



# Classification and Ordination of the *Pinus taiwanensis* forest on Daiyun Mountain, Fujian Province, China

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(Manuscript received 26 March 2019; Accepted 22 December 2019; Online published 19 February 2020)

**ABSTRACT:** Daiyun Mountain plays a fundamental role in maintaining stability of subtropical evergreen broad-leaved forest in China. To explore the distribution of vegetation on Daiyun Mountain, two-way indicator species analysis (TWINSPAN) method was used to classify the *Pinus taiwanensis* forest. The effects of 10 environmental factors on the distribution of *P. taiwanensis* forest were studied using canonical correspondence analysis (CCA). The results showed that (1) the *P. taiwanensis* forest could be divided into seven associations, *P. taiwanensis* Hayata + *Schima superba* Gardn. & Champ - *Oligostachyum oedogonatum* (Z.P. Wang & G.H. Ye) Q.F. Zhang & K.F. Huang + *Photinia parvifolia* (Pritz.) Schneid., *P. massoniana* Lamb. + *Acer davidii* Franch. - *Sarcandra glabra* (Thunb.) Nakai + *Styrax odoratissimus* Champ., *P. taiwanensis* + *S. superba* - *Clethra delavayi* Franch. + *Eurya groffii* Merr., *P. taiwanensis* + *Cunninghamia lanceolata* (Lamb.) Hook - *E. groffii* + *Vaccinium carlesii* Dunn., *P. taiwanensis* + *Machilus thunbergii* Sieb. & Zucc - *Camellia sinensis* (L.) O. Kuntze + *Rhododendron mariesii* Hemsl. & Wils., *P. taiwanensis* + *S. superba* - *Syzygium buxifolium* Hook. & Arn. + *Itea oblonga* Hand. - Mazz and *P. taiwanensis* + *Ilex crenata* Thunb. - *E. saxicola* H. T. Chang + *R. eudoxum* Balf. f. & Forrest, respectively; (2) associations I–III, V, and VII were distributed along elevation and nutrient gradients, whereas associations IV and VI were distributed on the southern slope with low soil acidity; (3) the CCA results showed that elevation and soil organic carbon played a greater role in the distribution of the seven associations; and (4) the soil and terrain factors accounted for 33.28% of the spatial distribution of the seven associations on Daiyun Mountain, and other unexplained factors accounted for 66.72%. We recommend creating different community protection areas based on elevation, and communities can be managed according to elevation.

**KEY WORDS:** Association, China, Daiyun Mountain, ordination, *P. taiwanensis*, vegetation classification.

## INTRODUCTION

The Daiyun Mountain National Nature Reserve is in the transitional zone between the southern subtropical and the mid-subtropical zones, and it preserves the typical mountain forest ecosystem of the Chinese southeast coast. Regarded as a significant biodiversity center in midland Fujian province (Chen *et al.*, 2016, Xu *et al.*, 2017). The *Pinus taiwanensis* Hayata forest is a representative component of subtropical forests in Eastern China. Covering an area of 64 km<sup>2</sup>, the *P. taiwanensis* on Daiyun Mountain is the largest and the most well-preserved in southern mainland China (Liu *et al.*, 2013). Daiyun Mountain, with a vital subtropical evergreen broad-leaved forest in China, plays a fundamental role in maintaining forest stability. The classification of *P. taiwanensis* forest on Daiyun Mountain and research on the relationships between communities and environment contributes to understanding local vegetation and preference for suitable environments, crucial for protecting local vegetation and improving management efficiency according to the adaptation to local conditions. The

quantitative classification method can be applied to objectively and accurately classify plant community on Daiyun Mountain in combination with species distribution (Vittoz *et al.*, 2010, Wehn and Johansen, 2015). Vegetation classification is closely associated with the relationship between plants and the local environment (Sanctis *et al.*, 2012, Skalski *et al.*, 2018), providing an avenue for exploring the distribution patterns of vegetation on Daiyun Mountain along environmental gradients.

Due to regionalism and diversity of vegetation, the boundaries between different types of vegetation are blurred. No consensus has been reached on the continuity and discontinuity of plant communities, and the method of vegetation classification based on continuity has not yet been unified. Weaver and Clements (1938) proposed the concept that plant communities should be regarded as a whole, whereas Braun-Blanquet (1964) supported community discontinuity. Eventually, two different classification systems were formed as the result of early arguments about community. However, the view that plant association acts as the basis of vegetation classification



is supported by both classification methods (Whittaker, 1978). An increasing number of people are holding that both continuity and discontinuity should be considered when classifying vegetation. The classification of vegetation has evolved into the current quantitative classification method (Wu, 1980; Chahouki, 2013). Vegetation quantitative classification is based on similarity coefficient, merging entities or attributes into various groups. Common classification methods include the hierarchical clustering method, the hierarchical differentiation method, fuzzy mathematics method and other methods. Two-way indicator species analysis (TWINSPAN) considers the relationship between plants and plots, and the classification results are more objective and accurate. It is one of the primary methods currently used to study vegetation classification (Legendre and Legendre, 1983; Sanctis *et al.*, 2012).

Vegetation determined by classification methods are a product of the interaction between plants and the environment (Khan *et al.*, 2019). Vegetation is an aggregation of species living under certain ecological conditions. The spatial distribution of vegetation is affected by environmental factors such as climate, topography and soil on large scales, and then certain species interact with each other to adapt to local habitat on a small scale (Wehn and Johansen 2015; An *et al.*, 2018). Canonical correspondence analysis (CCA) and redundancy analysis (RDA) can be used to objectively and accurately reveal the relationship between associations and environment (Castillon *et al.*, 2015; Li *et al.*, 2018). These ordination methods are widely used for determining the spatial distribution of vegetation.

Some studies have been conducted on the classification and ordination of *P. taiwanensis* forest in Daiyun Mountain. In terms of *P. taiwanensis* forest classification, Ren *et al.* (2011) analyzed the relationship between plant associations and diversity instead of considering the distribution pattern of species among plots. For community ordination, Liu *et al.* (2013) reported the plant community distribution amongst major tree species along the environmental gradients using the detrended canonical correspond analysis (DCCA) method. However, these studies cannot explore the spatial distribution of associations and the impact of the environment on their distribution. Therefore, we aimed to classify the *P. taiwanensis* forest and determine the effects of environmental factors on its vegetation distribution. We designed three questions that we wanted to answer through our research: (1) What kind of associations can be distinguished on Daiyun Mountain? (2) How are the associations in Daiyun Mountain distributed along the environmental gradients? (3) Which environmental factor is the most important factor affecting the distribution of associations? The results could provide a scientific basis for the rational restoration and management of mountain vegetation resources.

## MATERIALS AND METHODS

### Study Area

Daiyun Mountain National Nature Reserve (25°38'07"–25°43'40" N, 118°05'22"–118°20'15" E) is in Dehua County, Fujian province, China (Figure 1). The highest elevation is 1856 m, with a total area of 134.72 km<sup>2</sup>. A subtropical marine monsoon climate dominates this area with an annual precipitation of 1700–2000 mm. The annual average temperature falls in the range of 15.6 to 19.5 °C, and the extreme minimum and maximum temperature are –16.8 and 36.6 °C, respectively. The main soil types of Daiyun Mountain are red soil, yellow soil, lateritic red soil, mountain yellow-red soil, and peat mire soil. Daiyun Mountain is rich in plant resources and the forest coverage rate is 93.4%. Forest vegetation on Daiyun Mountain has notable vertical distribution characteristics. With increasing elevation, the vegetation distribution changes from bamboo forest, to evergreen broad-leaved forest, coniferous and broad-leaved mixed forest, to warm coniferous forest, dwarf forest, swamp, and finally to alpine, forming a natural vertical structure (Liu *et al.*, 2017, Xu *et al.*, 2017).

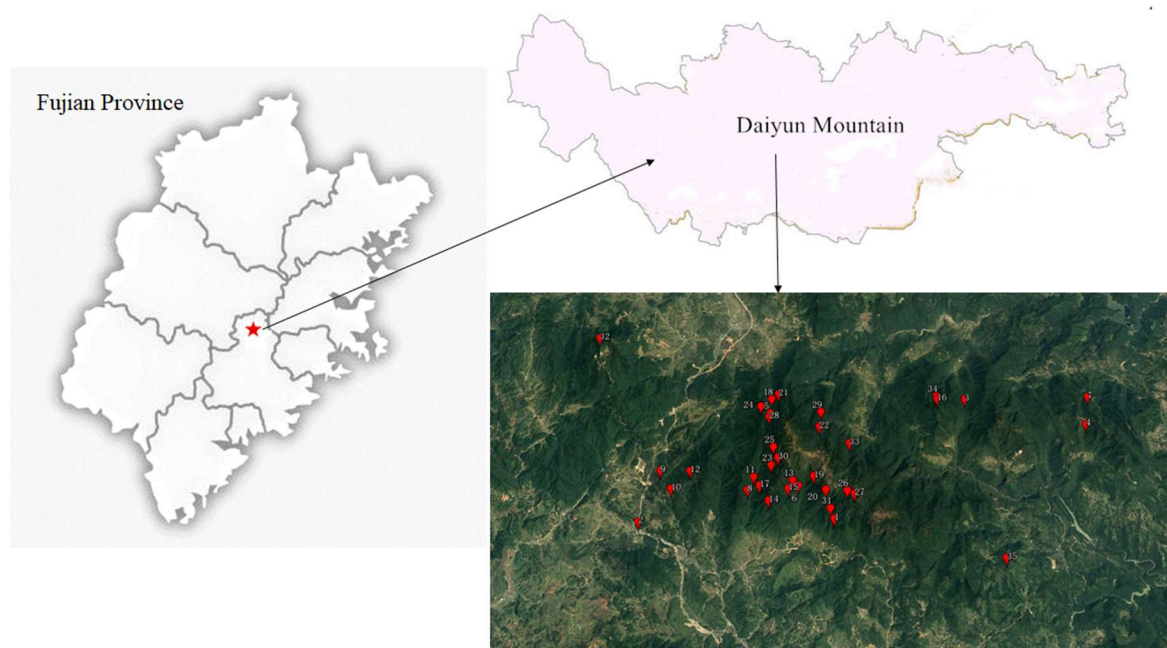
### Sampling Method

Based on comprehensive reconnaissance of the *P. taiwanensis* forest on Daiyun Mountain conducted in 2015 (Liu *et al.*, 2013), 35 sample plots with an area of 25 × 25 m were set in the undisturbed typical forest (Appendix S1 and S2). The diameter and height were measured for all vascular plants with a diameter at breast height (DBH) ≥ 1 cm at the tree layer in all plots, and the species name was recorded. Four types of topographical factors were selected: elevation (ELE), aspect (ASP), slope (SLOP), and slope position (SPO). The elevation was measured using a hand-held global positioning system (Jisibao G639, Jisibao Corporation, Beijing, China). A theodolite (DQL-16ZJ, Haerbin Optical Instrument Factory, Haerbin, China) was used to measure the slope. The aspect and slope position were measured using geological compass (DQL-8, Haerbin Corporation, Haerbin, China). The soil sampling points were set at the midpoints and diagonal position (northeast and southwest) of each plot. A total of 105 soil samples from 0 to 20 cm in the soil layer were collected and returned to the laboratory for soil physical and chemical analysis.

### Data Analysis

#### Species Data

The importance value can be used to comprehensively reflect the relative importance of species in a community by calculating indicators such as abundance, frequency, and dominance of species (Maarel and Franklin, 2013). The importance value is a primary indicator for determining the dominant species



**Fig.1.** Location of the study area and the sampling sites.

in a community, and the dominant species is the basis for vegetation classification (Maarel and Franklin, 2013). Therefore, we used the importance value of species to classify and ordinate vegetation on Daiyun Mountain. Species that are less frequent and more random in the community are called rare species (Kang *et al.*, 2015). In TWINSpan classification, the weight value of the rare species is higher, which will reduce the accuracy of classification results. Thus, when using TWINSpan for quantitative classification, we did not consider rare species (Kang *et al.*, 2015). The species data are based on the importance value of species with the rare species removed (importance value < 5 in all samples). We took the importance value of all species in each corresponding plot as the species data matrix, which was used for vegetation quantity classification and ordination analysis. The importance value is calculated as follows (Maarel and Franklin, 2013):

Importance value = relative abundance (*RA*) + relative frequency (*RF*) + relative dominance (*RD*)

Relative abundance (*RA*) = the number of individuals of a certain species / the sum of individuals of all species × 100

Relative frequency (*RF*) = the frequency of a certain species / the sum of frequency of all species × 100

Relative dominance (*RD*) = the dominance of a certain species / the sum of dominance of all species × 100

#### Environment Data

Environmental data included elevation, slope, aspect, slope position, soil pH (pH), soil organic carbon (SOC), total nitrogen (TN), total phosphorus (TP), total potassium (TK), and soil water content (SWC), for a total of 10 indicators. Among them, the ELE, SLOP, ASP, and SPO are topographic factors, whereas soil pH, SOC, TN, TP, TK, and SWC are soil factors. All the

following physical and chemical indicators of soil samples are referenced to the Bao (2000). Soil pH was measured via potentiometry. Soil organic carbon was evaluated using potassium dichromate heating method. Total nitrogen and total phosphorus were measured using the Kjeldahl method and molybdenum anti-colorimetric method, respectively, after the soil samples were dehydrated using  $\text{H}_2\text{SO}_4\text{--HClO}_4$ . Total potassium in soil was measured via flame photometry. Soil water content was measured using the oven drying method.

ELE, SLOP, pH, SOC, TN, TP, TK, and SWC are numerical variables that can be directly calculated by software. However, SPO and ASP are categorical variables that are represented by characters during the measurement process in field. They cannot be directly input into software to complete the calculation; they need to be converted into numerical variables. The slope position is divided into seven grades: 1 for valley, 2 for depression, 3 for flat, 4 for downslope, 5 for mid-slope, 6 for upper slope, and 7 for peak. The numbers from small to large indicate that the slope gradually changes from the valley to the peak (Zhang *et al.*, 2013). The north direction is defined as  $0^\circ$  and is divided into 8 grades in a clockwise direction in  $45^\circ$  angle increments. The results of ASP are divided into: north slope ( $0^\circ\text{--}22.5^\circ$  and  $337.5^\circ\text{--}360^\circ$ ) is grade 1, northeast slope ( $22.5^\circ\text{--}67.5^\circ$ ) is grade 2, northwest slope ( $292.5^\circ\text{--}337.5^\circ$ ) is grade 3, east slope ( $67.5^\circ\text{--}112.5^\circ$ ) is grade 4, west slope ( $247.5^\circ\text{--}292.5^\circ$ ) is grade 5, southeast slope ( $112.5^\circ\text{--}157.5^\circ$ ) is grade 6, southwest slope ( $202.5^\circ\text{--}247.5^\circ$ ) is grade 7, and south slope ( $157.5^\circ\text{--}202.5^\circ$ ) is grade 8. We defined non-slope as grade 9. The larger the number, the more the slope approaches the sun aspect (Zhang *et al.*, 2013).



### Taxonomic Designation

Association naming follows the naming rules proposed by Song (2004). First, the importance value of each species in the community is calculated, and the top two species with the two highest ranking importance value are denoted the dominant species (Song, 2004). The species with the highest value of the two is placed in front, and the two species are connected by "+". The characteristic species of the underlying layer are determined using the indicator value in the community, and the two species with the highest indicator value are denoted the characteristic species. The characteristic species are also connected by "+" and placed before the dominant species, and the symbol "-" connects the characteristic species and the dominant species. The association naming format is: dominant species 1 + dominant species 2 - characteristic species 1 + characteristic species 2 (Song, 2004). Among them, the indicator value (*Indval*) is calculated as follows:

$$IndVal_{i,j} = \frac{N_{individuals_{i,j}}}{N_{individuals_i}} \times \frac{N_{sites_{i,j}}}{N_{sites_j}} \times 100$$

where *IndVal<sub>i,j</sub>* denotes the indicator value of species *i* in community *j*, *Nindividuals<sub>i,j</sub>* is the average number of individuals of species *i* in community *j*, *Nindividuals<sub>i</sub>* is the average number of individuals of species *i* in each community, *Nsites<sub>i,j</sub>* is the number of plots occupied by species *i* in community *j*, and *Nsites<sub>j</sub>* is the number of plots contained in cluster *j*. The indicator value is the quantitative indicator of characteristic species. The higher the indicator value, the stronger the indication of the characteristic species to a certain association. The indicator value of a species in association ranges from 0 to 100. An indicator value is 100 indicates that a species appears only in a certain association, and the species is distributed in all plots in this association (Song 2004). In other words, the species can be used as an indicator species for this association. Both importance value and indicator value were calculated in Excel 2016.

### CCA Ordination

The steps for CCA are as follows: Firstly, the *P. taiwanensis* forest were divided by the two-way indicator species analysis (TWINSpan) based on species data, and then DCA was used to select an appropriate ordination method. Generally, if the distribution of the research object changes considerably, the CCA with a single-peak model is better. Conversely, the redundancy analysis (RDA) with linear model is better if the distribution does not change considerably. The commonly-used discriminant method is to calculate the axis length in DCA. When the maximum of the top four axes is greater than 4, CCA is recommended. When the maximum between 3 and 4, both CCA and RDA analysis can be used. When the maximum is less than 3,

RDA should be used (Hill and Gauch, 1980; Borcard *et al.*, 2011). Because environmental factors could be related to each other, we needed to remove the collinearity amongst environmental factors. We calculated the variance inflation factors (VIFs). The larger the VIF, the higher the collinearity amongst variables (Li *et al.*, 2009). After deleting the environmental variable with the highest VIF, we repeated these steps to remove the highest VIF variable until all VIFs were less than 10. Finally, partial analysis was used for a variance stratification. This method involves partitioning the contribution of topographical and soil factors to the spatial distribution of the associations on Daiyun Mountain. The DCA, VIFs calculation, CCA ordination and variation stratification were completed using the vegan package, and TWINSpan analysis was conducted using the vegan and cluster packages in R 3.4.2. (R core team *et al.*, 2017).

## RESULTS

### Classification of plant Communities

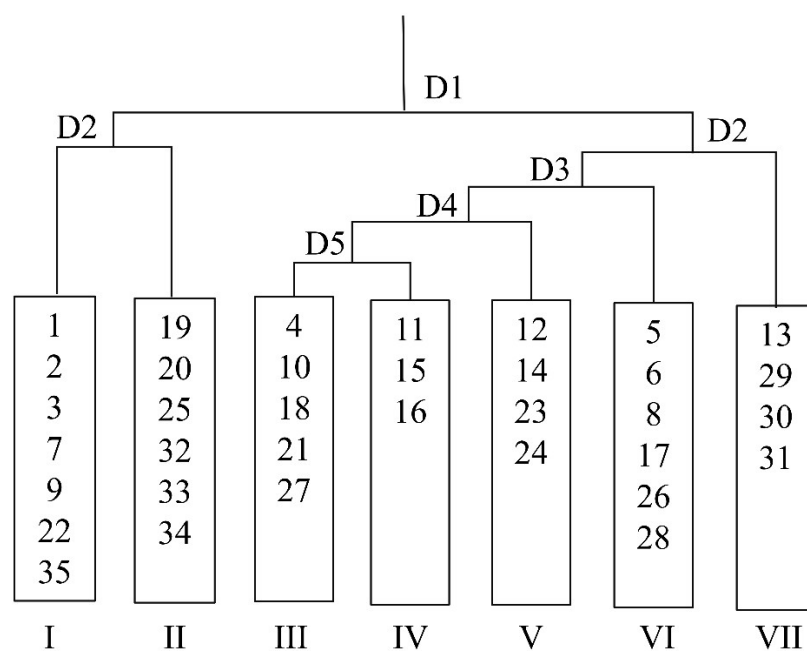
The 35 plots of *P. taiwanensis* forest on Daiyun Mountain were classified by TWINSpan. Combined with the actual ecological significance, the *P. taiwanensis* forest was divided into seven associations. The results of the vegetation classification are shown in Figure 2. Association naming includes two parts: the dominant species and the characteristic species, with the dominate species listed first and the characteristic species afterward. The dominant species and characteristic species of each association are listed in Table 1. The main environmental characteristics of each association is described in Appendix S3. The description of these seven associations are as follows"

(1) *P. taiwanensis* Hayata + *Schima superba* Gardn. & Champ - *Oligostachyum oedogonatum* (Z.P. Wang & G.H. Ye) Q.F. Zhang & K.F. Huang + *Photinia parvifolia* (Pritz.) Schneid. This association was representative in plots 1, 2, 3, 7, 9, 22, and 35, distributed at a medium elevation of 1200–1400 m, with a slope of 0°–33° on the downslope. The average soil pH was 4.74 in this association. The SOC, TN, TP, and TK contents were 67.83, 4.64, 0.29, and 24.89 g/kg, respectively. The soil water content was 51.67%. There are 87 species of plants in this association. The dominant species in the arbor layer are *P. taiwanensis* and *S. superba*. *O. oedogonatum* has some advantage in the undergrowth. The characteristic species were *O. oedogonatum* and *P. parvifolia*.

(2) *P. massoniana* Lamb. + *Acer davidii* Franch – *Sarcandra glabra* (Thunb.) Nakai + *Styrax odoratissimus* Champ. This association was representative in plots 19, 20, 25, 32, 33, and 34, which was distributed at lower elevation of 1000–1100 m, with slope of 0°–30°. The association was mainly distributed on the northeast slope and had a flat terrain. The average soil pH was 4.79.

**Table 1** The dominated species and indicated species of seven communities in Daiyun Mountain.

Communities	Dominant species	Importance value	Indicated species	Indicator value
<b>Community I</b>	<i>Pinus taiwanensis</i> Hayata	38.54	<i>Oligostachyum oedogonatum</i> (Z. P. Wang & G. H. Ye) Q. F. Zhang & K. F. Huang	92.92
	<i>Schima superba</i> Gardn. & Champ	9.33	<i>Photinia parvifolia</i> (Pritz.) Schneid.	23.92
<b>Community II</b>	<i>P. massoniana</i> Lamb.	16.01	<i>Sarcandra glabra</i> (Thunb.) Nakai	26.38
	<i>Acer davidii</i> Franch.	8.32	<i>Styrax odoratissimus</i> Champ.	16.67
<b>Community III</b>	<i>P. taiwanensis</i>	54.56	<i>Clethra delavayi</i> Franch.	48.34
	<i>S. superba</i>	4.18	<i>Eurya groffii</i> Merr.	25.4
<b>Community IV</b>	<i>P. taiwanensis</i>	39.06	<i>E. groffii</i>	35.79
	<i>Cunninghamia lanceolata</i> (Lamb.) Hook.	14.37	<i>Vaccinium carlesii</i> Dunn	31.46
<b>Community V</b>	<i>P. taiwanensis</i>	52.72	<i>Camellia sinensis</i> (Linn.) O. Kuntze	44.44
	<i>Machilus thunbergii</i> Sieb. & Zucc.	4.89	<i>Rhododendron mariesii</i> Hemsl. & Wils.	21.63
<b>Community VI</b>	<i>P. taiwanensis</i>	40.81	<i>Syzygium buxifolium</i> Hook. & Arn.	32
	<i>S. superba</i>	8.64	<i>Itea oblonga</i> Hand.-Mazz.	28.57
<b>Community VII</b>	<i>P. taiwanensis</i>	50.07	<i>E. saxicola</i> H. T. Chang	93.3
	<i>Ilex crenata</i> Thunb.	4.95	<i>R. eudoxum</i> Balf. f. & Forrest	54.05



**Fig. 2.** The classification results of *Pinus taiwanensis* forest in Daiyun Mountain. D1–D5 indicated the level of division. For example, D1 means the classification at one level, in this level, the classification method can divide the vegetation into two types. TWINSPLAN method can divide the *P. taiwanensis* forest in Daiyun Mountain into seven associations. Association I–VII are (I) *P. taiwanensis* Hayata + *Schima superba* Gardn. & Champ - *Oligostachyum oedogonatum* (Z.P. Wang & G.H. Ye) Q.F. Zhang & K.F. Huang+ *Photinia parvifolia* (Pritz.) Schneid., (II) *P. massoniana* Lamb. + *Acer davidii* Franch –*Sarcandra glabra* (Thunb.) Nakai + *Styrax odoratissimus* Champ., (III) *P. taiwanensis* + *S. superba* - *Clethra delavayi* Franch. + *Eurya groffii* Merr., (IV) *P. taiwanensis* + *Cunninghamia lanceolata* (Lamb.) Hook - *E. groffii* + *Vaccinium carlesii* Dunn., (V) *P. taiwanensis* + *Machilus thunbergii* Sieb. & Zucc - *Camellia sinensis* (L.) O. Kuntze + *Rhododendron mariesii* Hemsl. & Wils., (VI) *P. taiwanensis* + *S. superba* - *Syzygium buxifolium* Hook. & Arn. + *Itea oblonga* Hand. –Mazz and (VII) *P. taiwanensis* + *Ilex crenata* Thunb – *E. saxicola* H. T. Chang + *R. eudoxum* Balf. f. & Forrest, respectively. The number in Fig.2 represent the plot number in Daiyun Mountain.

The SOC, TN, TP, and TK contents were 36.38, 3.56, 0.25, and 20.33 g/kg, respectively. The soil water content was 54.68%. There are 85 species of plants in this association. The dominant species in the arbor layer are *P. massoniana* and *A. davidii*. *O. oedogonatum* and *Glochidion puberum* (L.) Hutch has some advantage in the undergrowth. The characteristic species were *S. glabra* and *S. odoratissimus*.

(3) *P. taiwanensis* + *S. superba* - *Clethra delavayi* Franch. + *Eurya groffii* Merr. This association was

representative in plots 4, 10, 18, 21, and 27, distributed at an elevation of 1200–1500 m, with a slope of 10°–30°, middle hill, and a north to east slope. The average soil pH was 4.49. The SOC, TN, TP, and TK contents were 66.53, 4.91, 0.28, and 16.95 g/kg, respectively. The soil water content was 48.49%. There are 85 species of plants in this association. The dominant species in the arbor layer are *P. taiwanensis* and *S. superba*. *E. rubiginosa* var. *attenuata* and *E. groffii* has some advantage in the undergrowth. The



characteristic species were *C. delavayi* and *E. groffii*.

(4) *P. taiwanensis* + *Cunninghamia lanceolata* (Lamb.) Hook - *E. groffii* + *Vaccinium carlesii* Dunn. This association was representative in plots 12, 14, 23, and 24, distributed at high elevation of 1500–1600 m, slope 0°–15°, and mid-upper hill. The average soil pH was 4.79. The SOC, TN, TP, and TK contents were 59.17, 5.78, 0.34, and 14.08 g/kg, respectively. The soil water content was 61.56%. There are 43 species of plants in this association. The dominant species in the arbor layer are *P. taiwanensis* and *C. lanceolata*. *Rhododendron simsii* Planch. and *R. mariesii* Hemsl. & Wils has some advantage in the undergrowth. The characteristic species were *E. groffii* and *V. carlesii* Dunn.

(5) *P. taiwanensis* + *Machilus thunbergii* Sieb. & Zucc - *Camellia sinensis* (L.) O. Kuntze + *R. mariesii* Hemsl. & Wils. This association was representative in plots 11, 15 and 16, which was distributed at high elevation of 1400–1600 m, with a slope of 0°–19°, on the south slope. The terrain was low, mainly valleys. The average soil pH was 4.56. The SOC, TN, TP, and TK contents were 84.81, 5.52, 0.35, and 20.25 g/kg, respectively. The soil water content was 51.67%. There are 57 species of plants in this association. The dominant species in the arbor layer are *P. taiwanensis* and *M. thunbergii*. *R. mariesii* and *E. groffii* has some advantage in the undergrowth. The indicator species were *C. sinensis* and *R. mariesii*.

(6) *P. taiwanensis* + *S. superba* - *Syzygium buxifolium* Hook. & Arn. + *Itea oblonga* Hand. -Mazz. This association was representative in plots 5, 6, 8, 17, 26, and 28, distributed at low elevation of 1000–1300 m, south slope, downhill, and slope of 10°–30°. The average soil pH was 4.71. The SOC, TN, TP, and TK contents were 58.95, 3.48, 0.31, and 15.67 g/kg, respectively. The soil water content was 45.25%. There are 68 species of plants in this association. The dominant species in the arbor layer are *P. taiwanensis* and *S. superba*. *Lindera aggregate* (Sims) Kosterm. and *E. rubiginosa* var. *attenuata* has some advantage in the undergrowth. The indicator species were *S. buxifolium* and *I. oblonga*.

(7) *P. taiwanensis* + *Ilex crenata* Thunb - *E. saxicola* H. T. Chang + *R. eudoxum* Balf. f. & Forrest. This association was representative in plots 13, 29, 30, and 31, distributed at high elevation of 1500–1700 m, north slope, mid-up hill, and slope of 15°–20°. The soil pH average was 4.74. The SOC, TN, TP, and TK content were 60.60, 7.91, 0.38 and 21.31 g/kg, respectively. The soil water content was 45.25%. There are 27 species of plants in this association. The dominant species in the arbor layer are *P. taiwanensis* and *I. crenata*. The indicator species were *E. saxicola* and *R. eudoxum*.

### CCA Ordination Analysis

The DCA results showed that the maximum axis length was 5.0918, which is greater than 4 (Appendix S4).

CCA was more appropriate for flowing ordination analysis. The CCA ordination results of the *P. taiwanensis* forest on Daiyun Mountain are shown in Table 2. As all VIFs were less than 10 (Appendix S5), there was no collinearity amongst the variables. Therefore, all environmental factors were used for CCA. The total eigenvalue of the CCA was 7.0705. The sum of eigenvalues of all constrained axes was 2.353. All 10 environmental factors explained 33.28% of the species distribution (2.353/7.0705). The Monte Carlo permutation test results showed that the 10 environmental factors could significantly explain the spatial distribution of the seven associations in Daiyun Mountain ( $P = 0.002$ ).

Table 2 shows that Environmental factors were significantly correlated with species distribution. To investigate which environmental factors were significant, each environmental factor was tested. The results are provided in Table 3. The correlations between ELE, SOC and species distribution were extremely significant. ASP, SPO, TN, and TP were significantly correlated with species distribution. ELE and SLOP had the strongest correlation with CCA 1, followed by TN, SOC, and TP. ASP had the strongest correlation with CCA 2, followed by TK and SPO. Table 3 shows that ELE and SOC were the main factors affecting the species distribution of associations on Daiyun Mountain.

**Table 2** CCA ordination of *P. taiwanensis* forest in Daiyun Mountain

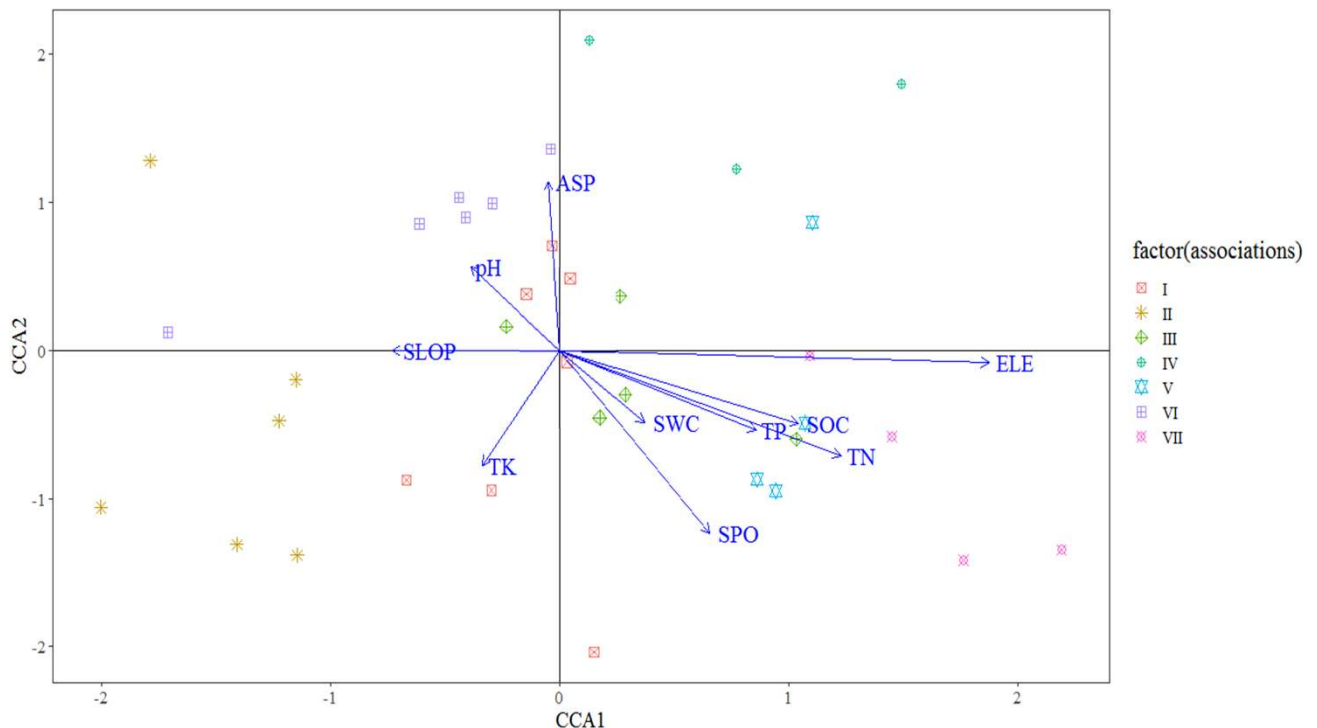
CCA	Axis1	Axis2	Axis3	Axis4
eigenvalue	0.5005	0.3122	0.294	0.2593
species-environment variance	21.27	34.53	47.03	58.05
accumulation proportion				
sum eigenvalues of all		2.353		
constraints axes				
total eigenvalue		7.0705		
Significance test of all axes		$P=0.002$		

**Table 3.** Significance test of environment factors.

	CCA1	CCA2	r <sup>2</sup>	P-value
ELE	0.99951	-0.03114	0.8129	0.001***
ASP	-0.03516	0.99938	0.2812	0.005**
SLOP	-0.99993	-0.0117	0.1226	0.113
SPO	0.4898	-0.87184	0.4233	0.002**
pH	-0.58992	0.80746	0.1026	0.163
SOC	0.88254	-0.47024	0.4525	0.001***
TN	0.91755	-0.39761	0.301	0.003**
TP	0.86571	-0.50054	0.2296	0.015**
TK	-0.42938	-0.90312	0.1571	0.053*
SWC	0.63045	-0.77623	0.0816	0.236

Note : \*\*\*, \*\* and \* indicate significance at the 0.001, 0.01, and 0.05 levels, respectively.

There is a strong correlation between elevation and soil carbon content, and elevation gradients was the most important environmental gradient for Daiyun Mountain (Figure 3). With the increase of elevation, it was successively distributed by associations II, VI, I, III, IV, V, and VII. *P. massoniana* was the main dominant species of association II in low elevation, whereas *P. taiwanensis* was the dominant species at middle and high

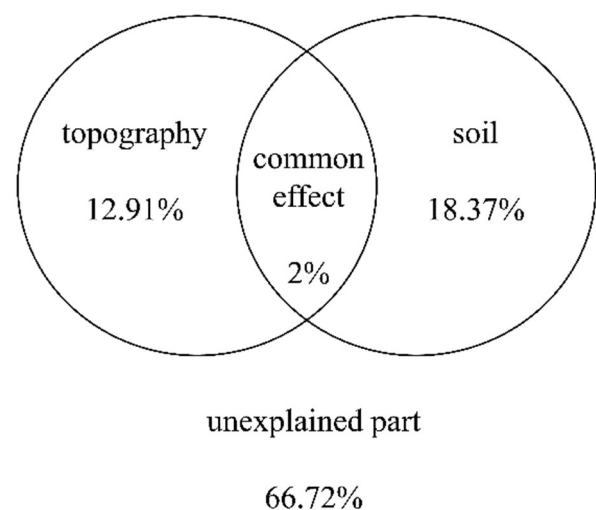


**Fig. 3.** The CCA ordination of *P. taiwanensis* community in Daiyun Mountain. Note: ELE: elevation; ASP: aspect; SPO: slop position; SLOP: slope; pH: soil pH; SOC: soil organic content; TN: total nitrogen; TP: total phosphorus; TK: total potassium; SWC: soil water content.

elevations. Each association has its own preferred habitat conditions in Daiyun Mountain. Associations IV and VI were more suitable for the more acidic soil on the southern slope than other associations. Associations II and VI were distributed in lower elevation areas with lower soil nutrient contents. Associations I and III were distributed at middle elevation and middle slope with medium soil nutrient contents. Associations IV, V, and VII were distributed at high elevation, where the habitat was characterized by high soil nutrient content and medium to upper hill. Association IV was more suitable for the south slope, whereas association VII was more suitable for growing on the north slope.

#### Variation partitioning of Environmental Factors in Associations' Spatial Distribution

The 10 environmental factors accounted for 33.28% of the spatial distribution of the associations, and the unexplained part accounted for 66.72% (Figure 4). The terrain alone contributed 12.91%, and the total explanatory quantity was 14.91%. The soil factor alone explained 18.37%, and the total explanatory quantity was 20.37%. The common contribution of terrain and soil was 2%. The results showed that the contribution of soil factors to the spatial distribution of *P. taiwanensis* forest on Daiyun Mountain was the highest, followed by topographic contribution, and the common contribution was the lowest.



**Fig. 4.** Quantitative separation of topography and soil factors to vegetation spatial distribution.

## DISCUSSION

### Classification and Naming of Associations on Daiyun Mountain

Chinese vegetation classification system adopted the classification unit of association, and dominant species play a crucial role in association (Song *et al.*, 2017). However, the species composition of subtropical





evergreen broad-leaved forests and tropical rain forests in Southern China is complex, especially the undergrowth layer, which poses challenges for the accurate determination of dominant species. A study on Wuyi Mountain indicated an obvious flora of evergreen broad forests, mainly in the pantropical element, but determining the dominant species was difficult (Ding *et al.*, 2015). Previous study found that tree seedlings and large shrubs infiltrated the undergrowth layer, resulting in a diverse species composition, and the dominant species were not obvious in Dinghu Mountain (Wen *et al.*, 2018). Therefore, vegetation classification based on the dominant species is difficult to implement in Southern China. The results of this study also showed that recognizing the dominant species in different tree layers is challenging, but that the difference in indicator species is obvious. The use of indicator species as one of the criteria may be an important basis for classifying vegetation. The indicator value of *O. oedogonatum* in association I and *E. saxicola* in association VII both were above 90, indicating that *O. oedogonatum* and *E. saxicola* had strong unicity in association I and VII, respectively. They were representative species in their communities. The naming method of the dominant species in the tree layers combined with indicator species in the undergrowth layer can be applied in the forest in Southern China.

#### **Spatial Distribution Characteristics of Associations on Daiyun Mountain**

Many studies have reported that the distribution pattern of vegetation is the result of combined effects of environment, biology, space, and other factors on different scales (Wang *et al.*, 2012). On the regional scale, climate plays a decisive role in vegetation distribution, whereas on landscape scale and below, other factors were dominant (Ivonne and Burkhardt, 2008). The influence of topography and soil on vegetation is more prominent, especially in mountainous areas (Wehn and Johansen, 2015; An *et al.*, 2018). For higher altitude mountains, elevation is usually the decisive factor affecting the species distribution pattern in mountain areas. Research on Daiyun Mountain showed that the main factor influencing associations distribution pattern was elevation, consistent with the results reported in Xishuangbanna (Zhang *et al.*, 2018). Based on the classification results and local environmental data, the habitat characteristics of the associations can be understood, which could help guide species conservation. With increasing elevation, the temperature gradually decreases, and precipitation and solar radiation also change, which in turn cause redistribution of hydrothermal conditions, thus affecting the habitat selection of plants. Seven associations on Daiyun Mountain have good adaptability to elevation and soil nutrition, and each association has its own unique ecological adaptability. Association II is

dominated by *P. massoniana* and *A. davidii*, distributed in low elevation and low nutrition areas. Although the soil nutrition is low, *P. massoniana* can tolerate the dry and infertile environment, which create a suitable environment for *P. massoniana* in the low elevation areas (Ou *et al.*, 2017). Thus, association II includes vegetation suitable for low mountain afforestation. Associations I, III, and VI are dominated by *P. taiwanensis* and *S. superba*, distributed at the medium elevations and soil nutrition. Association VI is resistant to poor nutrient conditions and prefers high-slope habitats. This association could help restore vegetation in the areas affected by serious soil erosion on Daiyun Mountain. Association III has strong adaptability to various ecological factors and is the most widely distributed vegetation type on Daiyun Mountain. Association IV prefers the southern slope with high light intensity, is dominated by pioneer species, which is a suitable association for strong solar light environment. Associations V and VII are distributed in areas with high elevation and high nutrition. The proportion of shade-tolerant species gradually increases in association V. Association VII grows at the highest elevations, with an increasing proportion of shrubs, and *P. taiwanensis* is the constructive species of this association. In high elevation areas, soil organic carbon is high, the litter layer is thick, light is sufficient, and the soil condition is good, which was beneficial to the growth and regeneration of the *P. taiwanensis* (Liu *et al.*, 2013). Therefore, *P. taiwanensis* forest in Daiyun Mountain can be protected within distinct elevation zones, and the main protection area should be the middle to high elevation areas.

#### **Relative Importance of Environmental Factors**

In the study of the *P. taiwanensis* forest on Daiyun Mountain, a total of 10 environmental factors accounted for 33.28% of the community spatial distribution, whereas the unexplained parts accounted for 66.72%. Shen and Zhang (2000) proposed that the degree of interpretability of environmental factors affecting vegetation distribution is mainly determined by the diversity of vegetation (Shen and Zhang, 2000). The more diverse the vegetation, the less control environment exerts on vegetation, which led to the lower contribution of environment (Shen and Zhang, 2000). The contribution of the environmental factors to the wetland plant community distribution in Tumen River wetland in Northeast China was 61.9% (Zheng *et al.*, 2019). The contribution of environmental factors to plant communities in the arid regions of Saudi Arabia was 51.15% (Alanazi and Alqahtani, 2019). The multivariate statistical analysis of forest vegetation in the Western Himalayas showed that environmental factors explained 34.8% variability of vegetation (Khan *et al.*, 2019). The contribution of environmental factors to the associations distribution was 33.28% on Daiyun Mountain, which





indicates that the *P. taiwanensis* forest was highly diverse. The comprehensive effect of various ecological mechanisms dictates the spatial distribution of associations. The external environment is the main factor restricting the survival of local plants and habitat filtration, and affecting the spatial distribution of local associations. When vegetation diversity was high, environmental factors such as topography and soil have less of an impact on the vegetation pattern. In diverse vegetation, plants adapt to the fierce competition environment and compete for limited resources, affecting the spatial distribution of plants through niche differentiation, negative density constraints, and random dispersal (Hillerislambers *et al.*, 2012). The unexplained part of the spatial pattern of seven associations was 66.72% in our study. The processes of niche differentiation, negative density restriction, and random dispersal may affect the spatial distribution of vegetation on Daiyun Mountain. Therefore, in the future, we will deeply explore the main forces driving the unexplained part, and comprehensively reveal the community assembly on Daiyun Mountain.

We divided the environmental factors into two categories: soil and topography. The soil contribution was 18.37% and the topographic contribution was 12.91%. The results inferred that topographic factors and soil factors play a similar role in the spatial distribution of seven associations on Daiyun Mountain. The common contribution of soil and topographic factors on Daiyun Mountain was 2%, indicating that the coupling relationship between soil and topographic factors was weak, and the interaction of topography and soil nutrients did not significantly affect the distribution of associations on Daiyun Mountain. Soil and topographic factors were relatively independently affecting the spatial distribution of associations on Daiyun Mountain.

## CONCLUSION

The vegetation on Daiyun Mountain was divided into seven associations using the TWINSpan method. The naming method of the dominant species of the dominant layer combined with the characteristic species in the undergrowth layer reasonably represents the vegetation classification in Southern China. Elevation and soil organic carbon content were the main factors driving associations distribution. We recommend creating different community protection areas based on elevation, and *P. taiwanensis* forest can be managed according to elevation. Association VI can be used as restoration vegetation in areas with serious soil erosion on Daiyun Mountain. Association II is suitable for low mountain afforestation. Association VII is the dominant association in high elevation habitats. The characteristics of each association need to be considered when managing the forest on Daiyun Mountain.

## ACKNOWLEDGMENTS

The authors wish to thank Ruijie Yao, Weizu Lin, Yulong Sun, Zuochao Ya, Zongkai Zhang and staffs of Daiyun Mountain National Nature Reserve for the assistance in the raw data collected. This study was supported by the National Natural Science Foundation of China (31700550;31770678), Guiding Project of Fujian Science and Technology Department (2015Y0042), Daiyun Mountain Nature Reserve Administration Project (KH1401450). The authors also record sincere appreciation for helpful and constructive comments made by the reviewers of the manuscript.

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