Research paper

Syntaxonomic and Gradient Analysis of *Keteleeria davidiana* var. *formosana* Forests in Taiwan

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【Summary】

In this study we present a comprehensive multivariate analysis of *Keteleeria davidiana* var. *formosana* forest vegetation in Taiwan. In total, 65 sample plots were compiled, partly from the relevant literature and partly from new and unpublished data. We used only woody vascular plant species for the analysis. The syntaxonomy of forest types was determined by a 2-way indicator species analysis (TWINSPAN) and tabular comparison method. A detrended correspondence analysis (DCA) was applied to the ordination analysis to clarify floristic variations of the 65 sample plots. One alliance, 2 associations, and 4 subassociations were distinguished and described: the *K. davidiana* var. *formosana* alliance was recognized and divided into *Cyclobalanopsis hypophaea-Keteleeria davidiana* var. *formosana* association including the *Callicarpa remotiflora* and *Antidesma hiiranense* subassociations and a *Diospyros morrisiana-Keteleeria davidiana* var. *formosana* association including the *Pinus luchuensis* and *Illicium arborescens* subassociations. Synonyms in the recent literature on forests relating to these associations and subassociations are given. The ordination program confirmed the differentiation of *K. davidiana* var. *formosana* forests.

Key words: *Keteleeria davidiana* var. *formosana*, syntaxonomy, TWINSPAN, DCA, Taiwan.

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研究報告

台灣油杉森林的統整分類與梯度分析

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摘 要

本研究使用65個台灣油杉的森林樣區進行植群多變數分析，樣區的資料部份是來自相關的文獻，部分是來自作者新調查的樣區與未發表的樣區，僅使用木本的維管束植物進行分析。使用雙向指標種分析法及列表比較法進行林型的統整分類，並使用降趨對應分析法來了解樣區在植相空間上的分布。共劃分出1個群團、2個群叢、4個亞群叢，分別是台灣油杉群團、灰背櫟－台灣油杉群叢、山紅柿－台灣油杉群叢、疏花紫珠亞群叢、南仁五月茶亞群叢、琉球松亞群叢、紅花八角亞群叢。本文經詳細比對，將文獻中的植群型異名納入本研究的分類單位。降趨對應梯度分析的結果顯示台灣油杉森林的植群在南北兩地有明顯的分化，且南部及北部的台灣油杉森林亦各自有分化的情形。

關鍵詞：台灣油杉、統整分類、雙向指標種分析法、降趨對應分析法、台灣。

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INTRODUCTION

In Taiwan, *Keteleeria davidiana* var. *formosana* (Pinaceae) usually grows in association with broadleaf trees in low-elevation mountain areas. Its habitats are restricted to the northern and southern parts of the main island of Taiwan. Early ecologists were highly interested in its special disjunct geographical distribution pattern. According to the description by Kanehira (1936), the species is naturally distributed in the Pinglin area of northern Taiwan and in Dawu area of southern Taiwan. In the Pinglin area, the *K. davidiana* var. *formosana* population was largely destroyed by extensive logging in the early of 20 century. A few small stands only exist at 300~600 m on a mountain ridge between the watershed of Gupoliao Creek and the watershed of Jingualiao Creek. In southern Taiwan, it was distributed at 900 m on a mountain near Fangshan Village, Chaozhou Township of the western Hengchun Peninsula and is now distributed at 500 m in sun-oriented habitats in the Dawu Forest District of the eastern Hengchun Peninsula. There were many trees of this species on the Hengchun Peninsula, but its population size was obviously decreased by extensive logging for building materials for aboriginal houses. Kanehira (1936) assumed that the discontinuous geographical distribution pattern of the species at that time was due to an earlier connection of Taiwan with China. Thus the population was capable of migrating from different parts of the Asian mainland. Liu (1966) agreed with the opinion of Kanehira, and conjectured that Taiwan had been merged with Fujian Province, with its northern part being connected to Zhejiang Province and its southern part being connected to Guandong Province when Taiwan was formerly connected to the Asian mainland during glacial maxima. Therefore, the northern population of *K. davidiana* var.

formosana on Taiwan probably came from Zhejiang and Fujian Provinces and southern populations of *K. davidiana* var. *formosana* came from Yunnan Province by way of Guangxi and Guandong Provinces to Taiwan. When sea levels rose and the Taiwan Strait reappeared, the discontinuous geographical distribution pattern was formed.

Yeh and Fan (1997) surveyed 5 plots at the Dawu *K. davidiana* var. *formosana* Nature Reserve and divided the vegetation into the *Cinnamomum osmophloeum-Keteleeria davidiana* var. *formosana* type and *Elaeocarpus sylvestris-Cycloblanopsis longinux* type which included the *Rhododendron mariesii-Cycloblanopsis longinux* and *Ardisia sieboldii-Keteleeria davidiana* var. *formosana* subtypes. Lo and Lin (1999) investigated 18 sampled quadrats in Pinglin *K. davidiana* var. *formosana* habitat and described the *Castanopsis carlesii* var. *sessilis-Machilus thunbergii* type including the *Daemonorops margaritae-Zanthoxylum scadens* and *Selaginella doederleinii-Euonymus laxiflorus* subtypes. In 2001, Chen established 5 permanent plots at Pinglin a *K. davidiana* var. *formosana* nature reserve and grouped the 5 plots into the *Castanopsis carlesii* var. *sessilis* type including the *Aralia bipinnata-Castanopsis carlesii* var. *sessilis* and *Myrsine sequinii-Castanopsis carlesii* var. *sessilis* subtypes. Lin et al. (2003) established 42 permanent plots in Pinglin and Dawu *K. davidiana* var. *formosana* forest stands and recognized the *Melastoma candidum-Alsophila podophylla* subtype in the north and the *Cinnamomum randaiense-Cyclobalanopsis salicina* subtype in the south, and grouped the 2 subtypes into the *Castanopsis carlesii* var. *sessilis-Machilus thunbergii* type.

At present, many countries are developing a standardized classification system to integrate vegetation types. Some researches have resulted in syntaxonomic work aimed at a special vegetation type (Dzwonko and Loster 2000, Lawesson 2000, Bergmeier and Dimopoulos 2001), a regional vegetation scheme (Sardinero 2000, Sari 2000), and a national system (Grossman et al. 1998, Bruelheide and Chytry 2000). Su (2004) pointed out that the diversification of vegetation classification in Taiwan is due to differences in vegetation schools and technical details of the algorithm. To the present, no comprehensive syntaxonomic analysis has been made of *K. davidiana* var. *formosana* forest communities. Therefore, this study aimed to produce a numerical syntaxonomic revision of the *K. davidiana* var. *formosana* forest vegetation in Taiwan. We made use of available published data on the above-described plots and a set of unpublished data. We studied natural forests and considered only woody plants.

MATERIALS AND METHODS

Compilation of data

Available data from studies of vegetation ecology and inventories of *K. davidiana* var. *formosana* forests in Taiwan were edited using the PC-ORD software (McCune and Mefford 1999). Forty published datasets from Yeh and Fan (1997) and Lin et al. (2003) were compiled together with unpublished data from 25 sample plots collected by Chen in 2001 and Yang in 2007. Only sample plots that fulfilled the following criteria were considered: (1) a natural forest with *K. davidiana* var. *formosana* dominance in the canopy; (2) the sample size within the range of 100~500 m^2; (3) synoptic tables not used, because single sample plots could not be separated; (4) an ordinal 1~9 scale according to Gauch (1982); and (5) only woody vascular plant species included. The scientific names of the vascular plants followed the *Flora of Taiwan* (Huang 1993~2000).

Data analysis

Classification was assisted by the TWINSPAN polythetic, hierarchical, divisive method (Hill 1979) run using PC-ORD software (McCune and Mefford 1999). TWINSPAN pseudospecies cut levels for species importance values were set to ordinal 1~9 scale units according to Gauch (1982). The maximum level of divisions was 5, the number of indicators per division was 5, and the minimum group size for division was 5. Based on the hierarchical TWINSPAN classification, a synoptic table sorting (Mueller-Dombois and Ellenberg 1974) was used to detect and characterize vegetation types in the data matrix with 65 plots and 191 taxa. We calculated the synoptic IVI value and constancy value as follows:

$S = (Np/N) \times \overline{n}$ and

$C = (Np/N) \times 100\%$;

where S and C, respectively, are the synoptic IVI value and constancy value of each tree species in the *i*th association, $\overline{n}$ is the average of the octave value of each tree species at each association, and Np and N are the number of plots appearing in the *i*th association and the total number of plots in the *i*th association, respectively. We took the ceiling S and C values to be integers, so as to avoid many rare species values bing 0.

The hierarchical vegetation classification system we adopted was according to the US National Vegetation Classification (USNVC) (Grossman et al. 1998). The naming of communities was done using the major characteristic species in front followed by the dominant species. The characteristic species appears to be the most characteristic of the community and the most differential compared to related communities. The dominant species appears in the canopy with a higher importance value. A detrended correspondence analysis (DCA) was applied to the floristic analysis, using the PC-ORD software (McCune and Mefford 1999). The analysis was performed on a data matrix obtained from the TWINSPAN analysis. All runs were made with the options of detrending by segment, non-linear rescaling, and downweighting rare species. Classification results were used to visualize the vegetation pattern represented by the sample scores along the first 2 axes.

RESULTS

Syntaxonomic classification

According to the TWINSPAN classification results, a hierarchical forest vegetation system was developed by the tabular comparison method. One alliance and 2 associations were distinguished in the synoptic table (Table 1). Each association and subassociation were distinguished by a unique set of diagnostic species. Descriptions of the major floristic composition and habitat type for all communities are given below.

***Keteleeria davidiana* var. *formosana* alliance**

Castanopsis carlesii var. *sessilis-Machilus thunbergii* type (Lin et al. 2003).

At present, forests characterized by *K. davidiana* var. *formosana* are often considered the natural forest type in southern Taiwan, yet forests in northern areas with that type are semi-natural or planted stands, which have long been managed through selective timber cutting and elimination of competing species. The physiognomy belongs to subtropical montane evergreen mixed conifevous-broadleaf forests. Geographically, these forests are distributed in the Pinglin area of northern Taiwan and in the Dawu area of southern Taiwan. According to the diagnostic species group, the alliance can be divided into *Cyclobalanopsis hypophaea-Keteleeria*

Table 1. Synoptic table of the *Keteleeria davidiana* var. *formosana* forests in Taiwan. The digits of columns contain the synoptic IVI value and constancy (1 = 1~20%; 2 = 21~40%; 3 = 41~60%; 4 = 61~80%; 5 = 81~100%) of species within each association. Shading area means diagnostic species of forest types

***Keteleeria davidiana* var. *formosana* alliance**
- **A. *Cyclobalanopsis hypophaea-Keteleeria davidiana* var. *formosana* association**
  - **A1. *Callicarpa remotiflora* subassociation**
  - **A2. *Antidesma hiiranense* subassociation**
- **B. *Diospyros morrisiana-Keteleeria davidiana* var. *formosana* association**
  - **B1. *Pinus luchuensis* subassociation**
  - **B2. *Illicium arborescens* subassociation**

Alliance Association	A		B	
Subassociation	A1	A2	B1	B2
Number of plots	17	17	18	13
Bredia gibba	1,1	0	0	0
Machilus japonica	1,1	0	0	0
Cyclobalanopsis globosa	1,1	0	0	0
Rododendron ovatum	1,1	0	0	0
Sloanea formosana	1,1	0	0	0
Hydrangea angustipetala	1,1	0	0	0
Ventilago leiocarpa	1,1	0	0	0
Symplocos sasakii	1,1	0	0	0
Lasianthus tsangii	1,1	0	0	0
Pasania nantoensis	1,1	0	0	0
Ficus aurantiaca	1,1	0	0	0
Ormosia formosana	1,1	0	0	0
Vaccinium bracteatum	1,1	0	0	0
Lasianthus chinensis	1,2	0	0	0
Pasania hancei	1,2	0	0	0
Symplocos wikstroemiifolia	1,2	0	0	0
Illicium anisatum	1,2	0	0	0
Symplocos shilanensis	1,2	0	0	0
Ardisia crenata	1,3	0	0	0
Lasianthus curtisii	1,3	0	0	0
Podocarpus fasciculus	1,3	0	0	0
Callicarpa dichotoma	2,4	0	0	0
Callicarpa remotiflora	2,5	0	0	0
Ficus nervosa	0	1,1	0	0
Reevesia formosana	0	1,1	0	0
Symplocos heishanensis	0	1,1	0	0
Castanopsis indica	0	1,1	0	0
Eurya hayatae	0	1,1	0	0
Cyclobalanopsis pachyloma	0	1,1	0	0

(con't)

Subassociation	A1	A2	B1	B2
Number of plots	17	17	18	13
Castanopsis fabri	0	1,1	0	0
Lithocarpus amygdalifolius	0	1,1	0	0
Fraxinus insularis	0	1,1	0	0
Ficus benjamina	0	1,1	0	0
Glycosmis citrifolia	0	1,1	0	0
Symplocos morrisonicola	0	1,2	0	0
Adinandra lasiostyla	0	1,2	0	0
Tarenna gracilipes	0	1,2	0	0
Machilus obovatifolia	0	1,2	0	0
Hydrangea chinensis	0	1,3	0	0
Podocarpus macrophyllus	0	1,3	0	0
Euonymus tashiroi	0	1,3	0	0
Garcinia multiflora	0	1,3	0	0
Osmanthus marginatus	0	2,4	0	0
Antidesma hiiranense	0	2,4	0	0
Ardisia virens	1,1	0	1,1	0
Ficus formosana	1,1	0	1,2	0
Rododendron rubropilosum	1,2	0	1,1	0
Fissistigma oldhamii	1,2	0	1,1	0
Heliotropium formosanum	1,2	0	1,1	0
Mussaenda pubescens	1,2	0	1,2	0
Lasianthus wallichii	1,3	0	1,2	0
Wendlandia uvariifolia	1,1	0	0	1,1
Broussonetia kaempferi	1,1	0	0	1,1
Symplocos caudata	1,1	0	0	1,1
Eurya loquaiana	1,1	0	0	1,1
Acer albopurpurascens	1,1	1,1	0	0
Croton cascarilloides	1,1	1,1	0	0
Neolitsea parvigemma	1,1	1,1	0	0
Drypetes karapinensis	1,1	1,1	0	0
Pasania glabra	1,1	1,1	0	0
Viburnum aboricolum	1,1	1,1	0	0
Helicia cochinchinensis	1,1	1,2	0	0
Osmanthus lanceolatus	1,1	1,2	0	0
Pasania chiaratuangensis	1,1	1,2	0	0
Schima superba	1,1	2,3	0	0
Wikstroemia lanceolata	1,2	1,1	0	0
Cryptocarya concinna	1,2	1,2	0	0
Lasianthus cyanocarpus	1,2	1,2	0	0
Castanopsis fomosana	1,3	1,1	0	0
Anneslea lanceolata	1,3	1,3	0	0

(con't)

Subassociation	A1	A2	B1	B2
Number of plots	17	17	18	13
Beilschmiedia erythrophloia	1,3	2,4	0	0
Magnolia kachirachirai	1,3	2,4	0	0
Symplocos congesta	2,4	1,2	0	0
Litsea acutivena	2,4	2,4	0	0
Cyclobalanopsis hypophaea	4,5	4,5	0	0
Ormosia hengchuniana	4,5	2,5	0	0
Cinnamomum subavenium	3,5	4,5	0	0
Syzygium formosanum	3,5	5,5	0	1,1
Cyclobalanopsis longinux	3,4	4,4	0	3,5
Rhododendron oldhamii	1,1	1,1	0	1,1
Osmanthus matsumuranus	1,3	2,4	0	1,1
Limlia uraiana	1,1	1,1	0	1,2
Eurya chinensis	1,2	1,3	0	2,2
Rhaphiolepis indica var. *tashiroi*	2,4	2,4	1,1	0
Litsea hypophaea	1,2	1,2	1,1	0
Scolopia oldhamii	1,2	1,1	1,1	0
Cyclobalanopsis glauca	1,1	1,2	1,1	0
Pasania harlandii	1,1	1,1	1,3	0
Litsea acuminata	1,1	1,2	1,1	1,1
Fissistigma glaucescens	1,1	1,3	1,1	1,1
Ilex rotunda	1,1	2,4	1,1	1,2
Diospyros eriantha	2,3	4,5	1,2	1,2
Ilex uraiensis	2,4	3,5	1,1	1,1
Tricalysia dubia	2,5	3,5	1,3	1,2
Psychotria rubra	4,5	4,5	4.5	4,5
Keteleeria davidiana var. *formosana*	7,5	5,5	8,5	4,5
Engelhardia roxburghiana	3,5	4,5	3,4	2,3
Rhododendron leptosanthum	1,3	2,4	1,2	1,2
Elaeocarpus sylvestris	1,3	3,5	1,2	1,3
Daphniphyllum glaucescens	2,4	2,3	1,2	2,4
Archidendron lucidum	2,4	2,4	1,2	1,2
Ardisia quinquegona	1,3	2,4	1,3	1,3
Myrsine seguinii	2,4	3,5	2,4	4,5
Gordonia axillaris	1,3	2,4	1,3	2,4
Schefflera octophylla	2,4	3,5	2,4	5,5
Elaeocarpus japonicus	1,3	1,1	1,2	2,3
Wendlandia formosana	1,2	1,2	3,4	4,5
Machilus thunbergii	1,3	2,4	4,5	5,5
Castanopsis carlesii var. *sessilis*	2,4	2,3	3,5	6,5
Ardisia sieboldii	1,2	1,3	1,2	1,3
Styrax suberifolia	1,2	1,3	1,3	2,4

(con't)

Subassociation	A1	A2	B1	B2
Number of plots	17	17	18	13
Cinnamomum osmophloeum	1,1	1,2	1,1	1,1
Gardenia jasminoides	1,1	1,3	1,1	1,2
Nageia nagi	1,1	1,3	1,1	1,2
Cryptocarya chinensis	1,1	1,1	1,2	1,2
Itea parviflora	1,1	1,2	1,2	1,1
Cleyera japonica	1,2	1,2	1,2	1,2
Eurya japonica	1,1	1,1	1,2	1,2
Glochidion rubrum	1,1	1,1	1,3	1,2
Ilex formosana	1,1	1,2	1,3	2,4
Illicium arborescens	1,1	1,1	1,2	4,5
Symplocos theophrastifolia	0	1,3	1,2	1,2
Mallotus paniculatus	0	1,1	1,2	2,4
Ilex goshiensis	0	1,1	1,1	1,3
Meliosma rigida	0	1,1	1,1	2,5
Ardisia cornudentata	0	1,1	1,2	1,1
Bridelia balansae	1,1	0	1,3	1,1
Ficus fistulosa	1,1	0	1,1	1,1
Cryptomeris japonica	1,1	0	1,1	1,2
Rhus succedanea	1,1	0	1,1	1,2
Adinandra formosana	1,1	0	1,3	1,2
Mallotus japonicus	1,1	0	1,2	1,1
Antidesma japonicum	3,5	0	1,2	2,5
Symplocos stellaris	1,1	0	1,1	1,2
Saurauia tristyla	1,1	0	1,1	1,2
Diospyros morrisiana	1,1	1,1	4,5	6,5
Randia cochinchinensis	1,1	1,1	1,2	5,5
Michelia compressa	1,1	0	1,2	4,5
Syzygium buxifolium	1,1	0	1,3	3,5
Itea oldhamii	0	0	2,4	1,3
Clerodendrum cyrtophllum	0	0	2,4	2,4
Melastoma candidum	0	0	2,4	1,2
Blastus cochinchinensis	0	0	2,4	1,2
Pinus luchuensis	0	0	4,4	1,2
Callicarpa formosana	0	0	1,2	1,2
Maesa perlaria	0	0	1,2	1,2
Maesa japonica	0	0	1,2	1,1
Symplocos glauca	0	0	1,3	2,4
Myrica rubra	0	0	1,1	1,3
Machilus zuihoensis	0	0	1,1	1,2
Cinnamomum camphora	0	0	1,1	1,2
Turpinia formosana	0	0	1,1	1,2

(con't)

Subassociation	A1	A2	B1	B2
Number of plots	17	17	18	13
Cyclobanlanopsis gilva	0	0	1,1	1,1
Ilex asprella	0	0	1,1	1,1
Litsea cubeba	0	0	1,1	1,1
Eriobotrya deflexa	0	0	1,1	1,1
Lasianthus fordii	0	1,1	1,1	0
Lasianthus obliquinervis	0	1,1	1,1	0
Pourthiaea lucida	0	1,1	1,1	0
Ficus septica	0	1,1	1,1	0
Pasania kawakamii	1,1	0	1,1	0
Osmanthus enervis	1,1	0	1,1	0
Aleurites montana	1,1	0	1,1	0
Sapium discolor	1,1	0	1,1	0
Syzygium euphlebium	1,1	0	1,2	0
Vaccinium wrightii	0	1,1	0	1,2
Meliosma squamulata	0	1,1	0	2,4
Rhododendron mariesii	0	1,1	0	1,1
Daphniphyllum himalaense	0	0	1,2	0
Cyclobanlanopsis sessilifolia	0	0	1,2	0
Osmanthus heterophyllus	0	0	1,1	0
Castanea mollissima	0	0	1,1	0
Diospyros oldhamii	0	0	1,1	0
Antidesma pentandrum var. *barbatum*	0	0	1,1	0
Vaccinium dunalianum var. *caudatifolium*	0	0	1,1	0
Camellia sinensis	0	0	1,1	0
Zanthoxylum ailanthoides	0	0	1,1	0
Cinnamomum kanehirae	0	0	1,1	0
Randia canthioidea	0	0	1,1	0
Bridelia tomentosa	0	0	1,1	0
Glochidion acuminatum	0	0	0	2,5
Cinnamomum micranthum	0	0	0	1,3
Pyrenaria shinkoensis	0	0	0	1,3
Prunus phaeosticta	0	0	0	1,2
Euonymus laxiflorus	0	0	0	1,2
Ilex pubescens	0	0	0	1,2
Pieris taiwanensis	0	0	0	1,2
Ilex ficoidea	0	0	0	1,2
Ficus virgata	0	0	0	1,1
Ternstroemia gymnanthera	0	0	0	1,1
Alnus formosana	0	0	0	1,1

davidiana var. *formosana* and *Diospyros morrisiana-Keteleeria davidiana* var. *formosana* associations.

A. *Cyclobalanopsis hypophaea-Keteleeria davidiana* var. *formosana* association (Group A in Fig. 1)

This association is confined to 900-m mountain habitat near Fangshan Village, Chaozhou Township of the western Hengchun Peninsula and also occurs at 500 m on sun-oriented habitat in the Dawu Forest District of the eastern Hengchun Peninsula. This association is mainly characterized by *Cyc. hypophaea*, *Cinnamomum subavenium*, *Ormosia hengchuniana*, and *Litsea acutivena* (Table 1). The canopy is primarily formed by tall trees of *K. davidiana* var. *formosana*, *Cyc. hypophaea*, *Magnolia kachirachirai*, *Anneslea lanceolata*, *Engelhardia roxburghiana*, *Machilus thunbergii*, *Castanopsis carlesii* var. *sessilis*, and *Cyc. longinux*. The subcanopy layer

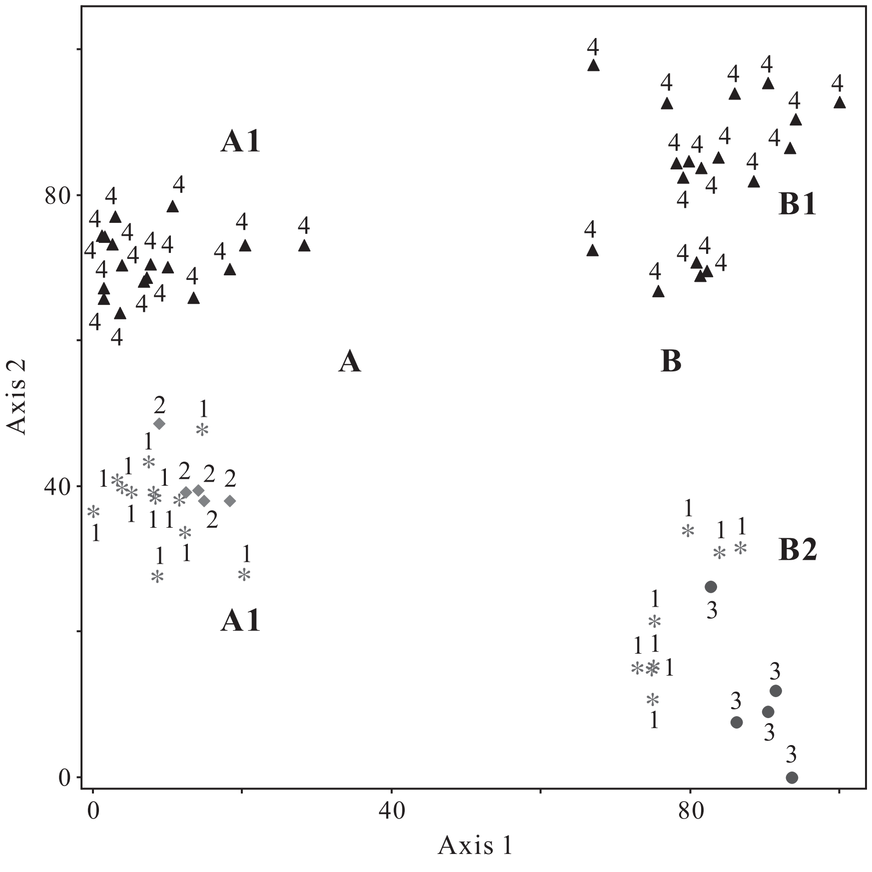

Fig. 1. Ordination of plots for the first 2 axes of the detrended correspondence analysis A: *Cyclobalanopsis hypophaea-Keteleeria davidiana* var. *formosana* association, A1: *Callicarpa remotiflora* subassociation. A2: *Antidesma hiiranense* subassociation. B: *Diospyros morrisiana-Keteleeria davidiana* var. *formosana* association. B1: *Pinus luchuensis* subassociation. B2: *Illicium arborescens* subassociation. Sources and numbers of plots used in the analyses: ✱1: unpublished by Yang (2007; 20), ◆2: Yeh and Fan (1997; 5), ●3: unpublished by Chen (2001; 5), ▲4: Lin et al. (2003; 35).

is dominated by *Ormosia hengchuniana*, *Tricalysia dubia*, *Osmanthus matsumuranus*, *Lit. acutivena*, *Ilex uraiensis*, and *Archidendron lucidum*. The shrub layer is mainly dominated by *Psychotria rubra*. Within this association 2 subassociations were further separated.

A1. *Callicarpa remotiflora* subassociation (Group A1 in Fig. 1)

Cinnamomum randaiense-Cyclobalanopsis salicina subtype (Lin et al. 2003).

The 17 plots of the *Callicarpa remotiflora* subassociation all belong to Lin et al. (2003). This is differentiated by a number of species such as *Callicarpa remotiflora*, *Cal. dichotoma*, *Podocarpus fasciculus*, *Lasianthus curtisii*, and *Ardisia crenata*.

A2. *Antidesma hiiranense* subassociation (Group A2 in Fig. 1)

Cinnamomum osmophloeum-Keteleeria davidiana var. *formosana* type and *Elaeocarpus sylvestris-Cycloblanopsis longinux* type, *Rhododendron mariesii-Cycloblanopsis longinux*, and *Ardisia sieboldii-Keteleeria davidiana* var. *formosana* subtypes (Yeh and Fan 1997).

The *Antidesma hiiranense* subassociation comprises 12 unpublished plots by Yang in 2007 and 5 published plots by Yeh and Fan (1997). This is indicated by *Ant. hiiranense*, *Osm. marginatus*, *Garcinia multiflora*, *Euonymus tashiroi*, *Pod. macrophyllus*, and *Hydrangea chinensis*.

B. *Diospyros morrisiana-Keteleeria davidiana* var. *formosana* association (Group B in Fig. 1)

This association is confined to a 300~600-m mountain ridge between the watershed of Gupoliao Creek and the watershed of Jingualiao Creek. This is mainly characterized by *Diospyros morrisiana*, *Michelia compressa*, *Syzygium buxifolium*, *Randia cochinchinensis*, *Itea oldhamii,* and *Clerodendrum cyrtophyllum* (Table 1). The canopy is primarily formed by tall trees of *K. davidiana* var. *formosana*, *Eng. roxburghiana*, *Mac. thunbergii*, *Cas. carlesii* var. *sessilis*, and *Cyc. longinux*. The subcanopy layer is dominated by *Diospyros morrisiana*, *Syz. buxifolium*, *Randia cochinchinensis*, and *Illicium arborescens*. The shrub layer is mainly dominated by *Psy. rubra*.

B1. *Pinus luchuensis* subassociation (Group B1 in Fig. 1)

Castanopsis carlesii var. *sessilis-Machilus thunbergii* type, *Daemonorops margaritae-Zanthoxylum scadens*, *Selaginella doederleinii-Euonymus laxiflorus* (Lo and Lin 1999), and *Melastoma candidum-Alsophila podophylla* subtypes (Lin et al. 2003).

The 18 plots of the *Pinus luchuensis* subassociation all belong to Lin et al. (2003). This is differentiated by a number of species such as *Pin. luchuensis*, *Blastus cochinchinensis*, and *Melastoma candidum*.

B2. *Illicium arborescens* subassociation (Group B2 in Fig. 1)

The *Illicium arborescens* subassociation comprises 8 new plots by Yang in 2007 and 5 unpublished plots by Chen in 2001. This is indicated by *Ill. arborescens*, *Meliosma rigida*, *Mel. squamulata*, and *Glochidion acuminatum*.

Ordination

The ordination diagram (Fig. 1) shows the dispersion of plots with respect to the first 2 axes. Eigenvalues were 0.438 for axis 1 and 0.244 for axis 2. Figure 1 shows a good separation of plots along the first axis, and there is discontinuity between group A (*Cyclobalanopsis hypophaea-Keteleeria davidiana* var.

formosana association) on the left and group B (*Diospyros morrisiana-Keteleeria davidiana* var. *formosana* association) on the right obtained from the synthetic table (Table 1). Along the second axis, there are discontinuities between group A1 (*Callicarpa remotiflora* subassociation) in the upper and group A2 (*Antidesma hiiranense* subassociation) in the lower, and between group B1 (*Pinus luchuensis* subassociation) in the upper and B2 (*Illicium arborescens* subassociation) in the lower.

DISCUSSION

Our studies show that the differentiation of *K. davidiana* var. *formosana* forests is related to several different historical and phytogeographical elements. The local diversity of the southern plots is much higher than that of the northern ones, and strong floristic-geographical differentiation of the *K. davidiana* var. *formosana* forests in Taiwan was observed. According to the first division of TWINSPAN, all sample plots were divided into 2 groups, reflecting southern and northern plots. This result corresponds with the first axis of the DCA and confirms the conspicuous differentiation of *K. davidiana* var. *formosana* forests. In the second division of TWINSPAN, both northern and southern plots were divided into 2 groups, representing 2 subassociations. The southern group (A1) and northern group (B1) happen to be the plots sampled by Lin et al. (2003), which are only 100 m^2. Judging from the differential species, these subassociations contain many intolerant trees and shrubs. It is reasonable to infer that these small plots could be located near trails or locally disturbed spots. The northern plots are actually mixed with pine plantations. Thus the 2 subassociations can be considered to be locally disturbed variants of the *Keteleeria* forest type.

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