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RESEARCH ARTICLE

Abiotic Factors and *Yushania* Influences on *Abies* Forest Composition in Taiwan

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ABSTRACT: *Abies kawakamii* forests are generally distributed above 3,000 m in Taiwanese high mountains. The community data used in our analysis were derived from the database of the National Vegetation Diversity Inventory and Mapping Project of Taiwan (NVDIMP), and environmental data were obtained from the WorldClim and NVDIMP databases. We used non-metric multidimensional scaling (NMDS) to identify vegetation composition of *Abies* communities and the structural equation models (SEMs) were used to examine the complex relationships between environmental factors and vegetation composition. The results of ordination showed the most important factors determining species composition of *Abies* forests involved habitat rockiness, heat load index, warmth index and summer and winter. SEM results approved the warmth index and winter precipitation were the main drivers determining the latent variable—climate, which significantly affect the overstory composition of *Abies* communities. The relative frequency of *Yushania niitakayamensis* also had a minor effect on the overstory. However, the relative frequency of *Yushania* had strong and significant effects on the understory flora and it was also strongly correlated with rock ratio and winter precipitation. Moreover, the overstory displayed a negative but insignificant coefficient on the understory composition, and this might be attributed to the fragile and high heterogeneous habitat in Taiwanese high mountain areas.

KEY WORDS: *Abies kawakamii*, abiotic factor, vegetation composition, multivariate analysis, structural equation model (SEM), *Yushania niitakayamensis.*

INTRODUCTION

One of the main issue of community ecology is to address the question of how assembly rules of living organisms work in community structure or composition, while most recent discussion focuses on ecological processes and principles of assembly in communities (Keddy, 1992; Weiher et al., 1998; Götzenberger et al., 2012). In recent studies, the ecological assembly rules restricting community composition would be generalized as influences by filters of species dispersal, abiotic factors and biotic interactions (McGill et al., 2006; Götzenberger et al., 2012). The abiotic factors usually refer to climate (e.g. temperature, precipitation, solar radiation), soil properties (e.g. nutrients, structure, textures) and physiographic factors (e.g. aspect, sky view factor, slope inclination), while biotic factors would be associated with interspecific interactions (Barnes et al., 1997). However, the general model employing assembly rules in community among complex species interactions and environmental variables is gaining attention in recent studies (Grace, 2008; Matthews et al., 2009; Rooney and Bayley, 2011; Gazol et al., 2012). Such studies could help us to understand and test the generalizations in regarding complex and heterogeneous ecosystems (Grace et al., 2010).

The understory layer of boreal and temperature coniferous or mixed broad-leaved forest is mainly composed by small herbs or dwarf shrubs, such as *Carex* spp., *Rubus* spp., *Vaccinium* spp. (Nakashizuka and Numata, 1982; Nakamura and Krestov, 2005), but the significance of dwarf bamboo in the understory layer in certain sites, such as species of genus *Pseudosasa*, *Sasa*, *Sasamorpha*, and *Yushania*, is a remarkable feature in temperate zones or mountainous areas of the subtropical zone of East Asia (Liu, 1971; Taylor and Qin, 1988; Krestov, 2003; Okitsu, 2003). The dwarf bamboo can expand in many forest understories by rhizome over several decades, while the dense and dominant population could be the major factor affecting mature trees, the regeneration of tree seedlings and diversity of herbaceous species (Nakashizuka and Numata, 1982; Nakashizuka, 1988; Iida and Nakashizuka, 1995; Takahashi, 1997; Gratzer et al., 1999; Takahashi et al., 2003; Ito and Hino, 2004). Although the overstory trees can sustain more resources than understory species, the dense population of dwarf bamboo in the understory could be influential to the soil water and nutrient availability and then affect overstory species in advance (Takahashi et al., 2003; Tripathi et al., 2006). Nevertheless, the question of how the dwarf bamboo affects the vegetation composition and their causation is still unclear.

In Taiwan, the dwarf bamboo, *Yushania niitakayamensis* (Hayata) Keng f., is a species widely inhabiting from 1000–3800 m above sea level (a.s.l.). Above 2,500 m a.s.l., it usually forms grassland in open habitats, such as mountain ridges, flat planes, or can be found in the understories of coniferous forest dominated by *Abies kawakamii* Ito, *Picea morrisonicola* Hayata and *Tsuga chinensis* var. *formosana* (Hayata) H. L. Li et H. Keng. In the understory, the stature of this species can reach up to 1–3 meters. In contrast, its individuals only attain maximum heights of 10–60 cm and forms open grasslands in disturbed habitats (usually by fire) or above forest line. Previous studies mentioned that the dense *Yushania* in the understory could inhibit the growth of seedlings and juvenile coniferous trees (Liu et al., 1984; Lai and Chen, 1995), and furthermore, the interactions between *Yushania* and coniferous species could be inferred as competition, and could be found in different successional stages or in post-fire habitats (Liu, 1963, 1971; Su, 1974; Liu and Su, 1978; Chen, 1993). However, the role of *Yushania* in the causation and interactions among coniferous species and other abiotic factors, such as aspect, soil properties, macroclimate, is still unclear.

In this study, we try to use explanatory analysis method, such as non-metric multiple dimensional scaling, to find potential environmental variable, which would affect the species composition of *Abies kawakamii* forests. We also aim to use structural equation modeling (SEM) to quantify the multiple direct and indirect interactions among the abiotic, biotic and latent variables. Through the SEM procedure we establish a latent variable reflecting unmeasured causal abiotic variables, which are estimated by observed variables. In particular, we also try to find the major limiting factors affecting vegetation composition and the interactions among the relative frequency of *Yushania* and floristic composition of the overstory and understory of *Abies kawakamii* forests.

MATERIALS AND METHODS

Study area and vegetation description

The study area is located in high-mountain regions of Taiwan above 3,000 m a.s.l. (around 22.5–24.5º N, 120.5–121.5º E), which includes the Central Mountain Range, Hsueh-Shan Range and Yu-Shan Range. The average annual temperature in the high-mountain regions ranges from 5–11 ºC, and the annual precipitation is around 3000 mm (recorded by the Yu Shan meteorological station, 3,845 m a.s.l.; 23º29'21" N, 120º57'06" E). The characteristic of precipitation in Taiwan is highly contributed by topography and the prevailing wind directions, while the summer and winter precipitations are mainly influenced respectively by the southwestern and northeastern monsoons (Chen and Huang, 1999; Chen and Chen, 2003). There is also extreme rainfall in summer caused by typhoons, while over half of the annual precipitation falls from June to October (Su et al., 2012).

There are six vegetation zones along the altitudinal gradient in Su's classification system: *Ficus-Machilus* zone (< 500 m a.s.l.), *Machilus-Castanopsis* zone (500–1500 m a.s.l.), *Quercus* zone (1500–2500 m a.s.l.), *Tsuga-Picea* zone (2500–3100 m a.s.l.), *Abies* zone (3100–3600 m a.s.l.) and alpine vegetation (> 3600 m a.s.l.; Su, 1984a). The forest vegetation in Taiwan is distinguished by an obvious cloud belt ranging from 1,500–2,500 m a.s.l. (i.e. *Quercus* zone) and includes zonal coniferous forest dominated by *Tsuga chinensis* var. *formosana*, *Abies kawakamii* and *Juniperus squamata* above this cloud belt. Below the cloud belt, the forests are mainly dominated by Fagaceae and Lauraceae, such as *Castanopsis cuspidata* var. *carlesii* (Hemsl.) Yamazaki, *Cyclobalanopsis morii* (Hayata) Schottky, *C. glauca* (Thunb. *ex* Murray) Oerst., *Litsea acuminata* (Bl.) Kurata, etc. According to the novel floristic classification, the *Abies kawakamii* vegetation includes three associations: *Junipero squamatae-Abietetum kawakamii* Lin et al. 2012, *Yushanio niitakayamensis-Abietetum kawakamii* Lin et al. 2012 and *Tsugo formosanae-Abietetum kawakamii* Lin et al. 2012 (Lin et al., 2012). The dominated species in the canopy layer are *Abies kawakamii* and *Tsuga chinensis* var. *formosana*, and mixed with *Juniperus squamata* and *Picea morrisonicola* Hayata in some places. The understory flora includes various species depending on habitat and topography conditions. The shrub layer is usually formed by dense dwarf bamboo *Yushania niitakayamensis* in thick soil and gentle slope habitat, and the other woody species are small trees such as *Eurya glaberrima* Hayata and *Sorbus randaiensis* (Hayata) Koidz. Species composition in the herb layers comprises mainly of shade-adapted species such as *Ainsliaea latifolia* subsp. *henryi* (Diels) H. Koyama, *Cystopteris moupinensis* Franchet, *Oxalis acetosella* subsp. *griffithii* (Edgew. & Hook. f.) Hara and *Elatostema trilobulatum* (Hayata) Yamazaki.

Data sets

The raw plots were derived from the National Vegetation Diversity and Inventory Mapping Project (NVDIMP; 2003–2008) database (Chiou et al., 2009).

In the NVDIMP database, 3,564 plots were sampled from the whole National Forests in Taiwan. The standard size of each plot is 400 m^2, which has four subplots within each plot. We estimated the percentage values of total and canopy cover in each plot and subplot. There were two layers in the floristic data. The first layer (hereafter overstory layer) included all trees and shrubs greater than 1.5 m in height and their diameter at breast height (DBH) was measured. The second layer (hereafter understory layer) included all the other species (shrubs and juveniles lower than 1.5 m, herbs, epiphytes) and their percentage cover values (the only one individual with coverage less than 0.1% was recorded as 0.1%; the others were recorded between 0.1% and 100%) were also estimated in the field. Species occurring in less than two plots were omitted from the dataset to reduce noise. We calculated the importance value index (IVI; Curtis and McIntosh, 1951) of overstory (IVI = average of relative dominance [represented by basal area] and relative density) and understory layers (IVI = average of relative dominance [represented by percentage cover] and relative frequency). A total of 95 plots were selected for analyses, which represented the *Abies kawakamii* forests according to the classification scheme of Lin et al. (2012).

Environmental factors such as topography (1: ridge; 2: upper slope; 3: middle slope; 4: lower slope; 5: valley; 6: flat plain), soil rockiness (proportion of rock greater than 5 mm in soil), habitat rockiness ratio (Rock_r; the proportion of rock without covering by woody debris, bryophytes and other plants), bare land ratio (BLR; the proportion of bare-land area within a plot), etc. were also estimated in the field. Geographical coordinates were also recorded by GPS device. Several topographic factors, such as aspect, elevation, heat load index (HLI; the approximation of potential direct incident radiation considering aspect, slope, latitude; see McCune, 2007), slope inclination and sky view factor (SVF; the indication of site openness) were interpolated using GIS software derived from a digital terrain model in 40 m grid of resolution. Climatic factors representing ecological limitations, such as summer/winter precipitation (PrS: May–September/PrW: October–February), summer radiation (May–September) were also calculated by the postgis geospatial database obtained from Chiou et al. (2004) and Lai et al. (2010). Kira's warmth index (WI = summation of monthly average temperature above 5°C; Kira, 1945) was calculated from monthly temperature obtained from the WorldClim database (Hijmans et al., 2005). The resolution of topographical and climatic factors were resampling to 1 km grid to make consistency. By reason of the very high cover of *Yushania* in present plots, we try to use relative frequency representing the prevalence of *Yushania*, which can be used as a biotic factor to assess its effect to *Abies kawakamii* forests. The relative frequency of *Yushania* (abbreviated as YUS) within each plot was calculated as count of *Yushania* in each plot divided by total species frequency.

Data analysis

We used 95 plots from NVDIMP databases, while their species composition was used for ordination analyses. Unconstrained ordination analyses, i.e. non-metric multidimensional analysis (NMDS) were used to identify relationships between the species composition of *Abies kawakamii* forests and environmental factors. The *metaMDS* function of *vegan* package (Oksanen et al., 2010) was used in R to perform the NMDS (R Development Core Team, 2011; version 2.14.0) until converging to minimum stress. The community data were square root transformed and submitted to Wisconsin double standardization and in *metaMDS* procedure when data values had large ranges, and then started randomly using iterative procedures to avoid falling into local minima (following McCune et al., 2002). We used maximum hundred iterations until converged and found a global solution with minimum stress throughout the procedure. To identify the relationship between species composition and environmental factors, principal component analysis (PCA) was used to analyze and project significant environmental vectors onto the NMDS diagrams. Environmental fit with PCA was also performed by the *envfit* procedure using *vegan* package in the R program with one thousand permutations (Oksanen et al., 2010). The final solution of each case was rotated to the first axis of NMDS with the most significant environmental factors explaining much of the variance in species composition (following McCune et al., 2002).

Recently SEM increasingly attracts the attention of ecologists to solve complex ecological interactions by its ability to quantify both direct and indirect effects (Grace, 2006; Vile et al., 2006; Laughlin and Abella, 2007; Martin et al., 2011; Rooney and Bayley, 2011). SEM itself is not only a multivariate statistic tool incorporating confirmatory factor analysis and path analysis (McCune et al., 2002; Arhonditsis et al., 2006; Grace et al., 2010), but also an ideal method to quantify causal effects, which is suitable for dealing with ecological hypotheses of multiple processes in ecological systems (Grace, 2008; Grace et al., 2010). The final solutions identified by the NMDS procedure were analyzed using SEM in the AMOS program (IBM Corporation, Somers, NY, version 18). The first NMDS axis scores of each vegetation layer were employed for species composition in SEM procedure. The exploitation of initial model examined covariances of all observed variables and chi-square fit statistics between data and model by maximum likelihood (ML) estimation and its regression weights of pathways with bootstrapping hundred times. Through ML estimation of the model, we considered a proper model fit by several criteria such as chi-squared fit, the ratio of chi-square and degree of freedom, goodness-of-fit index, adjusted goodness-of-fit index, Bentler-Bonnett normal incremental fit index, etc. (Bagozzi and Yi, 1988; Grace, 2006). Before presentation of SEM diagram, coefficients of direct and indirect pathways were standardized for the purpose of path measure comparisons, while total effects were evaluated to represent the sum of all pathways in the final step (Grace, 2006).

RESULTS

Species composition and NMDS results

Abies kawakamii usually had very high IVI in the plots (Table 1). *Juniperus squamata* was the second dominant species in the overstory layer, and followed by *Rhododendron pseudochrysanthum* Hayata, *Rhododendron pachysanthum* Hayata. Several deciduous species, such as *Viburnum betulifolium*, *Sorbus randaiensis* and *Ribes formosanum* Hayata were also found in the overstory layer. The understory layer included 104 species after excluding rare species or accidental species (Table 2). The *Yushania* possessed the highest IVI value, and other important species with IVI values greater than ten were *Pyrola morrisonensis* (Hayata) Hayata, *Ainsliaea latifolia* subsp. *henryi* and *Elatostema trilobulatum*. The result also revealed that the saplings of *Abies kawakamii* and shrubs of *Juniperus squamata* and *Rhodododendron pseudochrysanthum* were dominated in the understory flora of *Abies kawakamii* forests. The other important species with high IVI values were mostly shade-tolerant species, including *Ainsliaea macroclinioides* Hayata, *Oxalis acetosella* subsp. *griffithii*, and ferns such as *Dryopteris wallichiana* (Spr.) Alston & Bonner and *Cystopteris fragilis* (L.) Bernh.

The NMDS result of overstory layer showed that the species composition of *Abies kawakamii* forests was affected by YUS, WI, HLI and PrW (Fig. 1). Therefore, the YUS was rotated to the first axis in the overstory layer. The stress value of final NMDS solution was converged to 0.115 in the overstory layer. Both of the WI and YUS were strongly correlated to the first NMDS axis, and PrW was also positively correlated with the first NMDS axis, while the HLI was negatively correlated with this axis. The *Abies kawakamii*, *Pieris taiwanensis* Hayata, *Rhododendron pachysanthum* and

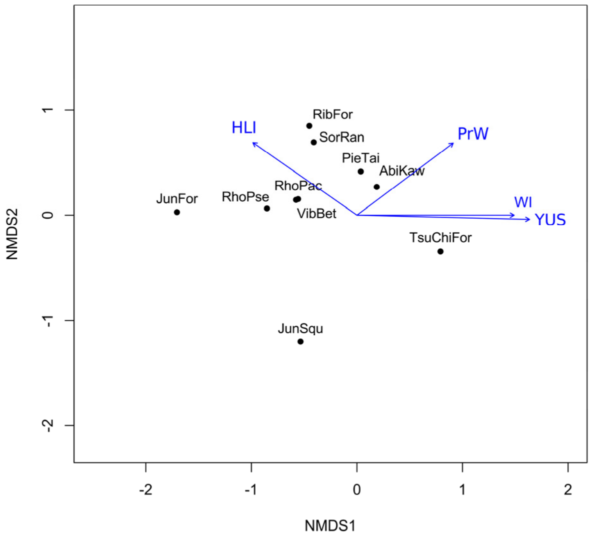

Fig. 1. Non-metric multidimensional scaling (NMDS) ordination of overstory species of *Abies kawakamii* forests vegetation. Species are abbreviated with the first three letters of the genus and the specific epithet. The environmental factors include HLI–heat load index; PrW–precipitation in winter; WI–Kira's warmth index; YUS–the relative frequency of *Yushania* (stress=0.115, bray-curtis distance).

Viburnum betulifolium Batal. were associated to lower HLI compared to *Ribes formosanum* Hayata and *Sorbus randaiensis* (Hayata) Koidz. The dominant *Tsuga chinensis* var. *formosana*, *Abies kawakamii*, *Juniperus formosana* and *Juniperus squamata* could be identified by WI and HLI along the first axis.

In the understory layer (Fig. 2), the final solution of NMDS stress value was converged to 0.223. Both YUS and WI were positively correlated with the first NMDS axis and PrS was positively correlated with the second axis, whereas PrW was negatively correlated with it, and Rock_r was associated with both axes negatively. The YUS along the first NMDS axis and PrW along the second axis implied that shade-adapted species could coexist with dense *Yushania* in the understory layer (group B), and these species included *Elatostema trilobulatum*, *Galium echinocarpum* Hayata, *Pyrola morrisonensis*, *Ainsliaea macroclinidioides* and *Rubus pungens* var. *oldhamii* (Miq.) Maxim. The species associated with high habitat rockiness (group C), such as *Geranium hayatanum* Ohwi, *Sedum nokoense* Yamamoto, *Veronica oligosperma* Hayata and *Cystopteris moupinensis* Franchet, were also related to lower WI. Higher PrS and lower PrW were associated with a group of understory species (group A) including high-mountain grassland herbs and shrubs, such as

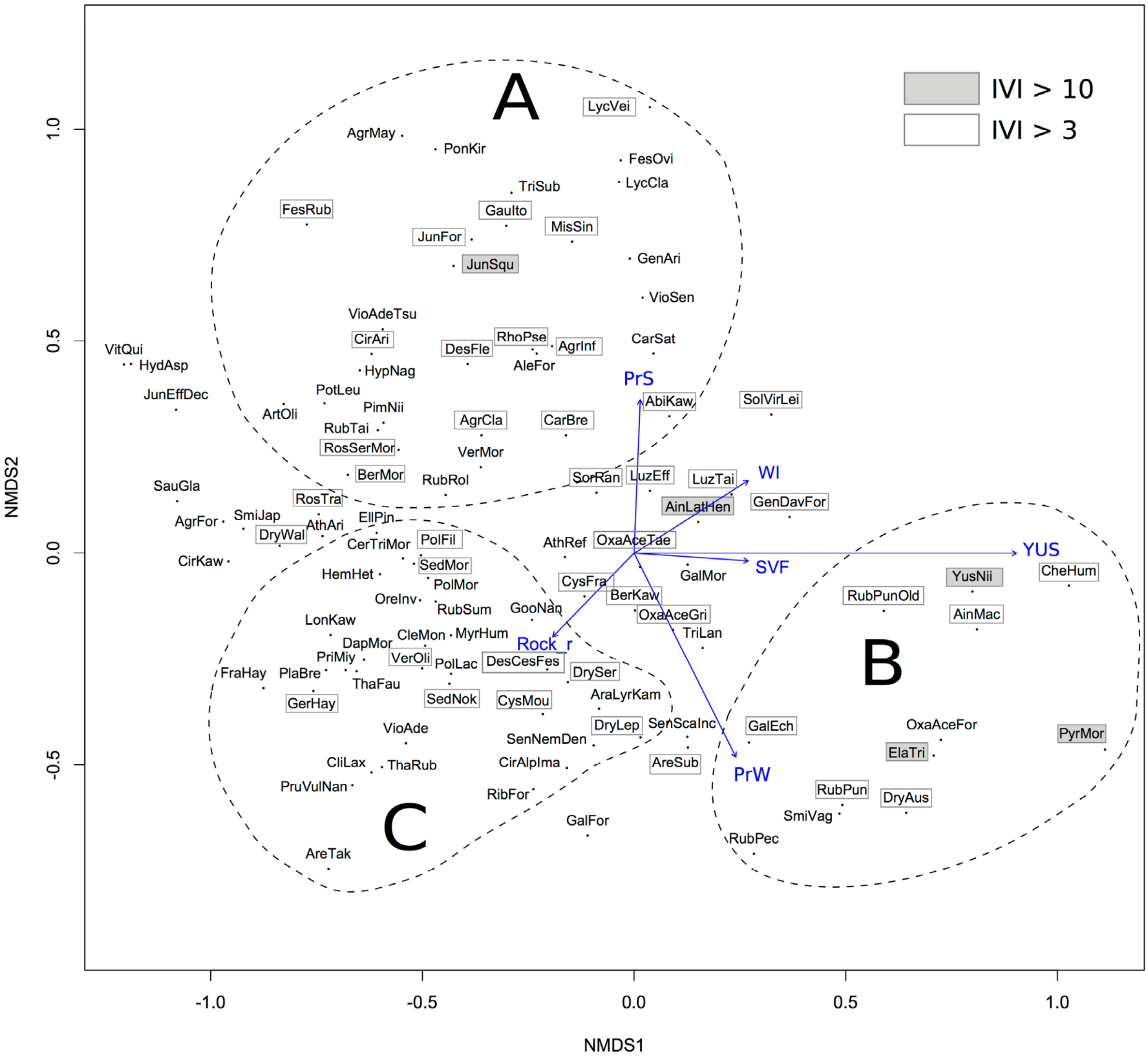

Fig. 2. Non-metric multidimensional scaling (NMDS) ordination of understory species of *Abies kawakamii* forests vegetation. Species are abbreviated with the first three letters of the genus and the specific epithet. The values of important value index (IVI) greater and equal than ten are filled in light-grey background and those IVI greater than three and less than ten are marked with light-grey frame. The biotic and abiotic factors include PrS–precipitation of summer; PrW–precipitation of winter; Rock_r–rock ratio; SVF–sky view factor, which is the index of site openness; WI–Kira's warmth index; YUS–the relative frequency of *Yushania niitakayamensis* (stress=0.223, bray-curtis distance).

Gaultheria itoana Hayata, *Miscanthus sinensis* (Anderson), *Deschampsia flexuosa* (L.) Trin., *Agrostis infirma* Buse, *Rhododendron pseudochrysanthum*, *Juniperus squamata*, etc. Species like *Ainsliaea latifolia* subsp. *henryi* with high IVI value was located around the center of the NMDS diagram and aggregated with *Luzula effusa* Buchen., *L. taiwaniana* Satake, *Oxalis acetosella* subsp. *taemoni* (Yamamoto) Huang & Huang, *Berberis kawakamii* Hayata, etc.

Structural equation modeling

The evaluation indices of our SEM result ($\chi 2$ = 14.066, d.f. = 11, P = 0.229, Table 3) revealed that the overall model performance was statistically acceptable. The error variances of vegetation composition and YUS indicated that our model explains 22% of the variance in the overstory layer, 14% of the variance in the understory layer, and 77% of the *Yushania* cover. Our result identified that YUS was a strong driver to the

Table 1. Species composition table of overstory layer (height ≥ 1.5 m) in *Abies kawakamii* forests. IVI is important value index (average of relative dominance and relative density). Rdo is the average of relative dominance and Rde is the average of relative density.

Species	Abbreviation	IVI	Rdo	Rde
Abies kawakamii	AbiKaw	89.5	93.0	85.9
Juniperus squamata	JunSqu	34.8	32.3	37.3
Rhododendron pseudochrysanthum	RhoPse	11.5	8.6	14.4
Rhododendron pachysanthum	RhoPac	10.3	1.5	19.1
Viburnum betulifolium	VirBet	9.6	5.5	13.7
Sorbus randaiensis	SorRan	9.1	0.6	17.7
Tsuga chinensis var. *formosana*	TsuChiFor	5.1	4.8	5.3
Ribes formosanum	RibFor	2.8	0.2	5.5
Juniperus formosana	JunFor	2.8	1.1	4.5
Pieris taiwanensis	PieTai	1.4	0.1	2.7

understory flora, and the latent variable "climate" of our model determined by WI and PrW (see Fig. 3). The latent variable was also a considerably strong driver to the overstory composition (standardised coefficient = 0.87) and understory composition (standardised coefficient = 0.58), although the coefficient was not significant between latent variable and understory flora. The HLI was significant in the ordination of overstory flora, but it had a negative influence to overstory composition. The latent variable was determined by WI and PrW. WI was an important factor (standardised coefficient = 0.29) but the PrW had an insignificant and weaker coefficient (standardised coefficient = 0.17). The Rock_r had a strong negative influence to YUS, while the PrW had a strong positive influence on it.

DISCUSSION

The influences of abiotic factors on *Abies kawakamii* forests

Our NMDS results identified that the WI and YUS had influential influence on both of canopy and understory species composition. The overstory species can be clearly identified by YUS and WI along the first axis, such as *Juniperus squamata*, *Abies kawakamii*, *Tsuga chinensis* var. *formosana*, and these dominant species are distributed along the elevation gradient (Liu et al., 1984; Su, 1984a). Although elevation plays an important role in vegetation composition and species distribution, WI represent the accumulated temperature for plant growth more effectively, and has been widely applied in species and vegetation distribution in East Asia (Su, 1984a; Song, 1991; Cao et al., 1995; Chen and Huang, 1999; Nakamura et al., 2007). The WI combining with other climatic factors, such as PrW, PrS and minimum temperature of coldest month was also

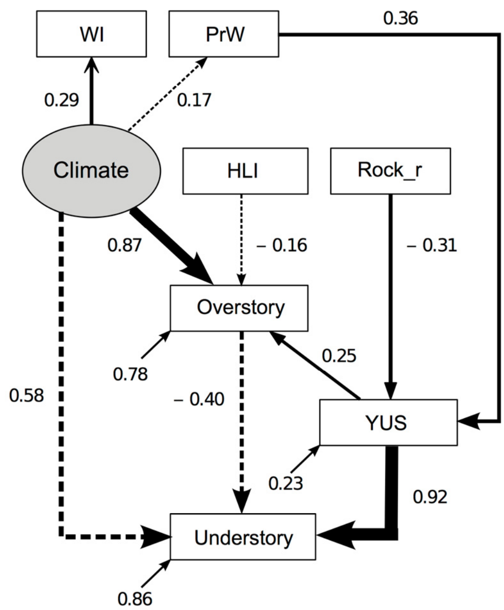

Fig. 3. Structural equation model (SEM) for overstory and understory layers of *Abies kawakamii* forests and environmental factors (χ^2=14.066, d.f.=11, P=0.229). All the pathway coefficients are standardized and the dashed line indicates the pathway coefficient is not significant (p>0.01). The left-bottom arrows of vegetation composition (overstory and understory) and YUS (relative frequency of *Yushania niitakayamensis*) indicate R^2. "Climate" is a latent variable indicated by warmth index (WI) and winter precipitation (PrW). The other observed environmental variables are heat load index (HLI) and rock ratio (Rock_r). Group A includes species of grassland herbs and shrubs in Taiwanese high mountains; group B includes shade-tolerant species which is usually associated with dense *Yushania* in the understorey of *Abies* forests; group C includes species associated with the habitat of high Rock_r.

Table 2. Species composition table of understory layer (height < 1.5 m) in *Abies kawakamii* forests. IVI is the important value index (average of relative dominance and relative frequency). Rdo is the average of relative dominance and Rfrq is the average of relative frequency. The species with IVI value less than three were excluded in this shortened table. See Appendix 1 for complete list of species and IVI values.

Species	Abbreviation	IVI	Rdo	Rfrq	Species	Abbreviation	IVI	Rdo	Rfrq
Yushania niitakayamensis	YusNii	51.8	83.1	20.5	*Geranium hayatanum*	GerHay	3.7	3.4	3.9
Pyrola morrisonensis	PyrMor	12.6	0.3	25.0	*Berberis morrisonensis*	BerMor	3.7	2.2	5.1
Ainsliaea latifolia subsp. *henryi*	AinLatHen	12.4	13.1	11.6	*Agrostis clavata*	AgrCla	3.6	1.5	5.7
Elatostema trilobulatum	ElaTri	10.1	3.4	16.7	*Galium echinocarpum*	GalEch	3.6	0.7	6.5
Juniperus squamata	JunSqu	9.6	12.0	7.3	*Rubus punguns* var. *oldhamii*	RubPunOld	3.6	1.1	6.1
Rhododendron pseudochrysanthum	RhoPse	8.2	9.4	6.9	*Lycopodim clavatum*	LycCla	3.6	2.3	4.9
Abies kawakamii	AbiKaw	7.9	7.5	8.3	*Cheilotheca humilis*	CheHum	3.6	0.4	6.7
Polygonum filicaule	PolFil	6.1	7.0	5.3	*Juniperus formosana*	JunFor	3.6	3.3	3.8
Ainsliaea macroclinidioides	AinMac	6.1	1.3	10.9	*Oxalis acetosella* subsp. *taemoni*	OxaAceTae	3.5	0.02	7.0
Miscanthus sinensis	MisSin	5.5	3.4	7.5	*Berberis kawakamii*	BerKaw	3.5	1.3	5.7
Oxalis acetosella subsp. *griffithii*	OxaAceGri	5.4	1.3	9.5	*Cystopteris moupinensis*	CysMou	3.5	0.9	6.1
Dryopteris wallichiana	DryWal	5.2	4.9	5.5	*Viola senzanensis*	VioSen	3.4	0.7	6.0
Agrostis infirma	AgrInf	4.9	3.3	6.4	*Solidago virgaurea* var. *eiocarpa*	SolVirLei	3.4	0.2	6.5
Deschampsia cespitosa var. *festicioides*	DesCesFes	4.8	2.6	6.9	*Rosa sericea* var. *morrisonensis*	RosSerMor	3.4	2.8	3.9
Cystopteris fragilis	CysFra	4.7	5.2	4.2	*Agropyron formosanum*	AgrFor	3.3	3.8	2.9
Carex breviculmis	CarBre	4.7	2.8	6.5	*Arenaria subpilosa*	AreSub	3.3	0.8	5.9
Sedum nokoense	SedNok	4.6	2.5	6.7	*Rubus pungens*	RubPun	3.3	0.01	6.6
Gaultheria itoana	GauIto	4.6	2.8	6.3	*Luzula effusa*	LuzEff	3.2	0.7	5.8
Oxalis acetosella subsp. *griffithii* var. *formosana*	OxaAceFor	4.5	0.5	8.5	*Fragaria hayatae*	FraHay	3.2	2.2	4.1
Deschampsia flexuosa	DesFle	4.0	1.7	6.2	*Dryopteris austriaca*	DryAus	3.1	0.4	5.9
Sedum morrisonense	SedMor	4.0	2.7	5.2	*Festuca ovina*	FesOvi	3.1	0.6	5.6
Luzula taiwaniana	LuzTai	3.9	1.5	6.3	*Galium formosense*	GalFor	3.1	0.4	5.8
Gentiana davidiana var. *formosana*	GenDavFor	3.8	0.3	7.4	*Dryopteris lepidopoda*	DryLep	3.1	1.3	4.8
Rosa transmorrisonensis	RosTra	3.8	3.4	4.1	*Lonicera kawakamii*	LonKaw	3.1	2.5	3.6
Lycopodium veitchii	LycVei	3.7	0.8	6.6	*Senecio scandens* var. *incisus*	SenScaInc	3.0	0.01	6.0

used to determine the species distribution and their response to climate change (Matsui et al., 2004; Nakao et al., 2011; Su et al., 2012). Our NMDS results revealed that both of the WI and PrW were significant factors. They also determined the latent variable, which was the most important driver on the overstory flora. The PrW is usually controlled by winter monsoon and its amount varies considerably with location in Taiwan (Su, 1984b), and it is an indicator of accumulation of snow in cool temperate regions (Nakao et al., 2011). However, the PrW determined the latent variable had minor contribution compared to the WI in our SEM result. We proposed that the PrW only controlled the overstory composition in windward habitat by monsoon. The HLI identified secondary pioneer species including *Juniperus formosana*, *Ribes formosanum*, *Sorbus randaiensis*, *Pieris taiwanensis* had negative effects in our model. Therefore we could approve that the climatic factors were more influential than the other factors to the vegetation composition of overstory species throughout the SEM process.

The results of NMDS identified three groups of understory flora in *Abies kawakamii* forests. Group A with high richness of understory species and low cover of *Yushania* was distributed along the positive direction of the first axis (Fig. 2) and characterized by relative high PrS. Most species of this group were typically found in high-mountain grassland and scrub vegetation, including *Juniperus squamata*, *J. formosana*, *Rhododendron pseudochrysanthum*, *Agrostis infirma*, *Deschampsia flexuosa*, etc. Group B included shade-adapted species coexisted with *Yushania* and was indicated by high YUS and PrW. The third group C was related to the high Rock_r, and higher PrW compared to group A. Group C also included many fern species, such as *Cystopteris moupinensis*, *Dryopteris lepidopoda* Hayata, *D. serratodentata* (Beddome) Hayata, *Polystichum morii* Hayata, *P. lachenense* (Hook.) Bedd., etc. They were also related to the association *Junipero squamatae-Abietetum kawakamii* Lin et al. 2012, with well-developed moss layer and the absence of *Yushania* in the understory (Lin et al., 2012). These ferns were also indicators of humid microhabitats, because the cracks of rocks could preserve water and provided suitable habitats for ferns.

The influences of *Yushania* on *Abies kawakamii* forests

The only biotic factor in our model was the relative frequency of *Yushania*, which was also a strong factor on the understory composition of *Abies kawakamii* forests. The interactions of *Abies kawakamii* and *Yushania niitakayamensis*, *Picea morrisonicola-Yushania niitakayamensis* or *Tsuga chinensis-Yushania niitakayamensis* depending on different migration processes and biotic interactions (Liu and Su, 1978). In particular, understanding how the understory species are affected by the overstory species is also important to the succession of coniferous forests in high-mountain regions of Taiwan. Our SEM result only showed the negative effect of overstory composition on the understory species. This might be attributed to the scattered microhabitats caused by fragile geology and extreme precipitation in the high mountains.

In summary, our study revealed that the major influential environmental factors in the vegetation composition of *Abies kawakamii* forests were the WI and the PrW, while minor factors were HLI, Rock_r, and PrS. The SEM result suggested that the above WI and PrW were strong indirect drivers to overstory composition and understory flora, but the coefficient between latent variable and understory flora was statistically insignificant. It would be affected by complex composition of understory species. The relative frequency of *Yushania* was also a strong driver to understory composition of the *Abies kawakamii* forests. In addition, the Rock_r was a strong negative driver directly to the relative frequency of *Yushania*, but the PrW was a positive direct factor. The growth and prevalence of *Yushania* would attribute to thick soil, and high habitat rockiness was an indirect factor to affect its cover. *Yushania* were often interpreted as competition in several local studies which often focused on the edge effects of *Abies kawakamii* forests and *Yushania* grasslands (Liu, 1971; Liu et al., 1984). In contrast, abiotic factors including soil thickness, topography and habitat rockiness have also been inferred as the important factors affecting the dominance of *Yushania* (Liu, 1968, 1971). Previous study reported that *Yushania* grassland has been attributed to heavy and acid soil (King et al., 1990a), but the soil properties and mother rocks underlying *Yushania* grassland and *Abies kawakamii* forests with *Yushania* understory were similar (King et al., 1990b). In other words, soil properties may not be the major determinant of the occurrences of *Yushania*. Our study showed that it could be simply interpreted in terms of Rock_r and PrW. Liu (1971) also observed that the prevalence of *Yushania* was associated with habitats with flat topography and relatively thick soil, for *Yushania* can spread widely by underground rhizomes. High soil rockiness and thin soil layer are probably the most important limiting factors for the expansion of *Yushania*.

Our model indicated that the understory floristic composition was determined directly by the relative frequency of *Yushania* rather than canopy flora or climate factors. Lin et al. (2012) classified the *Abies kawakamii*-dominated into three associations based on

Table 3. Structural equation model fit indices and thresholds. The abbreviations are as following: df–degree of freedom; GFI–Goodness-of-fit; AGFI–Adjusted goodness-of-fit; NFI: Bentler-Bonnett normal incremental fit index; TLI–Tucker-Lewis nonnormed fit index; CFI–Bentler's comparative fit index; RMSEA–root mean square error of approximation.

	$\chi 2$	df	$\chi 2$/df	p-value	GFI	AGFI	NFI	TLI	CFI	RMSEA
Model	14.066	11	1.279	0.229	0.960	0.898	0.922	0.963	0.981	0.054
Model-fit threshold	-	-	< 3	> 0.05	> 0.9	> 0.9	> 0.9	> 0.9	> 0.9	< 0.08

understory species composition. In the high-density habitats of *Yushania*, only few shade-tolerant species exist, such as *Ainsliaea latifolia* subsp. *henryi*, *Dryopteris austriaca* (Jacq.) Woynar *ex* Schinz & Thell., *Elatostema trilobulatum*. Some species occurring in the understory of *Abies kawakamii* forests are also widely distributed in the mountainous regions in Taiwan, such as *Ainsliaea latifolia* subsp. *henryi* (elevation ~1000–3800 m a.s.l.), *Cirsium arisanensis* Kitam. (~2000–3800 m a.s.l.), *Elatostema trilobulatum* (~1000–3600 m a.s.l.). Thus, the occurrence of these species would be affected by microhabitats, such as habitat moisture (e.g., *Elatostema trilobulatum* and *Myriactis humilis* Merr. usually distributed in moist and shaded habitats) or geology (e.g. *Sedum morrisonense* Hayata and *Viola adenothrix* usually distribute widely in rocky substrates throughout the mountainous region in Taiwan; Lin, C.-T., personal observation). Su (1974) and Liu and Su (1978) proposed that the climax forests of *Abies kawakamii* forests were developed through succession from *Yushania niitakayamensis-Juniperus squamata* and *Yushania niitakayamensis-Pinus taiwanensis* communities, while *Yushania* was regarded as an early secondary succession species appearing after forest fires. Nevertheless, the open *Yushania* grasslands would proceed to communities of *Pinus taiwanensis-*

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評估非生物因子及玉山箭竹對於臺灣冷杉林植群組成之影響

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摘要：在臺灣高海拔山區，臺灣冷杉（*Abies kawakamii* (Hayata) Ito）為優勢構成的森林分布於海拔三千公尺以上的山地。其植群組成資料來源為國家植群多樣性調查與製圖計畫資料庫（簡稱國家植群資料庫），而環境因子則是使用 WorldClim 及國家植群資料庫。我們使用非計量多元尺度法（non-metric multidimensional scaling）來鑑別臺灣冷杉林的物種組成，並使用結構方程模式來確認臺灣冷杉林與環境因子及玉山箭竹間的複雜因果關係。分析的結果顯示臺灣冷杉植群的組成受到棲地的岩石地比例、熱荷指數（heat load index）、溫量指數（warmth index）以及冬、夏季的降水等影響。結構方程模式之結果則證實了溫量指數及冬季降水是決定潛在變量—氣候的主要驅動變數，而氣候則是影響臺灣冷杉林上層植物組成的顯著的因子。玉山箭竹的相對頻度則是對冠層組成具有部分影響。對於地被植群來說，玉山箭竹的相對頻度則具有高度相關且明顯的影響，而其頻度本身則是受到土壤含石率及冬季降水的影響。此外，冠層植群組成對於地被具有負值且不顯著的相關係數，這可能肇因於臺灣高海拔地區破碎及異質性棲地的影響。

關鍵詞：臺灣冷杉、非生物性因子、植群組成、多變量分析、結構方程模式、玉山箭竹。

Appendix 1. Full species composition table of understory layer in *Abies kawakamii* forests. IVI is the average important value index (average of relative dominance and relative frequency). Rdo is the average of relative dominance and Rfrq is the average of relative frequency.

Species	Abbreviation	IVI	Rdo	Rfrq
Yushania niitakayamensis	YusNii	51.80	83.09	20.51
Pyrola morrisonensis	PyrMor	12.63	0.28	24.99
Ainsliaea latifolia subsp. *henryi*	AinLatHen	12.35	13.06	11.64
Elatostema trilobulatum	ElaTri	10.05	3.41	16.69
Juniperus squamata	JunSqu	9.62	11.98	7.26
Rhododendron pseudochrysanthum	RhoPse	8.16	9.38	6.94
Abies kawakamii	AbiKaw	7.90	7.46	8.33
Polygonum filicaule	PolFil	6.14	7.04	5.25
Ainsliaea macroclinidioides	AinMac	6.09	1.27	10.92
Miscanthus sinensis	MisSin	5.45	3.40	7.50
Oxalis acetosella subsp. *griffithii*	OxaAceGri	5.37	1.29	9.45
Dryopteris wallichiana	DryWal	5.18	4.87	5.49
Agrostis infirma	AgrInf	4.86	3.31	6.40
Deschampsia cespitosa var. *festucifolia*	DesCesFes	4.75	2.57	6.93
Cystopteris fragilis	CysFra	4.68	5.17	4.19
Carex breviculmis	CarBre	4.65	2.76	6.54
Sedum nokoense	SedNok	4.59	2.45	6.73
Gaultheria itoana	GauIto	4.56	2.82	6.29
Oxalis acetosella subsp. *griffithii* var. *formosana*	OxaAceFor	4.52	0.49	8.54
Deschampsia flexuosa	DesFle	3.95	1.74	6.16
Sedum morrisonense	SedMor	3.95	2.68	5.21
Luzula taiwaniana	LuzTai	3.87	1.45	6.30
Gentiana davidii var. *formosana*	GenDavFor	3.84	0.28	7.40
Rosa transmorrisonensis	RosTra	3.75	3.35	4.14
Lycopodium veitchii	LycVei	3.68	0.77	6.59
Geranium hayatanum	GerHay	3.66	3.40	3.93
Berberis morrisonensis	BerMor	3.65	2.18	5.12
Agrostis clavata	AgrCla	3.62	1.54	5.70
Galium echinocarpum	GalEch	3.62	0.70	6.54
Rubus pungens var. *oldhamii*	RubPunOld	3.59	1.11	6.07
Lycopodium clavatum	LycCla	3.57	2.25	4.88
Cheilotheca humilis	CheHum	3.55	0.36	6.74
Juniperus formosana	JunFor	3.54	3.31	3.76
Oxalis acetosella subsp. *taemoni*	OxaAceTae	3.53	0.02	7.04
Berberis kawakamii	BerKaw	3.49	1.28	5.69
Cystopteris moupinensis	CysMou	3.49	0.87	6.11
Viola senzanensis	VioSen	3.36	0.68	6.04
Solidago virgaurea var. *leiocarpa*	SolVirLei	3.35	0.16	6.54
Rosa sericea var. *morrisonensis*	RosSerMor	3.35	2.84	3.85
Agropyron formosanum	AgrFor	3.34	3.83	2.85
Arenaria subpilosa	AreSub	3.33	0.77	5.89

Rubus pungens	RubPun	3.31	0.01	6.61
Luzula effusa	LuzEff	3.24	0.70	5.78
Fragaria hayatae	FraHay	3.16	2.18	4.14
Dryopteris austriaca	DryAus	3.13	0.38	5.88
Festuca ovina	FesOvi	3.08	0.62	5.55
Species	Abbreviation	IVI	Rdo	Rfrq
Galium formosense	GalFor	3.08	0.39	5.76
Dryopteris lepidopoda	DryLep	3.07	1.30	4.83
Lonicera kawakamii	LonKaw	3.07	2.50	3.63
Senecio scandens var. *incisus*	SenScaInc	3.01	0.01	6.00
Sorbus randaiensis	SorRan	2.97	0.55	5.39
Arabis lyrata subsp. *kamtschatica*	AraLyrKam	2.97	0.96	4.97
Viola adenothrix	VioAde	2.96	0.24	5.67
Athyrium arisanense	AthAri	2.94	0.30	5.58
Cirsium arisanense	CirAri	2.93	0.81	5.04
Athyrium reflexipinnum	AthRef	2.90	0.43	5.37
Galium morii	GalMor	2.89	0.28	5.51
Hypericum nagasawai	HypNag	2.85	0.97	4.72
Rubus pectinellus	RubPec	2.83	0.36	5.30
Veronica oligosperma	VerOli	2.82	2.45	3.18
Dryopteris serratodentata	DrySer	2.80	0.29	5.30
Ponerorchis kiraishiensis	PonKir	2.76	0.19	5.32
Trichophorum subcapitatum	TriSub	2.75	1.20	4.31
Potentilla leuconota	PotLeu	2.63	0.54	4.72
Myriactis humilis	MyrHum	2.62	0.23	5.02
Tripterospermum lanceolatum	TriLan	2.61	0.25	4.97
Senecio nemorensis var. *dentatus*	SenNemDen	2.59	0.53	4.66
Ribes formosanum	RibFor	2.59	0.97	4.22
Festuca rubra	FesRub	2.59	2.19	2.98
Veronica morrisonicola	VerMor	2.54	0.77	4.32
Gentiana arisanensis	GenAri	2.49	0.23	4.75
Smilax vaginata	SmiVag	2.47	0.37	4.58
Vitex quinata	VitQui	2.42	0.02	4.81
Clematis montana	CleMon	2.38	0.19	4.58
Hemiphragma heterophyllum	HemHet	2.35	1.47	3.23
Agropyron mayebaranum	AgrMay	2.32	1.07	3.58
Cirsium kawakamii	CirKaw	2.32	0.63	4.02
Circaea alpina subsp. *imaicola*	CirAlpIma	2.28	0.17	4.40
Saussurea glandulosa	SauGla	2.27	0.77	3.76
Carex satzumensis	CarSat	2.22	0.55	3.90
Aletris formosana	AleFor	2.21	0.34	4.07
Thalictrum rubescens	ThaRub	2.12	0.34	3.90
Pimpinella niitakayamensis	PimNii	2.10	0.28	3.92
Oreomyrrhis involucrata	OreInv	2.10	0.28	3.92
Rubus sumatranus	RubSum	2.10	0.18	4.01

Cerastium trigynum var. *morrisonense*	CerTriMor	1.99	0.45	3.54
Clinopodium laxiflorum	CliLax	1.98	1.61	2.35
Thalictrum fauriei	ThaFau	1.98	1.27	2.69
Arenaria takasagomontana	AreTak	1.89	0.46	3.31
Viola adenothrix var. *tsugitakaensis*	VioAdeTsu	1.88	0.51	3.26
Prunella vulgaris subsp. *asiatica* var. *nanhutashanensis*	PruVulNan	1.82	0.51	3.12
Platanthera brevicalcarata	PlaBre	1.81	0.47	3.15
Primula miyabeana	PriMiy	1.78	0.38	3.17
Hydrangea aspera	HydAsp	1.73	0.04	3.41
Ellisiophyllum pinnatum	EllPin	1.63	0.11	3.15
Daphne morrisonesis	Dap Mor	1.63	0.83	2.43
Rubus taitoensis	RubTai	1.63	0.39	2.86
Species	Abbreviation	IVI	Rdo	Rfrq
Polystichum morii	PolMor	1.59	0.27	2.91
Smilacina japonica	SmiJap	1.52	0.87	2.17
Artemisia oligocarpa	ArtOli	1.46	0.18	2.73
Polystichum lachenense	PolLac	1.41	0.07	2.76
Juncus effusus var. *decipiens*	JunEffDec	1.20	0.02	2.39
Goodyera nankoensis	GooNan	0.95	0.03	1.86
Rubus taiwanicolus	RubTai	0.81	0.22	1.41