Study of the Structure and Competitive Coexistence of Subalpine Krummholz Species in Taiwan

Min-Chun Liao,[1] Wei Wang,[1] Hsy-Yu Tzeng[2,3]

【 Summary 】

Structural and spatial patterns of vegetation are essential to understanding the coexistence and competition among species in a community. In Taiwan, subalpine krummholz vegetation comprises 2 dominant species, *Juniperus morrisonicola* and *Rhododendron pseudochrysanthum*. We wanted to determine how these 2 species coexisted within a community on a high mountain in Taiwan. In total, characteristics of 403 individuals of these 2 species were examined at the Xue Mountain Glacial Cirque no. 1. Ripley's K function and a competition index were used to assess the coexistence relationship with intraspecific and interspecific competition between these 2 species. The spatial pattern revealed that trees at distances of 0-2 m had a random pattern, those at distances of 2-3 and 5-13 m had an aggregated pattern, and those at distances of > 13 m also had a random pattern. The sample species' competition index and traits were negatively correlated, indicating that the species with a greater diameter at the base were taller or had larger canopy and may thus have faced less competitive pressure. *J. morrisonicola* had a competitive advantage over *R. pseudochrysanthum*. These 2 species had different life strategies and supported each other through a mosaic distribution and a vertical canopy structure. Thus, they could coexist in a low-temperature, strong-wind, sunlight-intense, resource-deficient subalpine environment.

Key words: shrub, krummholz, spatial structure, coexistence, Xue Mountain Glacial Cirque no. 1.

Liao MC, Wang W, Tzeng HY. 2023. Study of the Structure and Competitive Coexistence of Subalpine Krummholz Species in Taiwan. Taiwan J For Sci 38(3):203-20.

[1] Forest Ecology Division, Taiwan Forestry Research Institute, 53 Nanhai Rd., Zhongzheng Dist., Taipei 100051, Taiwan
林業試驗所森林生態組，100051 臺北市中正區南海路53號。

[2] Department of Forestry, National Chung Hsing Univ, 145 Xingda Rd., South Dist., Taichung 402, Taiwan.
國立中興大學森林學系，402202 臺中市南區興大路145號。

[3] Corresponding author, E-mail: erecta@nchu.edu.tw 通訊作者

研究報告

臺灣亞高山矮盤灌叢植群結構和競爭共存研究

廖敏君[1] 王 偉[1] 曾喜育[2,3]

摘　要

植群的空間結構和型態對於理解植物社會中物種之間共存和競爭關係至關重要。地處亞熱帶臺灣雪山一號圈谷的亞高山矮盤灌叢植群主要包含兩個優勢植物：玉山圓柏 (*Juniperus morrisonicola*) 及玉山杜鵑 (*Rhododendron pseudochrysanthum*)。本研究主要探討為什麼這兩種植物可以在臺灣高山上的植物社會中共存？總計調查403株玉山圓柏及玉山杜鵑個體性狀特徵；並使用Ripley's K函數及競爭指數(CI)分析這兩個物種之間的種內競爭及種間競爭程度。根據Ripley's K水平空間分布顯示，在距離0-2 m處個體呈現隨機分佈，在2-3 m和在5-13 m處個體呈現聚集分佈，然而在距離大於13 m處個體之間也呈現隨機分佈。樣木的競爭指數與植物性狀特徵呈現負相關，表示地徑較大及樹冠幅面積較大的個體，受到較少的競爭壓力。玉山圓柏及玉山杜鵑具有不同的生活策略，且玉山圓柏比玉山杜鵑較具有競爭優勢，因此透過兩兩鑲嵌的分佈及樹冠層結構的相互支持下，能在低溫、強風、強日照且資源匱乏的高山環境中共同生存。

關鍵詞：灌木、矮盤灌叢、空間結構、共存、雪山一號圈谷。

INTRODUCTION

Alpine ecosystems combine elements such as diverse biological species, a population structure, tree boundaries, spatial distributions, tree ring development, plant growth, and microenvironmental changes. These elements are also direct or indirect evidence of global climate change (Hansen-Bristow et al. 1988, Guisan and Theurillat 2000, Grace et al. 2002). Forest lines are considered crucial landscape features at high elevations and latitudes worldwide. With changes in elevation and latitude, the physiognomy of the forest line changes from a continuous-canopy, closed forest to a treeless surface, such as the transition zone between krummholz vegetation and upright stands (Körner and Paulsen 2004, Resler 2006, Bader et al. 2007, Holtmeier 2009, Chiu et al. 2010, Harsch and Bader 2011, Körner 2012, Chiu et al. 2014) and transition zones for different biomes and plant communities (Gosz 1993, Fagan et al. 2003, Körner 2012).

Locations and spatial distributions of subalpine ecosystems reflect the climatic zone, biological boundaries, and the history of the habitat (Harsch and Bader 2011, Körner 2012). Furthermore, the tree species composition of a forest line reflects the influence of

vertical structural changes in climate and different climatic zones' characteristics. Therefore, temperature, humidity, and floristic composition are critical factors determining the composition at forest lines (Grace et al. 2002, Körner and Paulsen 2004, Holtmeier 2009). Holtmeier (2009) indicated that the species present in the "krummholz belt" above coniferous forests depend on the exposure of the mountain slope in the hemisphere. For example, willow scrub and *Rhododendron* species prevail on humid northern slopes. However, on the other side, *Rhododendron* species also live with a mosaic of junipers with mat-like growth that are significant subalpine vegetation, characteristic of sunny slopes in the dry northwest (Holtmeier 2009).

Environmental heterogeneity, stand development stage, competition among individuals and within the population, and seed dispersal and regeneration influence plant communities (Lingua et al. 2008). Thus, the vegetation structure is the result of complex vegetation dynamics. Spatial patterns of different plant communities reflect the type of horizontal forest structure. Random, aggregated, and regular spatial distributions are primary aspects of plant colonization (Heltshe and Ritchey 1984). Ripley's K function (Ripley 1977) used in multi-distance spatial cluster analyses is often used to analyze species' spatial distributions. For example, Camarero et al. (2000) used Ripley's K function to calculate tree-to-tree distances within a 2-dimensional space in subalpine forest pastures of Spain, providing an excellent example of how Ripley's K function can be employed to determine spatial distribution patterns. Zhang et al. (2009) investigated the population structure, spatial patterns, and associations of the species *Abies forrestii* var. *georgei* and *J. squamata* at the tree line and timberline on Mt. Baima Xueshan of the southeastern Tibetan Plateau. Zhao et al. (2008) used Ripley's K function to simulate vertical spatial distributions of different forest layers and tree species in a subtropical evergreen and deciduous broadleaf forest of southwestern Sichuan, China; they demonstrated that under vertical stratification, numerous scale turning points existed for different tree species in each spatial pattern. This phenomenon indicated that the internal structure of the forest stand was closely related to the external environment.

The site of interest in the present study was Xue Mountain Glacial Cirque in Shei-Pa National Park, Taiwan. Since the first scientific report on Taiwan's subalpine glaciers in 1932 (Tanaka and Kano 1934), this area has interested many geologists and ecologists (Hebenstreit 2006, Hebenstreit et al. 2006, Lu and Ou 2009). Diverse plant communities grow on Mt. Xue under harsh climatic conditions; at more than 3000 m above sea level (a.s.l.), the main plant community types are the *A. kawakamii* forest type, *Yushania niitakayamensis-Miscanthus transmorrisonensis* grassland type, and *J. morrisonicola-Rhododendron pseudochrysanthum* krummholz type (Wang et al. 2010). According to Taiwan's vegetation map, this study site is classified as C1A01-*Juniperus* subalpine coniferous woodland and scrub (Li et al. 2013). The present study explored relationships of the horizontal and vertical spatial structures of species using the competition index (CI). This is the first study to examine relationships among the spatial structure, distribution, competition, and coexistence of subalpine vegetation in the high-sunshine, snow-covered, low-temperature environment of high subtropical mountains in Taiwan. The 2 main species growing above the subalpine forest boundary line in Taiwan are *R. pseudochrysanthum* and *J. morrisonicola*. In this mosaic distribution

pattern, species must coexist.

MATERIALS AND METHODS

Study site and sampling

Taiwan is a subtropical continental island in the northwestern Pacific Ocean with numerous mountains from north to south through its central part. The study site is located at Xue Mountain Glacial Cirque no. 1, which is the central peak of Mt. Xue in Shei-Pa National Park, Taiwan (3500-3886 m a.s.l., 121°14′15″E, 24°23′24″N). This cirque has an oval shape and is open on its northeast side, with a maximum length of approximately 1000 m and a maximum width of approximately 600 m. The lowest point of the cirque is on the northeastern side of the long axis (at approximately 3500 m a.s.l.). The bottom of the cirque and the slopes on both sides of Mt. Xue are covered with gravel, which resulted from ice cracking and fragmentation (Hebenstreit 2006, Ho et al. 2010). The plot sampled in this study was located at approximately 3600 m a.s.l. (Fig. 1). Snow covers the study area for approximately 1~2 mon, depending on the temperature and moisture of the northeasterly monsoon. Plants lining the Glacial Cirque no. 1 are affected by strong winds and the snow weight load. The veg-
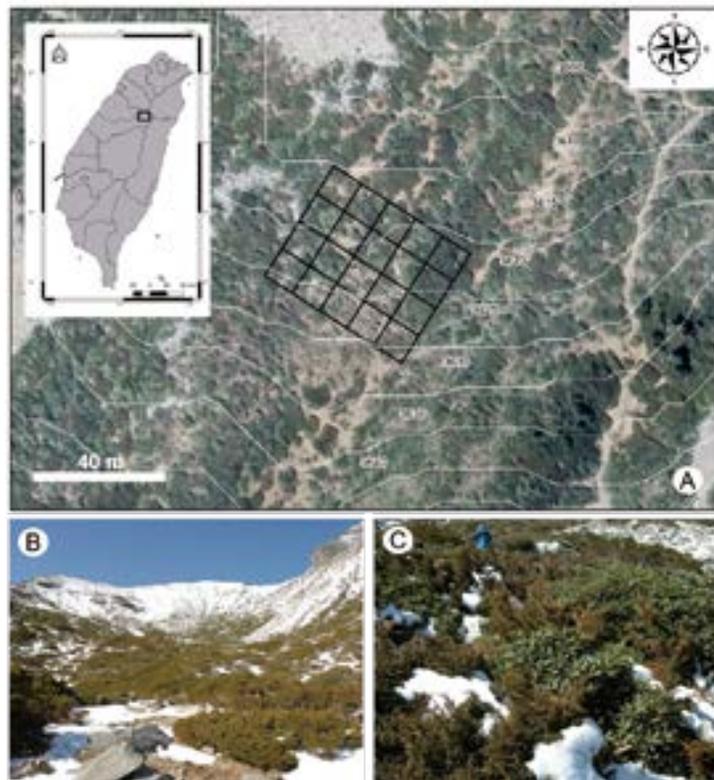
Fig. 1. Location and habitat of the study site, Xue Mountain Glacial Cirque no. 1 of Shei-Pa National Park in north-central Taiwan. (A) Study site of krummholz vegetation; (B) habitat of krummholz vegetation; and (C) coexistence of *Juniperus morrisonicola* and *Rhododendron pseudochrysanthum*.

etation at the study site is characterized as the *J. morrisonicola R. pseudochrysanthum* krummholz type (Chiu et al. 2010, Wang et al. 2010, Lin et al. 2012). Climatic data employed in this study were collected from the Mt. Xue Alpine Ecosystem Monitoring Database (http://syue.biodiv.tw/chi/day.php) and the Central Weather Bureau of Taiwan (https://www.cwb.gov.tw) and subsequently filtered. The annual average temperature at the Xue Mountain Glacial Cirque no. 1 is approximately 4.5 °C. The annual rainfall is approximately 2780.6 mm, and the average humidity is approximately 64%. The mountain is covered in snow from December to April in winter to spring every year (e.g., from December 2009 to December 2012, there were 105 d of snow cover. The average and total snow depths at this duration were 3.2 and 336.7 cm, respectively). Körner and Paulsen (2004) and Paulsen and Körner (2014) revealed that during the global tree growth season, the average soil temperature is 6 °C, limiting vertical tree growth.

Field sampling and diameter at base (DB) classification

We undertook 403 samplings in the plot (plot size 50 × 40 m) at the bottom of the Xue Mountain Glacial Cirque no. 1 in 2009~2010. We investigated individual tree characteristics including the relative position, DB, height, branch height, and crown radius of 8 orientations. Then according to the plant growth pattern, we used a 5-cm DB for 1 class of *J. morrisonicola* and a 3-cm DB for 1 class of *R. pseudochrysanthum* for our analysis.

Spatial pattern analysis

Spatial pattern analysis is currently the most commonly used approach for studying a population's spatial distribution pattern. We used Ripley's K function point pattern to analyze this study's spatial pattern (Ripley 1977, 1981). Using individual plant (target tree) coordinates as the center and a certain length (r) as the radius, the functions of other plants (objective trees) in the circle were calculated, and spatial distributions along different scales were estimated. Furthermore, calculation methods and functions have been modified by many scientists and have been applied to experiments with various designs (Diggle et al. 1976, Haase 1995, Camarero et al. 2000). The research algorithm was as follows:

$$K(t) = \left[\frac{A}{n^2}\right] \sum_{i=1}^{n} \sum_{j=1}^{n} \frac{1}{W_{ij}} I_t(u_{ij}), \text{for } i \neq j \cdots\cdots (1)$$

where A is the plot area containing n plants, I_t is a counter variable that is set to 1 if the distance u_{ij} between plants i and j is $\leq t$ (corresponding to the lag distance), and W_{ij} which is a weighting factor that corrects for edge effects (Haase 1995). Equation (2) shows the square root transformation, $L(r)$, that was employed to linearize $K(t)$ and stabilize its variance. $L(r)$ has an expected value of approximately 0 under the Poisson assumption:

$$L(r) = \sqrt{\frac{K(t)}{\pi}} - t \cdots\cdots\cdots (2)$$

If the value of $L(r)$ is positive and exceeds the confidence interval, an aggregated distribution can be inferred; if it is negative and exceeds the confidence interval, a regular distribution can be inferred; and if it lies within the confidence interval, a random distribution can be inferred. To investigate the relationship between 2-point patterns, we used the $K_{12}(t)$ function to examine bivariate spatial interactions (Moeur 1993). The function is as follows:

$$K_{12}(t) = \frac{n_1 K_{12}(t) + n_2 K_{21}(t)}{n_1 + n_2} \dots\dots\dots\dots\dots\dots\dots\dots (3)$$

where n_1 and n_2 represent the number of events in the 2 classes of points. We used the square root transformation again (Moeur 1993) as follows:

$$L_{12}(r) = \sqrt{\frac{K_{12}(t)}{\pi}} - t \dots\dots\dots\dots\dots\dots\dots\dots (4)$$

Competition index (CI)

We used the CI to analyze the degree of competitive pressure during growth and to predict temporal and spatial changes (Fajardo and McIntire 2007, Nishimura et al. 2010, Das et al. 2011). The CI and distance space relationship can be of 2 types: distance-independent and distance-dependent (Weiner et al. 1990, Sommer and Worm 2002, Shi and Zhang 2003). The CI was initially used to improve stand management. Subsequently, ecologists discovered that the distance between plants considerably affects interplant competition. Therefore, in this study, regarding CI as proposed by Hegyi (1974), plant diameters and the distance between plants were calculated. The following formula was employed:

$$CI_i = \sum_{j=1}^{n} D_j D_i^{-1} L_{ij}^{-1} \dots\dots\dots\dots\dots\dots\dots\dots (5)$$

where CI_i is the CI of sampled plant i, D_j is the diameter of the competitive tree at the ground height (cm), D_i is the diameter of the objective tree at the ground height (cm), and L_{ij} is the distance between the objective and competitive trees.

CI_i represents the competitive pressure exerted by other competitive trees on the target tree; a higher value reflects more-intense competition. A circle centered on the target tree was drawn to select a competitive tree, and objective trees within the circle radius were considered to affect neighboring trees. In most ecological studies, the search radius selected depends on experimental materials. However, when deducing the influence range of an individual plant, further analysis is needed to obtain an objective and reasonable distance. We referenced a variable search radius when the DB was used for the calculation. If the sum of the DB of the competitor and target species divided by 6 is greater than the distance between the 2 species, these individuals are considered competitors (Wang et al. 2021).

RESULTS

Species composition and shrub crown structure analysis

In total, 403 krummholz species, comprising 212 and 191 individuals respectively

Table 1. Basic characteristics of *Juniperus morrisonicola* and *Rhododendron pseudochrysanthum* in this study

Species	No. of Individuals	Diameter at the base (cm)	Height of shrub (cm)	Branch height of shrub (cm)	Shrub crown projection area (m^2)
Juniperus morrisonicola	212	20.58±14.49	97.41±41.85	49.18±26.96	4.30±4.86
Rhododendron pseudochrysanthum	191	9.22±7.02	71.70±29.75	38.33±22.30	2.52±3.01

belonging to *J. morrisonicola* and *R. pseudochrysanthum* were investigated (Table 1). The average number of krummholz species per hectare was 2015 at this study site. The average height of all individuals was 85 cm; those of *J. morrisonicola* and *R. pseudochrysanthum* were 97.4 and 71.7 cm, respectively (Table 1). According to the DB classification, the diameter structures of both *R. pseudochrysanthum* and *J. morrisonicola* were of the reverse-J type (Fig. 2). The average DB of *R. pseudochrysanthum* was 9.2 cm. The 3-6-cm DB class contained the most individual shrubs (51 individuals in total). The over-21-cm DB class included several

individual shrubs; no krummholz species was included in the DB classes of 30, 36, or 39 cm. The average DB of *J. morrisonicola* was 20.58±14.49 cm. The 10-cm DB class contained the most individual shrubs (36 individuals in total). All DB classes ranging from 5 to 25 cm had more than 25 individuals.

According to Table 2, the height and crown area were linearly related; individuals with a larger crown area also had a greater shrub height. The DB and average crown projection area of *R. pseudochrysanthum* were smaller than those of *J. morrisonicola* (Fig. 3). Average crown projection areas of *J. mor-*
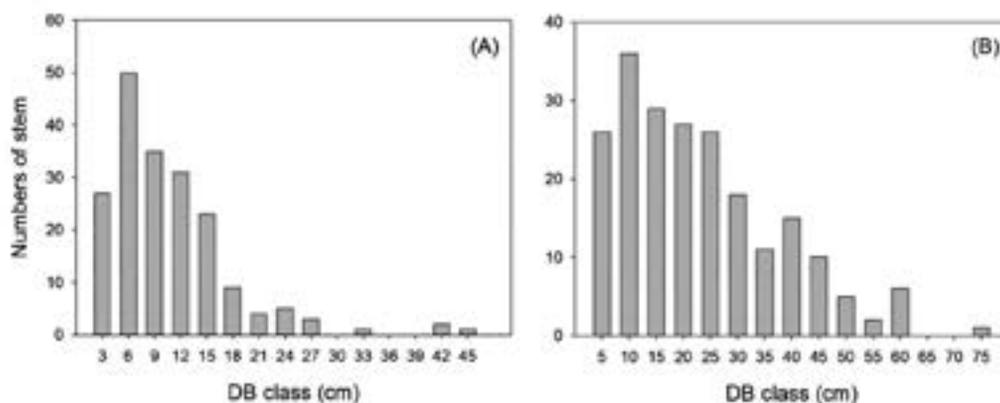
Fig. 2. Diameter at base (DB) classification of krummholz species: (A) *Rhododendron pseudochrysanthum* **and (B)** *Juniperus morrisonicola*.

Table 2. Correlations of characteristics of *Juniperus morrisonicola* **and** *Rhododendron pseudochrysanthum*

Characteristic	Diameter at base	Competition index	Shrub crown projection area	Height of shrub
Competition index	-0.50**			
Shrub crown projection area	0.66**	-0.35**		
Height of shrub	0.63**	-0.33**	0.67**	
Branch height of shrub	0.41**	-0.20*	0.51**	0.56**

* $p < 0.05$, ** $p < 0.01$.

risonicola and *R. pseudochrysanthum* were 4.30±4.86 and 2.52±3.01 m², respectively. The DB, height, and crown projection area were linearly related ($p < 0.05$; Fig. 3).

Spatial distribution analysis

Distribution patterns of all shrubs were determined using Ripley's K function. Results revealed that all individual shrubs within a distance of 0-2 m had a random distribution (Fig. 4), whereas those within distances of 2-3 and 5-13 m had an aggressive distribution. However, the spatial distribution pattern was random when the spatial scale was greater than 13 m. We separately determined the spatial structures of *R. pseudochrysanthum* and *J. morrisonicola.* Results revealed that *R. pseudochrysanthum* individuals aggregated
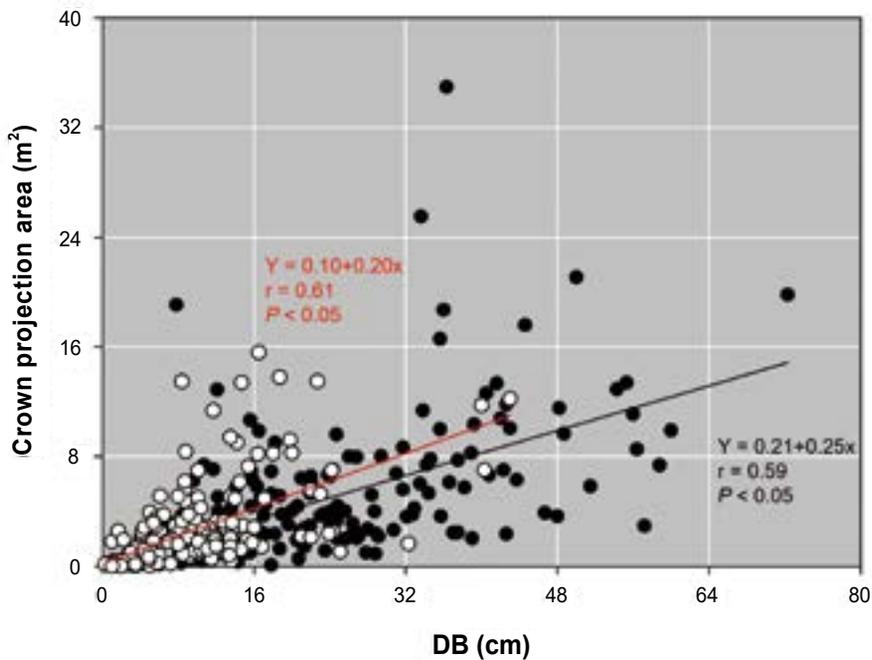
Fig. 3. Correlations between the diameter at base (DB) and crown projection area for (●) ***Juniperus morrisonicola* and (○) *Rhododendron pseudochrysanthum.***

Table 3. Interspecific and intraspecific competition indices (CIs) of species of krummholz vegetation

Species	No. of individuals	Intraspecific CI	Interspecific CI	Total
Juniperus morrisonicola	212	0.12±0.13[*]	0.03±0.04	0.16±0.16
Rhododendron pseudochrysanthum	191	0.23±0.35[*]	0.06±0.08	0.28±0.41

[*] Indicates that the CI was more than another source as examined by the Wilcoxon signed-rank test.

from a small to a large scale (1-19 m) and were distributed at distances exceeding 19 m. *J. morrisonicola* was randomly distributed at distance scales of < 1 m; trees showed an aggregated pattern at distances of 1-8 m and a random pattern at distances of > 8 m (Fig. 4).

Competition index (CI)
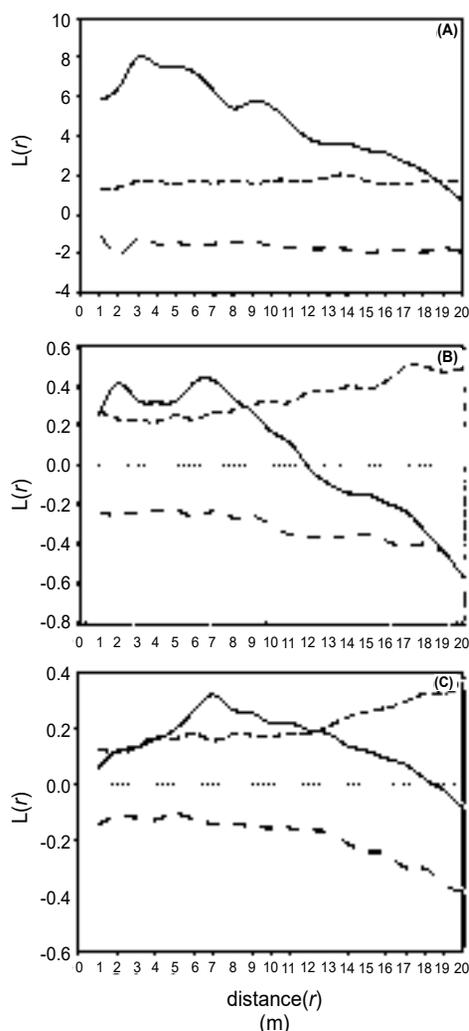
Fig. 4. Ripley's K function pattern analysis of krummholz vegetation for (A) *Rhododendron pseudochrysanthum*, (B) *Juniperus morrisonicola*, and (C) all individuals.

We analyzed the krummholz characteristics, and a significant negative correlation was observed between the CI and certain shrub traits. Significant linear relationships were discovered between the shrub height and DB ($r = 0.63$, $p < 0.05$) and between shrub height and tree crown projection area ($r = 0.67$, $p < 0.05$). A larger DB was associated with a greater shrub crown projection area, and a greater shrub height was associated with low competitive pressure (Table 2). The competitive pressure on *R. pseudochrysanthum* was higher than that on *J. morrisonicola* ($p < 0.05$; Table 3). We considered the study site to be located in a subalpine environment, and shrub height was affected by habitat weather factors.

Using the CI, we evaluated the intraspecific and interspecific competition of *J. morrisonicola* and *R. pseudochrysanthum*. We hypothesized that (1) the CI of intraspecific competitive pressure would be higher than that of interspecific competitive pressure within *J. morrisonicola* and (2) the CI of interspecific competitive pressure would be higher than that of intraspecific competitive pressure within *R. pseudochrysanthum*. *J. morrisonicola* was discovered to have a greater competitive capacity than *R. pseudochrysanthum*. So, the CI of intraspecific competitive pressure was higher than that of interspecific competitive pressure within *J. morrisonicola*, and the CI of interspecific competitive pressure was higher than that of intraspecific competitive pressure within the *R. pseudochrysanthum* population. These results supported the 2 hypotheses mentioned above (Table 3). However, none of the results were significant. Figure 5 shows that most trees with higher CIs had smaller DBs and were located near large trees, whereas shrubs with larger DBs had lower CI values. These findings reveal that intraspecific competitive pressure on the mature population

was higher than interspecific competitive pressure. Most trees with high intraspecific pressure were saplings or seedlings susceptible to environmental and resource effects.

DISCUSSION

Characteristics and growth traits of krummholz plants at the timberline

Böse (2006) compared the late Pleistocene and existing elevated terrain zones of Taiwan and suggested that tree line heights in mountainous regions such as on Mt. Jade, Mt. Nanhuda, and Mt. Xue had increased since the late Pleistocene Epoch. If they were estimated using the equilibrium line elevation (the snow line), the tree line commensurate with the climate should be 4000 m a.s.l. However, the current tree line is mainly located at 3200-3500 m a.s.l., presumably due to frost weathering and mass movements. Therefore, mountainous areas in Taiwan are characterized by the following features: (1) Pleistocene glacial forms, (2) tree lines located on the mountaintops, and (3) debris slopes caused by frost weathering (Böse 2006). Chiu et al. (2010) investigated whether tundra vegetation was present in subtropical Taiwan from an ecological climate perspective and discovered that krummholz vegetation at a modified warmth index of 15 °C under a bioclimatic index above the forest line could be identified simply as tundra vegetation. However, if a finer vegetation categorization was adopted, this type of subalpine vegetation in Taiwan
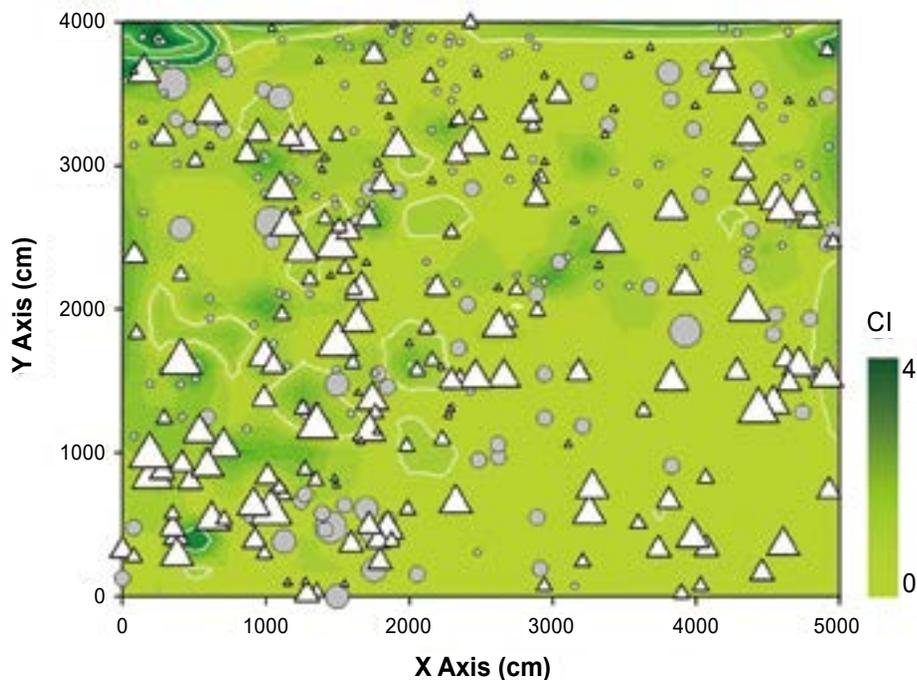
Fig. 5. Competition index patterns of krummholz species in this study. Triangles are *Juniperus morrisonicola* and circles are *Rhododendron pseudochrysanthum*. The size of the symbols indicate classifications of diameter at base.

would not be described as typical tundra vegetation but rather as "krummholz" vegetation. Krummholz vegetation belongs to the forest-tundra ecotone (Hammer and Walsh 2009, Zhang et al. 2009, Körner 2021), although the critical temperature limits its growth, and it cannot reach subalpine forests of subtropical Taiwan. The constant weathering and disintegration of bare rocks on mountain peaks—such as at Mt. Jade, Mt. Xue, and Mt. Nanhu—lead to shallow soils, gravel, or debris; shallow soils are the main reason upright trees cannot survive (Chiu et al. 2010). Therefore, the krummholz community in the subalpine forests of subtropical Taiwan is defined as a "forest line ecotone" community (Harsch and Bader 2011, Chiu et al. 2014).

J. morrisonicola and *R. pseudochrysanthum* are distributed in high montane areas of Taiwan (Wang et al. 2010). Their growth patterns greatly vary depending on the habitat. *J. morrisonicola* can grow into high trees in the leeward direction and usually develops into prostrate subshrubs in the windward direction and on ridgelines (Lin et al. 2012). This species can be considered krummholz (Wang et al. 2010, Lin et al. 2011). *R. pseudochrysanthum* grows into small shrubs in the lower layers of forests and on forest margins, whereas it forms krummholz vegetation in cirques. Both species are the main tree species at the forest line and are crucial topics for research in biology, species conservation, and climate change (Su 1974, Lin et al. 2011, Pan et al. 2013). According to the vegetation grouping of Su (1974), the vegetation community on the Xue Mountain Glacial Cirque mainly comprises shrubs of *J. morrisonicola* and *R. pseudochrysanthum*, with the understory vegetation consisting of *Deschampsia flexuosa, Potentilla tugitakensis, Berberis morrisonensis,* and *Veronica morrisonicola* (Lin et al. 2011). Because of the sampled plot's

relatively flat terrain and stability, the topsoil contained small amounts of humus, providing sufficient water for shrubs to survive. Thus, *J. morrisonicola* and *R. pseudochrysanthum* were the dominant trees as krummholz vegetation at the study site, with several flag-like trees distributed among them.

J. morrisonicola can live for over 2000 yr (Su 1974), whereas *R. pseudochrysanthum* can last only a few hundred to approximately 1000 yr. According to DB classes in this study, more *J. morrisonicola* and *R. pseudochrysanthum* individuals belonged to the small-diameter class, and the distributions of these 2 species were both a reverse-J-type pattern. The vegetation community should theoretically be supplemented from saplings, although numbers of both species in the smallest diameter class were lower than those in the second-smallest diameter class, indicating a declining trend in the number of saplings. Also, results of Lin et al. (2011) who performed field observations and those of the present study both demonstrated that seedlings of the 2 species are incredibly scarce. This signifies the difficulty in supplementing saplings for the 2 species, reflecting that the relatively harsh environment of cirques complicates the establishment of seedlings and indicates the sampled plot's microtopographic effects. The smallest diameter class in the DB classification may have included asexually reproducing plants of the 2 species that exhibited a krummholz growth pattern (Körner 2021), which requires further investigation through plant physiological research. In addition to innate differences in the growth patterns of the 2 species (Lin et al. 2011, 2012), we discovered that the average ground diameter of *J. morrisonicola* (21 cm) was significantly larger than that of *R. pseudochrysanthum* (9 cm), indicating the superiority of *J. morrisonicola* over *R. pseu-*

dochrysanthum; thus, larger species have a greater competitive advantage (Canham et al. 2004).

Horizontal spatial patterns and vertical structural associations

Determining the spatial distribution of vegetation communities is crucial to understanding their dynamics, because their horizontal spatial distributions can indicate whether the communities compete (Watt 1947). Results of the spatial distribution revealed that although all plants in the sampled plot were randomly distributed at the smallest scale, those between the small scale and mesoscale had an aggregated distribution. In addition to individual competitiveness, the environment could be a significant factor contributing to these shrubs' spatial distribution. The harsh environmental conditions in the studied region could have resulted in the successful renewal of seedlings and saplings only occurring when parent trees provided shelter for those younger plants. Furthermore, the microtopographic effect of the sampled plot caused differences in the spatial distribution of plants; that is, low-lying areas become waterways or watersheds when the snow melts, leading to difficulties in establishing seedlings. However, the spatial distributions of distinct tree species were influenced by the species' biological features, such as seed dispersal and germination, resulting in different spatial distribution patterns of the 2 dominant tree species.

Both *J. morrisonicola* and *R. pseudochrysanthum* are endemic to Taiwan (Li et al. 1998, Adams 2014). *J. morrisonicola* bears large berry-like seed cones, and it is wind pollinated; by contrast, *R. pseudochrysanthum* has capsular fruits with numerous tiny, winged seeds and is pollinated by bumblebees. Spatial distributions of individual *J.*

morrisonicola in the sampled plot varied with the distance between individual plants. At the spatial scale in the investigated region, individual plants were distributed along a distance scale of 1-8 m and exhibited an aggregated distribution, whereas those in the remaining scales had a random distribution. This may be related to the dependence of plants on the foraging behavior of rodents, which leads to the indirect dispersal of residual seeds (Lin et al. 2011). *R. pseudochrysanthum* had an aggregated distribution at all distance scales, which may be partly related to wind dispersal of its tiny seeds (Pan et al. 2013). The successful establishment of seedlings also mostly depends on symbiosis with mycorrhiza fungi (Cairney and Meharg 2003, Zhong and Yu 2012). Even if the tiny seeds of the *R. pseudochrysanthum* parent shrub are dispersed to a suitable environment by wind, if seedlings are established too far away from the parent tree, the lack of growth assistance from mycorrhiza fungi during the initial germination stage may endanger the seedlings once seed nutrients have become depleted.

The spatial distribution of plants of varying sizes (ages) may be influenced by the microtopography. Figure 5 shows that *J. morrisonicola* and *R. pseudochrysanthum* with higher canopy strata and greater ground diameters were mainly located on the plot's left and right sides, whereas the center of the sampled plot was composed of shrubs with lower crown strata and bare areas. Onsite topographic interpretation revealed that the microtopographic structure was higher on both sides than at the plot's center, and the plot's midline was near the bottom of the cirque, adjacent to its lower opening. Despite the low elevation of the study site, snow beds usually form at the end of the snow season, and the late melting of these snow beds causes the annual growth of

plants in the area to begin later than those in surrounding regions. In addition, the formation of waterways due to snow melting and glacial erosion following rising temperatures leads to difficulties establishing individual plants and their survival. Quinton et al. (2004) described how snow accumulation in alpine areas during winter initiates runoff that causes constant disturbance to the debris slope. Plants at the midline of the plot may be disturbed by the runoff of melted snow or ice sheets, complicating the survival of *J. morrisonicola* and *R. pseudochrysanthum* seedlings, which is disadvantageous to population establishment. This result was reflected in plants with smaller ground diameters at the center of the plots with more unused space.

In addition to microtopographic effects, an interaction between the northeast monsoon and terrain was identified by Chiou et al. (2010) as a factor affecting the distribution pattern of mid-to-high-elevation species in Taiwan. The 45° azimuth of the cirque is oriented to the northeast and is affected by the northeasterly monsoon all year long. Monsoon winds not only cause prostration in *J. morrisonicola* and *R. pseudochrysanthum* in the cirque but also result in a considerable canopy shift; canopy growth directions are also affected by alternations in the mountain-valley wind direction between daytime and nighttime. Canopy shifts may affect seedlings' spatial distribution characteristics during their establishment (Chen and Chang 2007). The prevailing northeasterly monsoon and mountain-valley winds may have affected *R. pseudochrysanthum* seed dispersal, which relies on these winds.

All woody plants and *J. morrisonicola* trees in the center of the plot exhibited an aggregated distribution at the mesoscale, which might be attributable to the dispersal of plant propagules or constraining factors during seedling establishment. Accordingly, the biological characteristics of the species and its environmental conditions should be considered when determining the spatial scale of the aggregated distribution. Suppose the species is located in a resource-poor and barren environment. Most vegetation communities gradually shift to a random distribution at larger spatial scales, and the absence or presence of plants may be influenced by environmental factors when the spatial scale exceeds a specific threshold. Due to the short distance limitation of saplings and the effects of parent trees, the correlation between individual plants is low, and *J. morrisonicola* may even exhibit a uniform distribution at larger spatial scales, revealing negative correlations among individual trees of the plant community at large spatial scales. Canham et al. (2004) stated that because tree species with larger diameters are mostly survivors of each growth period, individual plants maintain a specific distance from each other; thus, the CI is low, and correspondingly, the CI of plants with greater diameters or age is low following an increase in time. Also, Kikvidze et al. (2011) employed the stress-gradient hypothesis to determine the intensity of competitive interactions among high-elevation plants and concluded that this interaction did not change with increasing elevation; thus, the spatial distribution at the microscale can also predict the pattern formed as a result of interactions between plants.

Competition and coexistence of krummholz vegetation

The types of CI have been analyzed by numerous scholars, who have divided CIs into distance-dependent and distance-independent CIs (Shi and Zhang 2003). Li et al. (2002) reported that after a mature group has

experienced long-term growth and long-term intraspecific competition, seedlings grow in a suitable fertile place following natural seeding, although competition is also the strongest in this circumstance. Following the passage of time and an increase in the space available after the death of plants due to competition, more environmental and spatial resources are available to plants; thus, trees exhibit a uniform distribution. Intraspecific competitive pressure is more significant than interspecific competitive pressure. However, the present study discovered that although intraspecific competition was more significant than interspecific competition for *J. morrisonicola*, the difference was nonsignificant; competition may have been affected by other environmental factors. The competition level between individual plants depends on the environment; in particular, a harsher environment leads to more-intense competition between individual plants, resulting in no significant difference in intraspecific and interspecific competition.

With sufficient intraspecific aggregation, competing species can coexist, even when interspecific competition within neighborhoods is greater than intraspecific competition (Silvertown and Charlesworth 2001). Competition theory has 6 coexistence mechanisms: resource partitioning, spatial segregation, recruitment limitations, pest-pressure, storage effects, and density-independent mortality (Silvertown and Charlesworth 2001). If intraspecific competition is stronger than interspecific competition for all competitors, coexistence conditions can be met without niche separation (Silvertown and Charlesworth 2001). In this study, competing species could coexist with sufficient intraspecific aggregation, even when interspecific competition within neighborhoods was stronger than intraspecific competition.

Nishimura et al. (2010) proposed that reversals in competitive superiority between different growth stages and the trade-off between longevity and turnover are more-crucial factors in the coexistence of these species than is regeneration niche differentiation related to canopy gaps in a sub-boreal coniferous forest.

Competition should be the main factor causing the death of trees, and if it is genuinely the factor influencing inter-tree competition, dead wood should have been found in the sampled plot (Das et al. 2011). However, the CI of *J. morrisonicola* and *R. pseudochrysanthum* was low, and no dead-wood was discovered within the sampled plot, indicating the adaptability and tolerance of both species to the harsh environment, and that the individual competition process did not cause much pressure in terms of death. The 2 species' growth patterns exhibited environmental adaptability (Lin et al. 2011, Pan et al. 2013). Rhododendron's traits—such as the specific leaf area, size, and thickness—significantly differed depending on the environment (Chang et al. 2018). In a study on the groundcover composition of a Taiwan fir forest in Taiwan, Tseng and Tzeng (2016) discovered that *R. pseudochrysanthum* seedlings appeared in gaps and non-gap sampled plots and was nonselective in the undergrowth environment, indicating the high adaptability of this species to the environment.

The alpine environment is extremely harsh, involving snow accumulation (Nykanen et al. 1997), strong winds (Chen et al. 2007, Chiou et al. 2010), intense radiation, and dryness, which considerably affect the growth of trees. The canopy height and width of *J. morrisonicola* and *R. pseudochrysanthum* have long been affected by the pressure of accumulated snow and wind, and their distributions have evolved into distort-

ed patterns. This study verified that the CI was significantly negatively correlated with krummholz characteristics, indicating that a greater individual DB was associated with a more-significant shrub canopy and that a greater individual height was associated with lower competitive pressure on individual plants. Although the environment limited the height of trees investigated in this study, the DB, tree height, and canopy projection area of shrubs were all significantly linearly related; thus, trees with a more-massive canopy can obtain more environmental resources and have a more-significant advantage (Fraver et al. 2014).

Although the competitive ability of *J. morrisonicola* is superior to that of *R. pseudochrysanthum*, the 2 species can coexist in the subalpine environment and support each other through their mosaic distribution canopy structure (Figs. 1, 5). The following explains why the 2 species coexist in the Xue Mountain Glacial Cirque no. 1. (1) The seed dispersal mechanism affects krummholz vegetation's spatial patterns because of species' life strategies in the subalpine environment. The wind forms species' life strategies of both tree line and insect-pollinated taxa (Körner 2012). *J. morrisonicola* is a wind-pollinated taxon, whereas *R. pseudochrysanthum* is an insect-pollinated taxon. These 2 species can support each other in windy and snowy environments through the vertical structure of the tree height and tree crowns. *J. morrisonicola* has a longer lifespan in the habitat and thus produces more giant seeds, whereas the time for *R. pseudochrysanthum* to reach reproductive age and produce comparatively sized seeds is shorter. Finally, *J. morrisonicola* has a K-reproductive strategy. In contrast, the strategy of *R. pseudochrysanthum* is R-reproductive. (2) A harsh environment and deficiency of resources reduce competitive pressure for both species regardless of their strengths and life strategies.

CONCLUSIONS

Krummholz falls within the scope of subalpine ecosystem research; however, studies on the spatial distribution and competition of krummholz species are lacking. Because krummholz vegetation forms a specific type of tree line (Harsch and Bader 2011), Holtmeier (1981) argued that krummholz vegetation has a shrub shape due to its genes, whereas tree species that form a prostrate state due to climate factors should be known as crippled trees. Most studies collectively refer to shrubs in a prostrate state as krummholz. Therefore, tree species in subalpine areas have weaker growth potential and require a greater capacity and higher competitiveness to acquire environmental resources for survival. This study discussed the environmental factors, such as strong winds and snow accumulation in the subalpine climate, that cause this prostrate state of krummholz vegetation at the Xue Mountain Glacial Cirque no. 1. However, seedlings from parent plants in a rocky terrain develop into genetic clones in the adjacent space when covered by rocks (Böse 2006); errors may be present in the analysis and determination of the individual spatial distributions of clones. Thus, molecular biotechnology should be applied in future studies.

ACKNOWLEDGMENTS

Hsing University (NCHU), for help with the field investigation.

LITERATURE CITED

Adams RP. 2014. *Juniperus* of the world: The genus *Juniperus*, 4th ed. the United States of America Trafford.

Böse M. 2006. Geomorphic altitudinal zonation of the high mountains of Taiwan. Quat Int 147(1):55-61.

Bader MY, Rietkerk M, Bregt AK. 2007. Vegetation structure and temperature regimes of tropical alpine treelines. Arct Antarct Alp Res 39(3):353-64.

Cairney JWG, Meharg AA. 2003. Ericoid mycorrhiza: a partnership that exploits harsh edaphic conditions. Eur J Soil Sci 54(4):735-40.

Camarero JJ, Gutierrez E, Fortin MJ. 2000. Spatial pattern of subalpine forest-alpine grassland ecotones in the Spanish Central Pyrenees. For Ecol Manag 134(1-3):1-16.

Canham CD, LePage PT, Coates KD. 2004. A neighborhood analysis of canopy tree competition: effects of shading versus crowding. Can J For Res 34(4):778-87.

Chang YC, Tseng YH, Wang W, Tzeng HY, Pan CC. 2018. Variation of leaf traits of *Rhododendron pseudochrysanthum* along an altitudinal gradient at the East Xue Trail of the Xue Mountain. Q J For Res 40(3):191-210. [in Chinese with English summary].

Chen CT, Chang WY. 2007. Spatial heterogeneity of tree crown in Nanjenshan secondary forest. Q J For Res 29(2):27-42. [in Chinese with English summary].

Chiou CR, Song GZM, Chien JH, Hsieh CF, Wang JC, Chen MY, et al. 2010. Altitudinal distribution patterns of plant species in Taiwan are mainly determined by the northeast monsoon rather than the heat retention mechanism of Massenerhebung. Bot Stud 51:89-97.

Chiu CA, Lee MF, Tzeng HY, Liao MC. 2014. A concise scheme of vegetation boundary terms in subtropical high mountains. Afr J Agri Res 9(20):1560-70.

Chiu CA, Tseng YH, Wang CC, Liao MC, Tzeng HY. 2010. Deliberation of Taiwanese alpine tundra vegetation and its possible position based on an ecoclimatic viewpoint. Q J For Res 32(3):89-102. [in Chinese with English summary].

Das A, Battles J, Stephenson NL, van Mantgem PJ. 2011. The contribution of competition to tree mortality in old-growth coniferous forests. For Ecol Manage 261(7):1203-13.

Diggle PJ, Besag J, Gleaves JT. 1976. Statistical analysis of spatial point patterns by means of distance methods. Biometrics 32(3):659-67.

Fagan WF, Fortin MJ, Soykan C. 2003. Integrating edge detection and dynamic modeling in quantitative analyses of ecological boundaries. BioSci 53(8):730-8.

Fajardo A, McIntire EJB. 2007. Distinguishing microsite and competition processes in tree growth dynamics-a priori spatial, modeling approach. Am Nat 169(5):647-61.

Fraver S, D'Amato AW, Bradford JB, Jonsson BG, Jonsson M, Esseen PA. 2014. Tree growth and competition in an old-growth *Picea abies* forest of boreal Sweden: influence of tree spatial patterning. J Veg Sci 25(2):374-85.

Gosz JR. 1993. Ecotone hierarchies. Ecol Appl 3(3):370-6.

Grace J, Berninger F, Nagy L. 2002. Impacts of climate change on the tree line. Ann Bot 90(4):537-44.

Guisan A, Theurillat JP. 2000. Assessing alpine plant vulnerability to climate change: a modeling perspective. Integr Assess 1:307-20.

Haase P. 1995. Spatial pattern analysis in ecology based on Ripley's K-function: intro-

duction and methods of edge correction. J Veg Sci 6(4):575-82.

Hammer ES, Walsh SJ. 2009. Canopy structure in the krummholz and patch forest zones. In: Butler DR, Malanson GP, Walsh SJ, Fagre DB editors. The changing alpine treeline: the example of Glacier National Park, MT, USA. Amsterdam: Elsevier. p 119-50.

Hansen-Bristow KJ, Ives JD, Wilson JP. 1988. Climatic variability and tree response within the forest-alpine tundra ecotone. Ann Assoc Am Geogr 78(3):505-19.

Harsch MA, Bader MY. 2011. Treeline form−a potential key to understanding treeline dynamics. Glob Ecol Biogeogr 20(4):582-96.

Hebenstreit R. 2006. Present and former equilibrium line altitudes in the Taiwanese high mountain range. Quat Int 147(1):70-5.

Hebenstreit R, Böse M, Murray A. 2006. Late Pleistocene and early Holocene glaciations in Taiwanese mountains. Quat Int 147(1):76-88.

Hegyi F. 1974. A simulation model for managing jack-pine stands. p. 74-90 in Fries, J. (Ed.) Growth Models for Tree and Stand Simulation. Royal College of Forestry, Department of Forest Yield Research, Research Notes 30. Stockholm, Sweden.

Heltshe JF, Ritchey TA. 1984. Spatial pattern detection using quadrat samples. Biometrics 40(4):877-85.

Ho LD, Chen SH, Chyi SJ. 2010. Taiwan's quaternary mountain glacier retreat models. J Geogr Sci 59:19-38. [in Chinese with English summary].

Holtmeier FK. 1981. What does the term krummholz really mean? observations with special reference to the Alps and the Colorado Front Range. Mount Res Develop 1(3/4):253-60.

Holtmeier FK. 2009. Mountain timberlines--ecology, patchiness, and dynamics. Advances in global change research. The Netherlands: Springer.

Körner C. 2012. Alpine treelines: functional ecology of the global high elevation tree Limits. Basel, Switzerland: Springer.

Körner C. 2021. Alpine plant life: functional plant ecology of high mountain ecosystems. 3rd ed. Berlin and Heidelberg, Germany: Springer-Verlag.

Körner C, Paulsen J. 2004. A world-wide study of high altitude treeline temperatures. J Biogeogr 31(5):713-32.

Li CF, Chytrý M, Zelený D, Chen MY, Chen TY, Chiou CR, et al. 2013. Classification of Taiwan forest vegetation. Appl Veg Sci 16(4):698-719.

Li HL, Lu SY, Yang YP, Tseng YH. 1998. Ericaceae. Flora of Taiwan. 2nd ed. Vol 4:31. Taipei, Taiwan, the Editorial Committee of the Flora of Taiwan.

Li XK, Ou ZL, Ning SJ, Su ZM, Tang RQ, Li RT. 2002. A quantitative study on intraspecific and interspecific competition in *Abies yuanbaoshanensis* community. J Plant Resourc Environ 1:20-4.

Lin CC, Tzeng HY, Tsai ST, Wang CC, Wang W, Lu KC. 2011. Study on plant community of *Juniperus morrisonicola* forest at Cuei-Chih Area in Mt. Shye. Q J For Res 33(4):33-50. [in Chinese with English summary].

Lin CC, Tzeng HY, Wang CC, Tsai ST, Lu KC. 2012. Stand structure of *Juniperus morrisonicola* forest at Cuei-Chih Area in Mt. Shye. Q J For Res 34(1):53-62. [in Chinese with English summary].

Lingua E, Cherubini P, Motta R, Nola P. 2008. Spatial structure along an altitudinal gradient in the Italian central Alps suggests competition and facilitation among coniferous species. J Veg Sci 19(3):425-36.

Lu KC, Ou CH. 2009. Alpine ecosystem integrative survey in Xue Mountain. Taiwan: Shei-Pa National Park Headquarters. [in Chi-

nese with English summary].

Moeur M. 1993. Characterizing spatial patterns of trees using stem-mapped data. For Sci 39(4):756-75.

Nishimura N, Kato K, Sumida A, Ono K, Tanouchi H, Iida S, et al. 2010. Effects of life history strategies and tree competition on species coexistence in a sub-boreal coniferous forest of Japan. Plant Ecol 206(1):29-40.

Nykanen ML, Peltola H, Quine CP, Kellomaki S, Broadgatem M. 1997. Factors affecting snow damage of trees with particular reference to European conditions. Silva Fennica 31(2):193-213.

Pan CC, Tseng YH, Chiu CA, Tzeng HY. 2013. Phenology of *Rhododendron pseudochrysanthum* in Mt. Xue. Q J For Res 35(2):71-86. [in Chinese with English summary].

Paulsen J, Körner C. 2014. A climate-based model to predict potential treeline position around the globe. Alp Bot 124:1-12.

Quinton WL, Carey SK, Goeller NT. 2004. Snowmelt runoff from northern alpine tundra hillslopes: major processes and methods of simulation. Hydrol Earth Syst Sci 8(5):877-90.

Resler LM. 2006. Geomorphic controls of spatial pattern and process at alpine treeline. Prof Geograph 58(2):124-38.

Ripley BD. 1977. Modelling spatial patterns. J Roy Stat Soc Ser B (Methodol) 39(2):172-212.

Ripley BD. 1981. Spatial statistics. Hoboken, NJ: J Wiley & Sons.

Silvertown JW, Charlesworth D. 2001. Introduction to plant population biology. 4th ed. the United States of America, Wiley-Blackwell.

Shi H, Zhang L. 2003. Local analysis of tree competition and growth. For Sci 49(6):938-55.

Sommer U, Worm B. 2002. Competition and coexistence. Ecological Studies vol 161. Berlin and Heidelberg, Germany: Springer-Verlag.

Su HJ. 1974. The communities of *Juniperus squamata* in the alpine regions of Taiwan. Bull Exp For Natl Taiwan Univ. 113:101-12.

Tanaka K, Kano T. 1934. Glacial topographies in the Nankotaizan Mountain group in Taiwan. Geogr Rev Jpn 10(3):169-90. [in Japanese].

Tseng SH, Tzeng HY. 2016. Assessing the gap dynamics in a subalpine forest on Xue Mountain through aerial orthophotos. Q J For Res 38(4):227-40. [in Chinese with English summary].

Wang W, Chiu CA, Tsai ST, Hsu CK, Tzeng HY, Lu KC. 2010. Vegetation research along the East Trail of Mt. Shei. Q J For Res 32(3):15-34. [in Chinese with English summary].

Wang W, Liao MC, Tzeng HY. 2021. Competition in *Abies kawakamii* forests at subtropical high mountain in Taiwan. Plos One 16(7):e0254791. https://doi.org/10.1371/journal.pone.0254791.

Watt AS. 1947. Pattern and process in the plant community. J Ecol 35(1/2):1-22.

Weiner J, Berntson GM, Thomas SC. 1990. Competition and growth form in a woodland annual. J Ecol 78(2):459-69.

Zhang Q, Zhang Y, Peng S, Yirdaw E, Wu N. 2009. Spatial structure of alpine trees in mountain Baima Xueshan on the southeast Tibetan Plateau. Silva Fennica 43(2):197-208.

Zhao AJ, Hu TX, Huang CD, Chen XH. 2008. Spatial point pattern characteristics of mountainous evergreen and deciduous broad-leaved forest. J Zhejiang For Sci Tech 28:1-7. [in Chinese with English summary].

Zhong LF, Yu SJ. 2012. Research progress on Ericoid mycorrhiza. JASTA 14(3):145-50. [in Chinese with English summary].