus concentrations (Fig. 7h, k). This suggests that species in Group 2 favor habitats with higher moisture retention and enhanced nutrient availability - conditions typically found in soils with lower drainage capacities. Group 3, on the other hand, showed the highest values for slope and aspect, indicating a preference for more variable or sloped terrains (Fig. 7b, c). This pattern reflects an adaptation to specific topographical features, such as water drainage patterns, sunlight exposure, and temperature variations, all of which likely influence the suitability of habitats for the species in this group.

Finally, Group 4 was associated with elevated levels of silt, sand, CEC, TN, and elevation (Fig. 7a, f, g, l, j). These results suggest that species in Group 4 are linked to soils with a balanced texture (silt and sand), higher nutrient retention capacity (as indicated by CEC and TN), and are typically found at higher elevations, where environmental conditions such as temperature and humidity differ from those at lower altitudes.

## Discussion

### Overall interspecific association of tree species

The process of community succession involves dynamic changes in species interactions, which are crucial for understanding the mechanisms that maintain community stability and biodiversity (Chai et al. 2016, Detto et al. 2022). Shuai & Wang (2023) emphasize that environmental filtering and interspecific competition play central roles in shaping species' functional traits and ecological strategies during succession. In the early stages of succession, these processes often result in competitive exclusion or niche differentiation (Buche et al. 2022). However, as succession progresses, species traits tend to complement one another, leading to more mutualistic or neutral interactions (Cassini 2020, Falk et al. 2022, Löffler & Pape 2020). Our findings regarding the overall association among 194 woody species in the seasonal tropical forest of PKK National Park, Laos, align with this model, as evidenced by the overall positive association observed among species. This suggests that the woody plant communities in the study area are entering a more stable phase, characterized by cooperative or mutually beneficial interspecific relationships.

The shift in species interactions indicates that the community is approaching equilibrium, where species are better adapted to coexist (Chen et al. 2018). This transition reduces the likelihood of competitive exclusion and enhances the community's resilience (Li et al. 2020). The positive association observed among the 194 woody species in the study area points to a trend toward more stable, potentially symbiotic relationships as succession progresses. These interactions suggest that the woody plant communities in PKK National Park are nearing, or have already reached, the final stage of ecological succession, where the competitive dynamics of earlier stages are replaced by cooperative associations.

It is important to note that this equilibrium does not imply the complete absence of competition (Aarssen 1983). Rather, it signifies a balance between competitive interactions and cooperative relationships, allowing species to coexist without compromising the community's overall functionality (Shmida & Ellner 1984). Our results offer a deeper understanding of community dynamics by illustrating how interspecific relationships evolve from competitive dominance to cooperative stability as succession unfolds in the woody plant communities of PKK National Park. These findings support the idea that as communities mature, their internal interactions become more integrated, leading to a more stable and resilient ecological system (Jin et al. 2022).

Different letters below the boxplot (Fig. 7) indicate significant differences between various species groups in the study area ($p < 0.05$).

### Interspecific associations between dominant species

Interspecific associations provide valuable insights into the interactions between species across diverse habitats, offering a deeper understanding of their capacity to adapt to varying environmental conditions (Liu et al.

2014, Liu et al. 2019b). This study focused on analysing interspecific associations based on species pairs, revealing that dominant species exhibited both positive and negative associations in roughly equal proportions. However, a clear disparity emerged in the frequency of significant positive versus negative associations. Specifically, the number of species pairs with significant positive associations exceeded those with significant negative associations, suggesting a general trend of positive interspecific relationships among the 194 species in the study area.

Positive associations between species pairs typically indicate similar or shared environmental resource requirements, often pointing to potential mutualistic or symbiotic relationships (Nguyen et al. 2022). In contrast, negative associations generally reflect species' ability to adapt to environmental heterogeneity, where variations in biological traits can lead to competitive exclusion and niche differentiation (Phuong et al. 2022). The size of the sampling plot is a critical factor influencing the nature of interspecific associations (Nguyen et al. 2023c). Larger habitats tend to show predominantly positive associations, while smaller habitats are more likely to exhibit negative associations (Shuai & Wang 2023). Empirical studies in tropical forests suggest that optimal plot sizes range from 400 m² to 900 m² (Chen et al. 2018). In this study, the use of a larger plot size of 2500 m² enhanced the reliability of the findings by providing a broader, more representative analysis.

Although the plot size and number of plots in our study were comparable to those of Pham et al. (2021) and Huong & Cuong (2022), our results exhibited notable differences. Specifically, the proportion of species pairs showing no significant interspecific associations was considerably lower in our study. One key difference between our study and those of Pham et al. (2021) and Huong & Cuong (2022) lies in the statistical methods used. While their studies employed an unadjusted chi-square test, our analysis applied Yates’s corrected chi-square test. Yates's correction for continuity enhances the accuracy of the chi-square test, particularly in cases with small sample sizes in 2×2 contingency tables (Adler 1951). The unadjusted chi-square test is typically less conservative and can increase the likelihood of rejecting the null hypothesis (Haber 1982). In contrast, Yates’s correction is more conservative, reducing the risk of Type I errors and thus increasing the reliability of hypothesis testing (Li et al. 2020). This methodological refinement strengthened the robustness of our findings and aligns with contemporary statistical advancements (Nguyen et al. 2023c).

To further verify the robustness of our results, we employed both the AC and PC tests, which yielded findings consistent with the initial chi-square analysis of interspecific associations. The outcomes from these additional tests confirmed the reliability of our preliminary results. Specifically, the nine species pairs showing positive associations and the seven exhibiting negative associations, as identified through the chi-square test, all exhibited AC values greater than 0.5 and PC values exceeding 0.002. Consequently, the 16 species pairs with significant associations in the chi-square analysis also met the criteria established by the AC and PC tests, further reinforcing the strength and reliability of these associations.

## Division of ecological species groups

In our study, TWINSPAN analysis was applied to classify community types within PKK National Park. It was previously demonstrated by Dar & Parthasarathy (2023) that TWINSPAN provides a more accurate representation of study plot distribution and species composition compared to other clustering methods, such as hierarchical clustering, k-means, or model-based clustering. A key strength of TWINSPAN lies in its ability to identify indicator species that are strongly associated with specific environmental conditions or habitat types, making it a valuable tool in ecological studies focused on species-environment interactions (Hill 1979). Unlike other methods, TWINSPAN incorporates these indicator species into the clustering process, thereby enhancing the ecological relevance of the resulting groups (Clare 2000, Hugh G. Gauch & Whittaker 1981). Additionally, its binary division approach facilitates clear, dichotomous classification, producing well-defined, easily interpretable groups that effectively capture ecological gradients or differentiate distinct community types (Cui et al. 2009, Marshall & Elliott 1997). This feature is particularly beneficial in ecological data analysis, where identifying discrete community units is crucial for effective ecological management and conservation (Song & Zhang 2018). The incorporation of conservation strategies that utilize spatial patterns of species richness and diversity - such as prioritizing conservation areas based on key floristic groups - can improve forest policy and management effectiveness (Khan et al. 2011).

The application of TWINSPAN in this study enabled the identification and characterization of vegetation groups, facilitating an interpretation of their diversity and species distribution patterns (Siebert 2012). However, challenges arose due to the discontinuous distribution of communities, as effective classification depends on relatively stable species composition, structure, and habitat occupation (Li et al. 2020, van der Maarel & Sykes 1993). Differences in microhabitats, stages of community development, and species interactions within similar habitats were significant in distinguishing community types in tropical forests (Rees et al. 2001). The classification of species groups and communities in our study primarily relied on assessments of species abundance, presence/absence, and environmental factors, revealing significant correlations between species composition and various topographical and soil characteristics, as demonstrated by CCA analysis. These findings underscore the considerable influence of environmental factors on species distribution within the study area.

Four distinct ESGs were identified within the woody plant communities in PKK National Park. Vilches et al. (2013) emphasized that ESGs, when analysed in conjunction with physiographic, microclimatic, and soil variables, are effective tools for delineating ecosystems across multiple landscape scales. Our analysis confirmed that the distribution of these ecological groups was closely linked to the topographical and soil properties of the sampled plots. Through the use of CCA and ANOVA, clear relationships were found between ESG distribution and environmental factors. Specifically, aspect and slope were significant determinants of the third ESG, while elevation had a substantial influence on the fourth ESG. Soil variables such as pH, OM, TK, and sand content were key factors shaping the first ESG, whereas clay content and TP were central to the second ESG. The composition of the third ESG was most strongly influenced by silt content, sand, TN, and CEC.

Our findings align with previous research. For instance, Olivero & Hix (1998) emphasized the role of aspect in shaping ground flora distribution. The geographical distribution of plant species is influenced by factors such as water availability, light, and soil temperature (Buri et al. 2017, Huang et al. 2021). Topography indirectly affects these resources by modifying solar radiation, which in turn impacts temperature, soil moisture, humidity, vapor pressure deficits, and transpiration - all crucial for plant survival, growth, and distribution (Small & McCarthy 2005). Similarly, Dar & Parthasarathy (2023) suggested that altitude, along with slope and aspect, affects solar azimuth, hydrology, climate, and soil properties, influencing vegetation patterns through the creation of microenvironments.

Our study further emphasized the significant role of soil variables in environmental differentiation, ranking second only to topography. Through comprehensive analyses, including CCA and ANOVA, we observed that soil nutrient content plays a critical role in ESG distribution. This finding aligns with prior research demonstrating the impact of soil nutrients on plant community composition in tropical forests. For example, Mataji et al. (2009) examined soil characteristics within the Rusco-Fagetum ecological group in Iran, finding that clay soils influence plant community formation. Soil nutrients are essential for plant nutrition, as their concentration and availability largely determine soil fertility and site productivity (El-Ramady et al. 2014). Furthermore, Amorin & Batalha (2007) identified phosphorus as a key driver of plant community dynamics in Brazil, further underscoring the importance of soil nutrients in shaping ecological groupings.

## Conclusions

This study provides valuable insights into the stability and interspecific associations of plant communities in the natural forests of PKK National Park, Lao PDR. By analysing data from thirty-two permanent plots and documenting 5,477 individual trees across 194 species, we identified the key characteristics of tropical forests in the region.

The study revealed that plant communities are in a stable phase, with positive associations among most species and specific ecological groupings identified through indicator species analysis. Notably, environmental factors such as topography and soil properties were found to significantly influence plant distribution and the formation of ESGs.

Furthermore, the identification of dominant species and their interrelationships, particularly through the analysis of 45 species pairs, highlights the complex dynamics within the forest ecosystem. These findings not only enhance our understanding of plant community structure but also provide a basis for future monitoring efforts, which could serve as an early warning system for biodiversity conservation.

The results underscore the importance of continuous observation and the potential for using ecological indicators to inform conservation strategies.

## Conflict of interest

The authors declare that they have no conflict of interest.

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