

Article

Vegetation Types Attributed to Deforestation and Secondary Succession Drive the Elevational Changes in Diversity and Distribution of Terrestrial Mosses in a Tropical Mountain Forest in Southern China

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Abstract: (1) Background: Detailed diversity information regarding terrestrial mosses in a tropical forest ecosystem and an understanding of the drivers behind moss distribution provide crucial data for the management and conservation of forest ecosystems. Mosses are critical components of tropical forest ecosystems due to their high diversity and biomass, and they also fulfill essential ecological functions. Here, we report the first study into the relative importance of vegetation types and elevational gradient for the diversity, distribution and community structure of terrestrial moss species in southern China. (2) Methods: Five elevations spaced 200 m apart in the tropical mountain forest on the northern aspect of Tai Mo Shan were selected. The diversity, distribution, and geographical patterns of terrestrial mosses in response to altitudinal changes were examined. Differences in the biotic variables of terrestrial mosses between elevations were tested using a one-way ANOVA. Curve estimation regression models were used to describe the responses of the biotic variables to the elevation gradient. Canonical correlation analysis (CCA) was performed to identify and measure the associations among biotic variables of terrestrial mosses and abiotic environmental factors. (3) Results: Fifty-three terrestrial moss species belonging to 20 families and 31 genera were recorded along the altitudinal gradient on Tai Mo Shan. Microclimate factors including dew point and rainfall were strongly associated with the cover and thickness of the ground moss species. There were no obvious richness changes of terrestrial mosses along the elevation gradient. In total, 33 of the 51 species were tropically distributed, 14 species were found across East Asia and the tropical regions, 10 species had an East Asian pattern and 8 were temperate species. (4) Conclusions: Vegetation types significantly affect the diversity and distribution of terrestrial moss species. Although they are influenced by the East Asian and temperate climate with frequent human activities, terrestrial mosses on Tai Mo Shan are primarily tropical in nature. Forest conservation and restoration should be implemented to sustain and improve the diversity of terrestrial mosses and understory plants on Tai Mo Shan, especially at higher elevations.

Keywords: diversity and distribution; elevational gradient; growth; vegetation types; southern China; terrestrial mosses; tropical mountain forest



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1. Introduction

Bryophytes encompass more than 20,000 species recorded worldwide, of which more than 12,000 are mosses [1]. Tropical forest ecosystems harbor the highest biodiversity of all terrestrial habitats [2–4]. More than 40% of bryophytes occur in tropical habitats [5], which are hotspots and well-suited to the exploration of the potential influences of global climate change on moss diversity [6] from unexpectedly high rates of habitat degradation and biodiversity loss [7]. Mosses are critical components of tropical forest ecosystems due to their high diversity and biomass [8–11]. They also play critical roles in serving

as pioneer plants in soil development [12–14], nutrient cycling [15,16], the regulation of hydrology [17,18], vegetation restoration and succession [19,20]. However, compared with their non-vascular epiphyte counterparts, terrestrial mosses appear to be neglected in ecological studies, especially in terms of the relationship between biotic and abiotic variables [21,22]. Under the threat of habitat fragmentation and drastic global warming [23], the detailed diversity mapping of terrestrial mosses in montane forest and an understanding of the underlining drivers will provide crucial data for the management and conservation of forest ecosystems [24].

Environmental variables, specifically rainfall, relative humidity and temperature, vary along elevation gradient, resulting in the distribution of different ecosystems [25], which might exert a strong impact on the biotic communities of terrestrial mosses. Forest characteristics such as ground cover and canopy closure are two factors that affect terrestrial moss diversity [26,27]. Deforestation and vegetation development are other factors influencing moss species diversity patterns [28]. Terrestrial moss species are intimately dependent on the external environment due to their morphological and physiological specificities and have a wide geographic distribution because of the interactions of their dispersal history, climatic and environmental fluctuations and habitat availability. These make them the best candidates for depicting elevational zonation studies of forest ecosystems, as they are found from sea level to mountain peaks (with an elevational diversity gradient) [8,29–33].

Perspectives on factors influencing the diversity and distribution of terrestrial mosses in mountain forest ecosystem are still controversial. Although non-vascular epiphyte richness and distribution have been explored in many regions, ecological studies of terrestrial mosses in mountain forest ranges in tropical Asia are generally lacking. The cover and thickness of terrestrial mosses are two important parameters of the growth condition of moss species and are indicative of their responses to climate change. In addition, the distribution patterns of moss species can provide baseline information, which may reflect the physiological adaptation to their current habitats and possibly imply the potential response to predicted climate change. The vegetation types have changed greatly from 100 m to 900 m asl on Tai Mo Shan due to deforestation and subsequent secondary succession (Table 1), presenting us with different habitats. The objectives of this study were (1) to investigate the terrestrial moss community characteristics (composition, cover and thickness) and their distribution pattern on Tai Mo Shan in Hong Kong; (2) to analyze the phytogeographical characteristics; and (3) to assess if vegetation types are the major factor influencing moss diversity and distribution, and to provide implications for the conservation of terrestrial mosses.

Table 1. Environmental and climatic factors along the altitudinal gradient ($n = 3$).

Altitude	AT	DP	RH	RF	pH	GC	CC	WS	VT
100	27.2 a	23.4 a	84.8 d	1838 b	4.99 a	89.3 c	88.8 b	12.3 b	Dense broad-leaved lowland woodland (<i>Glochidion hongkongense</i>)
300	25.4 b	22.6 b	88.2 c	1917 ab	4.68 b	94.7 a	90.0 a	5.30 d	Dense broad-leaved lowland woodland (<i>Syzygium levinei</i>)
500	23.9 c	22.0 c	91.8 b	1992 ab	4.27 c	92.0 b	88.7 c	7.70 c	Dense broad-leaved low-hill forest (<i>Cinnamomum porrectum</i>)
700	23.2 d	21.9 c	92.6 ab	2077 ab	4.54 b	53.5 e	41.9 e	25.9 a	Grassland with small montane shrub patches (<i>Miscanthus sinensis</i>)
900	21.0 e	19.7 d	93.4 a	2271 a	4.60 b	68.4 d	45.0 d	25.3 a	Grassland with dense montane shrub patches (<i>Miscanthus sinensis</i>)

Values followed by different letters are significantly different ($p < 0.05$) among various altitudes. Altitude: m above sea level; AT: °C mean daily air temperature; DP: °C dew point; RH: % relative humidity; RF: mm rainfall; GC: % ground cover; CC: % canopy closure; WS: wind speed km/h; VT: vegetation type (with most dominant species for each elevation within brackets).

2. Materials and Methods

2.1. Study Area

Hong Kong is in the eastern Pearl River Delta of the South China Sea, 22°9′–22°33′ N, 113°50′–114°26′ E, with a territory of 1104 km². It lies 130 km south of the Tropic of Cancer and features a humid subtropical climate with distinct hot humid and cool dry seasons. Despite its small area, there are distinct horizontal and vertical climatic gradients in Hong Kong. The primary evergreen or semi-evergreen monsoon forests that used to cover Hong Kong were cleared 400 years ago, except for some small, undisturbed patches in elevated, remote and steep regions [34,35].

Hong Kong is one of the most densely populated places in the world, with less than 25% of the total land area being urbanized. A generally hilly to mountainous terrain with steep slopes occupies approximately 75% of the total land area. Undeveloped land is found in very few plane areas and consists mostly of secondary forests, grassland, shrubland or farmland [36–39]. About 40% of the undeveloped land area is designated as country parks and nature reserves [40]. Despite the small total extent of Hong Kong and the massive amount of human disturbance, diverse flora and fauna still survive [37,41]. A diverse ecosystem exists in this region, with more than 3000 species of vascular plants, of which 300 are endemic to Hong Kong [42,43]. The known bryophyte flora of Hong Kong consists of 372 species from 70 families and 159 genera, of which 238 are mosses and 134 are liverworts and hornworts [44].

Tai Mo Shan is the highest peak in Hong Kong, with an elevation of 957 m. It has an area of 1440 hectares and is situated in the Tai Mo Shan Country Park in the center of the New Territories, Hong Kong. Due to the height of the mountain, Tai Mo Shan is claimed to be Hong Kong's most misty area, as it is often covered in clouds. It is not uncommon for temperatures to drop below the freezing point during the winter [45]. The vegetation types in our study sites along the elevation gradient change greatly from lowland to the peak. Dense broad-leaved lowland woodlands are mainly distributed in hilly areas below 400 m, with the dominant species *Glochidion hongkongense* and *Syzygium levinei* at 100 m and 300 m, respectively. Dense broad-leaved low-hill forests are mostly located on uplands between 400 m–550 m. The species *Cinnamomum porrectum* is dominant at 500 m elevation. Grasslands are widely found at upper slopes above 550 m to the peak. At 700 m, small montane shrub patches are distributed, with the grass species *Miscanthus sinensis* being dominant. At 900 m and near the peak, dense montane shrub patches or montane forest patches exist, with *M. sinensis* again the commonest species. The area has become one of the major forest plantations with mainly native species selected in Hong Kong, starting from 2013 [46]. Trees planted here are mostly native species, such as *Ficus microcarpa*, *Endospermum chinense*, *Syzygium levinei*, *Antidesma bunius*, *Psychotria asiatica* and *Aquilaria sinensis*, with other non-natives, such as *Pinus massoniana*, *Acacia confusa*, *Lophostemon confertus* and *Melaleuca quinquenervia*. Forests are limited to a maximum altitude of 550 m, while the upper slopes are dominated by shrubs and grasses [35].

2.2. Moss Sampling

In April 2018, five sampling elevations were selected from the northern aspect of Tai Mo Shan (Figure 1), with an elevation interval of 200 m from 100 ± 20 m to 900 ± 20 m along the altitudinal gradient. Three 100 m transects were set up approximately 20 m apart at each altitude along the contour line according to vegetation type and accessibility, and six 0.5 m × 0.5 m quadrats were established along each transect line at intervals of ~20 m. All quadrats were marked using nylon threads. At each selected elevation, all three transects were homogenous and comparable to each other regarding vegetation type, canopy height and closure, ground cover and microclimate. Quadrats were moved to the nearest suitable location if boulders or dead wood occurred on the transect lines.

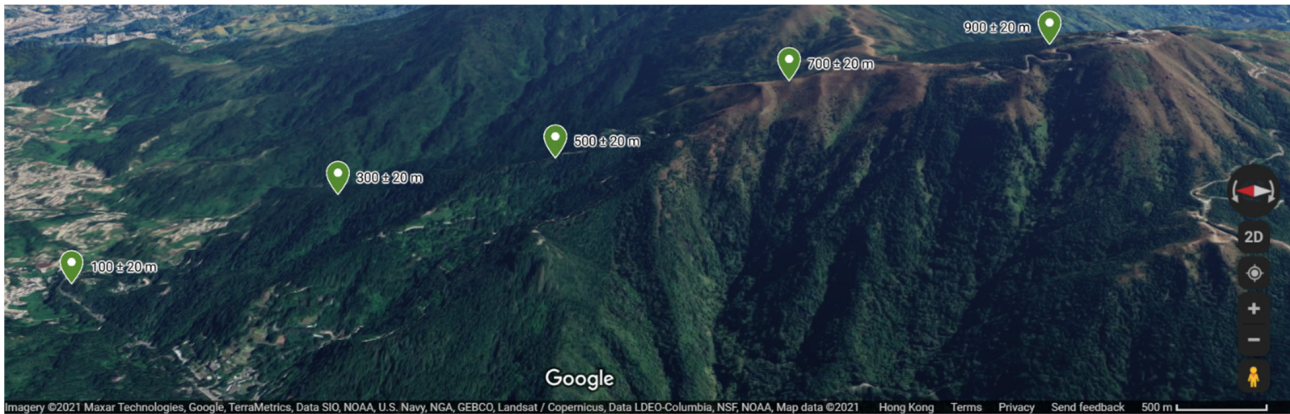
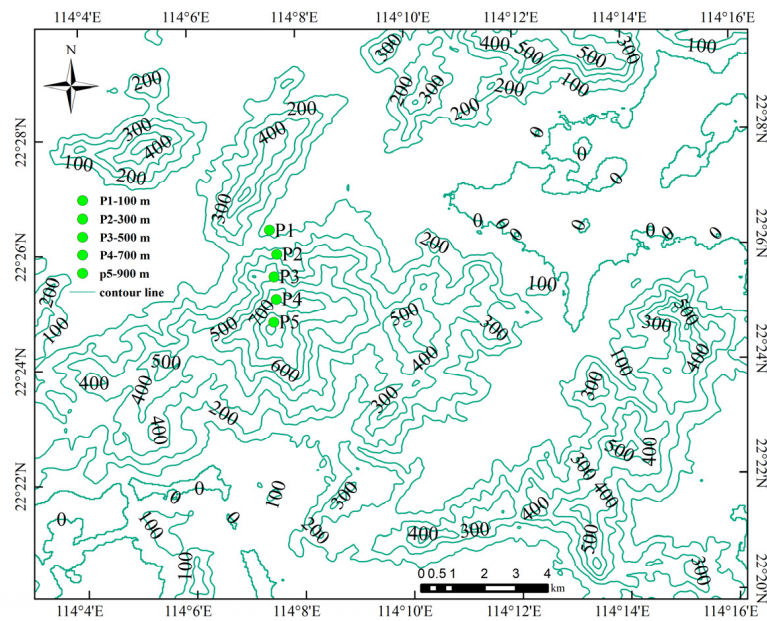


Figure 1. Map showing the study site on Tai Mo Shan in the central part of Hong Kong (**upper**), and Google map with the five sampling points on Tai Mo Shan from 100 m to 900 m with elevation intervals of 200 m (**lower**).

Field surveys were carried out from June to August in 2018 and 2019. Species composition, thickness, cover and life forms (such as tuft, tail, weft, mat and cushion) were examined in the 90 quadrats. For moss cover measurement, a transparent plastic sheet with 25 grid cells of 0.1 m × 0.1 m was placed on each quadrat. The percentage cover of terrestrial moss species was estimated based on the number of grids occupied by terrestrial mosses with an area cover larger than 50%. The thickness (height) of the moss layer was recorded in the four cardinal directions and the center of the quadrats. Moss species in each quadrat along each transect were collected and stored in paper bags for identification in the laboratory after June 2018. Moss specimens were identified under a microscope (YS100; Nikon) in the laboratory, and the nomenclature followed that in [47,48].

The geographical distribution of the recorded species was obtained from the data of the Discover Life (<https://www.discoverlife.org/> accessed on 19 July 2021), GBIF (<https://www.gbif.org/> accessed on 19 July 2021), eFlora (<http://www.efloras.org/index.aspx> accessed on 19 July 2021) and other published databases. A phytogeographical pattern division method of bryophytes with revised and more detailed tropical division was also adopted in this study to supplement data interpretation [49]. Each species was assigned to a phytogeographical pattern on the basis of its present worldwide distribution.

2.3. Environmental and Climatic Factors

Environmental and climate data (including air temperature, relative humidity (RH), rainfall, dew point and wind speed) at each site were obtained from a local weather station if possible. For two elevations (500 and 700 m asl) from the northern aspect, weather data were not available, and climate parameters were measured at the self-deployed weather stations or were estimated according to the nearest meteorological station. Three mini weather stations were set at each elevation to collect the air temperature, dew point, relative humidity, rainfall and wind speed. Vegetation type, canopy closure, ground cover and geographic location were recorded at each sampling site. Canopy closure was determined using the densiometer method by standing in the center of each quadrat and counting at the four cardinal directions of the sampling point [50]. The number of grids with >50% plant coverage in each direction was counted, and the average calculated. Ground cover was measured from images obtained from a densiometer mirror by placing it in the center of each quadrat. Soil pH was measured using a glass electrode after shaking a 1:2.5 solution (soil to water ratio) for approximately 30 mins [51]. The environmental and climatic factors along the altitudinal gradient are presented in Table 1.

2.4. Statistical Analysis

Species richness, cover and thickness were averaged for each transect line and elevation for statistical analysis. All environmental variables were averaged for each elevation. All statistical tests were performed using SPSS (Version 26.0; IBM). Data were checked for deviation from normality and homogeneity of variance before analysis. Differences in richness, cover and the thickness of terrestrial mosses among elevation gradients were tested using a one-way ANOVA and Tukey's HSD. Curve estimation regression models were used to describe the response of biotic variables such as species richness, cover and thickness to the elevation gradient with cubic and quadratic models. Durbin-Watson test was performed to check self-correlation in the environmental variables before canonical correlation analysis. Canonical correlation analysis (CCA) was performed to identify and measure the associations among biotic variables and environmental factors, including altitude, air temperature, dew point, relative humidity, rainfall, canopy closure, ground cover, soil pH and wind speed, using the MANOVA syntax command [52,53].

3. Results

3.1. Species Composition

A total of 134 specimens were collected from 90 quadrats and identified to belong to 53 species in 31 genera and 20 families (Appendix A Table A1). The terrestrial moss richness of different transect lines across the elevation gradient ranged from 3–10 species (Appendix B Table A2). The terrestrial moss community cover ranged from 7.2% to 23.8%, and the highest value was observed at the peak of Tai Mo Shan (Appendix B Table A2). *Pogonatum inflexum* dominated at 100 m, while *Pseudotaxiphyllum pohliaecarpum* was the most common species at 300 and 500 m asl, and *Hypnum plumaeforme* dominated at the peak. No dominant species was found at 700 m asl. Plant thicknesses at different altitudes ranged from 3.2 mm to 8.6 mm and increased with elevation. The most common families were Dicranaceae (consisting of three genera and seven species), Leucobryaceae (consisting of two genera and six species), Thuidiaceae (consisting of two genera and five species), Sematophyllaceae (consisting of three genera and five species) and Hypnaceae (consisting of four genera and seven species) (Appendix A Table A1).

3.2. Distribution of Terrestrial Mosses along the Elevation Gradient

Differences in species richness along the elevation gradient were not statistically significant ($F = 1.245$, $p = 0.353$, Table 2). No obvious trend was found between moss richness and elevation ($R = 0.541$, $p = 0.264$ for the cubic model, $R = 0.389$, $p = 0.374$ for the quadratic model, Figure 2a). By contrast, moss cover along the transect lines differed significantly with altitude ($F = 43.331$, $p < 0.001$, Table 2). Plant thickness differed

significantly along the elevation gradient ($F = 29.145$, $p < 0.001$, Table 2). Moss cover ($R = 0.892$, $p < 0.001$ for the cubic model, $R = 0.812$, $p < 0.01$ for the quadratic model, Figure 2b) and thickness ($R = 0.960$, $p < 0.001$ for the cubic model, $R = 0.953$, $p < 0.001$ for the quadratic model, Figure 2c) increased nonlinearly with the increasing elevation. The moss plants grew better with increasing elevation, and the highest cover and thickness occurred at the peak of Tai Mo Shan.

Table 2. One-way ANOVA showing the composition and distribution of terrestrial mosses along the elevation gradient ($n = 3$).

Site	Altitude (m asl)	Species Richness	Cover (%)	Thickness (mm)
1	100	8.0 ± 1.2 a	15.0 ± 1.0 b	3.23 ± 0.3 b
2	300	7.7 ± 1.2 a	10.4 ± 0.2 c,d	3.23 ± 0.2 b
3	500	7.0 ± 0.6 a	12.3 ± 1.8 b,c	3.47 ± 0.3 b
4	700	5.0 ± 1.2 a	7.2 ± 0.1 d	5.07 ± 0.5 b
5	900	7.7 ± 1.2 a	23.8 ± 0.6 a	8.60 ± 0.7 a

Values followed by different letters are significantly different ($p < 0.05$) among various sites.

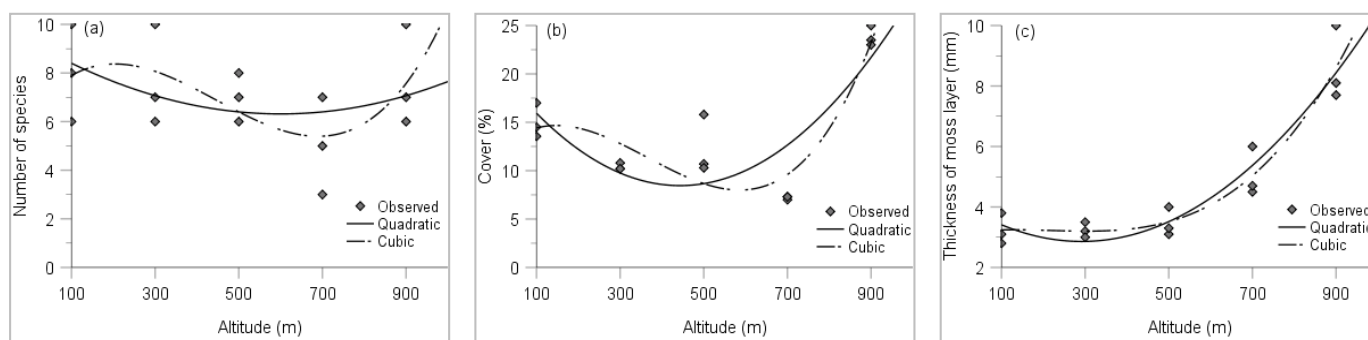


Figure 2. Characteristics of terrestrial moss distributed along the elevation gradient; (a): species richness along elevational gradient; (b): cover of terrestrial moss species along elevational gradient; (c): thickness of moss layer along elevation gradient.

3.3. Life Form Composition

Four different life forms were identified at the different study elevations of Tai Mo Shan. Smooth mat was the dominant moss life form overall, followed by turf (Appendix A Table A1). Different life forms prevailed at the five elevations. Smooth mat was the dominant life form at 100 m asl, turf and mat were dominant at 300 m asl, and cushion was dominant at 500 m asl. Weft, turf and mat life forms were common at 700 m asl, while at the peak, weft was most prevalent (Figure 3 and Appendix A Table A1).

3.4. Phytogeographical Elements

Nine elements of phytogeographic patterns were identified for all terrestrial mosses found in this study (Figure 4 and Tables A1 and A3). Excluding the cosmopolitan species, 33 of the 51 species were tropical, 14 species were continuously distributed between East Asian and tropical regions, 10 species had an East Asian pattern and 8 species were northern temperate (Table 3). *Dicranodontium didymodon* was the only species endemic to China.

Table 3. General phytogeographical elements of terrestrial moss species on Tai Mo Shan.

General Patterns	Moss Species (% Total)	Patterns in Appendix C Table A3
Tropical	33 (64.7%)	2, 3, 4, 5, 7
East Asian	24 (47.1%)	5, 6, 7, 9
Temperate	8 (15.7%)	8
Total	51	

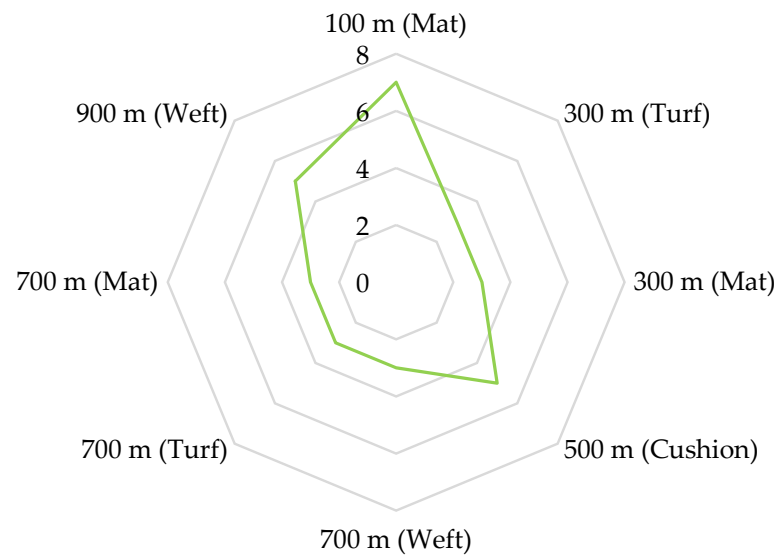


Figure 3. Dominant life forms of terrestrial mosses at five elevations.

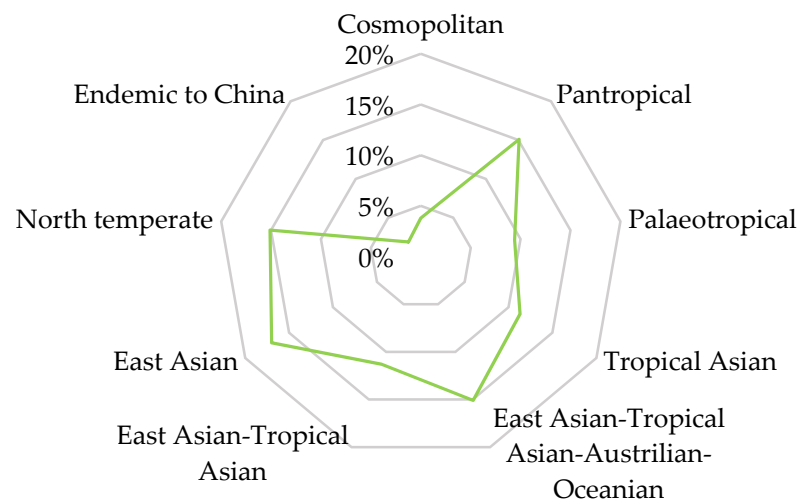


Figure 4. Nine phytogeographical elements of terrestrial mosses on Tai Mo Shan.

3.5. Environmental Variables and Species Composition

The results of Durbin–Watson test ranged from 1.5–2.5, which showed no self-correlations among the environmental variables. Based on the canonical correlation analysis results, canonical variables for biotic and environmental variables were strongly associated ($r_1 = 0.99$, $p < 0.001$; $r_2 = 0.93$, $p = 0.015$) (Figure 5 and Tables A4–A6). The first canonical coefficient explained 84.9% of the variance in the correlation and showed that the canonical variable for biotic factors (primarily coverage and thickness) was strongly related to the dew point (negative) and rainfall (positive) and, to a lesser extent, air temperature (negative) (Figure 5a). The first canonical variable for biotic factors explained 57% of the variance in these factors, whereas that for abiotic factors explained 28% of the variance. The second canonical variable suggests that the canonical factor for species richness was strongly related to ground cover and canopy closure (positive for the previous two) and, to a lesser extent, relative humidity, wind speed and altitude (negative for the latter three) (Figure 5b). The second canonical variable for biotic factors explained 24% of the variance in these factors, and that for abiotic factors explained 48% of the variance in the environmental factors.

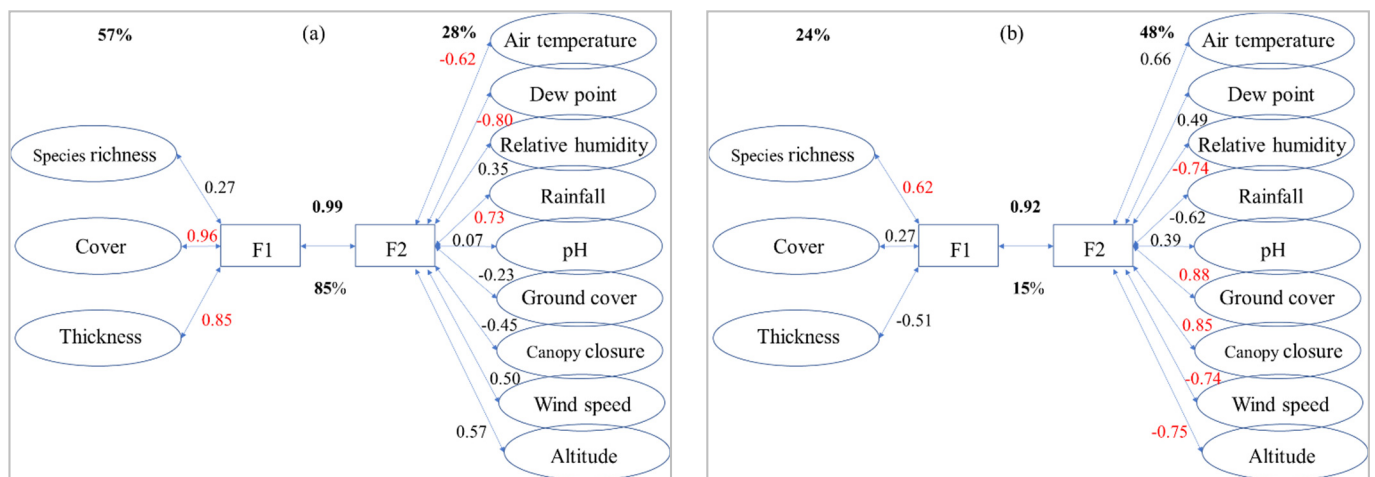


Figure 5. Structure of the first (a) and second (b) canonical variables sets of the CCA.

4. Discussion

In total, 53 terrestrial moss species from 20 families and 31 genera were found in the Tai Mo Shan, which has distinct horizontal and vertical climatic gradients. This species number is relatively low due to the fact that this study was conducted in a secondary mountain forest with a smaller number of moss species on grasslands at the higher elevations and that we focused only on terrestrial mosses, in contrast to the previous findings of tropical primary forest regions, which included not only mosses, but lichens, liverworts and other epiphytes [54,55].

Elevational diversity gradients differ among various organisms in different habitats [10]. Vegetation types might explain why no obvious species abundance changes of ground moss diversity was found in the present study. Due to the large-scale deforestation centuries ago, with subsequent secondary succession, different habitats developed along the elevation gradient with different climatic conditions and vegetation types, resulting in unique and fragmented habitats which is not conducive to the dispersal and colonization by mosses [7,56]. Forests are limited to a maximum altitude of 550 m asl; the upper slopes are dominated mainly by grasses and montane shrub patches or montane forest patches with significantly lower ground cover, canopy closure and higher wind speed in contrast to that of lowland woodlands and low-hill forest at the lower elevations. The results in Table 1 showed that the two most open habitats at 700 and 900 m most clearly stood out from the other three, which suggested that the observed species compositional patterns were mainly determined by basic ecological differences of each habitat between elevations. Ground cover and canopy closure were two factors that affected the terrestrial moss diversity, which was in line with the previous findings [26,27]. Bryophytes are often regarded as shade plants, with the ability to photosynthesize effectively under low photosynthetically active radiation, even for species in open habitats [57–59]. Excess exposure therefore inhibits the colonization and growth of terrestrial mosses [60–62]. Water loss increases at approximately the square root of the wind speed [63]. Consequently, a high wind speed will curb the development and growth of terrestrial mosses. Therefore, the two open habitats at higher elevation, especially at 700 m, featured less rich diversity of terrestrial mosses. Massive disturbance has influenced species diversity patterns, as large-scale deforestation and different vegetation developments have existed along elevation gradient in this region, which supported the findings of present study [28]. From the CCA results (Figure 5, Tables A4–A6), rainfall and altitude were negatively related to species richness, which indicated that vegetation types outweighed the positive effect of optimal environmental conditions of higher elevations [24,64–66]. No obvious trend was observed, whether increasing [29,31,33,54,55], decreasing [67] or a hump-shaped distribution [9,65,68] upon increasing elevation. The scale effect might explain the difference between these

patterns. When the elevation gradient is relatively long, a hump-shaped distribution instead of a linear pattern will occur [65,69]. However, in addition to climatic variables such as rainfall [70] and temperature [71], biotic variables such as productivity [72], competition [73] and resource abundance [74] also correlate with the elevational diversity of plants and animals.

The moss layer developed better at higher elevations, and the highest cover and thickness occurred at the peak, indicating optimum environmental conditions [69]. A thicker moss layer is often associated with high cover in some species, which consequently results in higher biomass. Therefore, cover and thickness are two important parameters to model the biomass of bryophytes [69]. The important role of air temperature, dew point, rainfall and relative humidity in bryophyte growth might be due to their poikilohydry [75], and the water content is a primary factor for bryophyte productivity [76,77], whereas increasing temperature decreases moss cover [78,79]. Table 1 shows that the environmental variables including the development of different vegetation types varied significantly along the altitudinal gradient, resulting in different habitats. The effect of altitude can be explained by differences in habitats along the elevation gradient. At altitudes higher than 550 m, herbaceous plants and litter at montane grassland have a good moisture-holding capacity and nutrient availability, thus favoring the growth of ground bryophyte species [80]. Ground cover may be a better factor than canopy closure for more realistically reflecting the microclimate of ground moss species. Moss cover was significantly related to elevation, which is in line with the findings in tropical rain forests [81] and the Appalachians in eastern North America [33].

The life form of bryophytes is driven by different environmental pressures to minimize water loss to maximize net carbon dioxide uptake [82]. The life form of bryophytes is closely related to humidity and light and, to a lesser extent, temperature [83]. Short turfs and cushions were predominant in brightly lit habitats. Tails and fans were observed in the shade beneath the tropical rain forest. In the case of mats and wefts, the capillary retention of water predominates with respect to physiological activity, especially photosynthesis, which enables these life forms to extend their duration of being fully active beyond the time of rainfall. Different life forms prevail at the five elevations on Tai Mo Shan. Smooth mats and turfs were the dominant forms. Mats dominated below 400 m, whereas wefts and mats dominated above 400 m. Different life form characteristics coincide with the humidity of a habitat, such as pendants in lowlands and submontane areas (<400 m), wefts and tails in the montane belt (400–900 m) and mats and cushions in high montane and subalpine belts (above 900 m) [32]. Furthermore, smooth mats are adapted to relatively dry habitats [84]. These differences might be explained by the different bryophyte types studied (i.e., epiphytic and terrestrial).

The nine phytogeographical patterns identified in this study were divided into three groups: tropical, East Asian and temperate, except for the cosmopolitan pattern (Table 3). Although Hong Kong lies on the margin of the Asian tropics with intense human activities, the tropical element was still the largest of the three, contributing two-thirds of the total taxa, which was higher than the total number of non-tropical taxa (i.e., the sum of the East Asian and temperate taxa). High similarities were found between Hong Kong and Hainan, and tropical taxa were the most shared due to the similar climate zone [85]. The distribution of seed plants is divided into 15 phytogeographical types [86], which are also applicable to bryophytes. However, bryophytes have a wider distribution than seed plants. The present diversity and distribution of terrestrial mosses have been significantly affected by deforestation in this region, but they also offer an opportunity to explore how they survive under microclimate and habitat degradation.

5. Conclusions

Our study shows that Tai Mo Shan features rich moss species, even in warmer and dryer lowlands. However, vegetation types significantly affect the diversity and distribution of terrestrial mosses. The highest cover and thickness of ground moss species occurred

at the peak of Tai Mo Shan. Cover and thickness can be used as predictors of biomass of terrestrial moss species. Life forms of terrestrial mosses were diversified, which was driven by different environmental pressures, with different life forms prevailing at different elevations. Although they are influenced by the East Asian and temperate climate and disturbed by human activities, terrestrial mosses on Tai Mo Shan are primarily tropical in nature. Under the threat of climate change, especially global warming and the uncertainty of rainfall, those lying at higher altitudes face great challenges. Forest conservation and restoration should be conducted to sustain and improve the biodiversity of terrestrial mosses and understory plants on Tai Mo Shan, especially at higher elevations.

6. Future Research

The present study only investigated terrestrial mosses, but further research on liverworts, hornworts and other understory plants should be carried out in to give more complete information of the impact of deforestation and subsequent vegetation development on understory and bryophyte communities. A comparison study in tropical primary forests in nearby Guangdong or Hainan province might provide us with more convincing evidence.

Author Contributions: J.H. and L.M.C. conceived the ideas. J.H. carried out the fieldwork, sample collection, laboratory procedures, and data analyses. L.M.C. commented on the data analyses. J.H. led the writing and L.M.C. edited the manuscript. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: The authors confirm that the data supporting the findings of this study are available within the article and its Appendix A.

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Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

Table A1. Characteristics of terrestrial mosses along altitudinal gradients.

Elevation	Species	Family	Life Form	Geographical Element
100	<i>Syrrhopodon gardneri</i>	Calymperaceae	Turf	Pantropical
	<i>Syrrhopodon armatus</i>	Calymperaceae	Turf	Palaeotropical
	<i>Hyoplia javanica</i>	Pottiaceae	Turf	Tropical Asian
	<i>Philonotis hastata</i>	Bartramiaceae	Cushion	Pantropical
	<i>Octoblepharum albidum</i>	Leucobryaceae	Cushion	Pantropical
	<i>Schwetschkeopsis fabronia</i>	Fabroniaceae	Weft	North temperate
	<i>Claopodium gracillimum</i>	Thuidiaceae	Mat	East Asian
	<i>Claopodium pellucinerve</i>	Thuidiaceae	Mat	North temperate
	<i>Entodontopsis anceps</i>	Stereophyllaceae	Mat	Tropical Asian
	<i>Fissidens guangdongensis</i>	Fissidentaceae	Turf	Tropical Asian
	<i>Sematophyllum subpinnatum</i>	Sematophyllaceae	Mat	Pantropical
	<i>Pseudotaxiphyllum densum</i>	Hypnaceae	Mat	East Asian
	<i>Ectropothecium zollingeri</i>	Hypnaceae	Mat	East Asian-Tropical Asian-Australian-Oceanian
	<i>Vesicularia montagnei</i>	Hypnaceae	Mat	East Asian-Tropical Asian-Australian-Oceanian
	<i>Pogonatum inflexum</i>	Polytrichaceae	Turf	East Asian Tropical Asian

Table A1. Cont.

Elevation	Species	Family	Life Form	Geographical Element	
300	<i>Pleurodium subulatum</i>	Ditrichaceae	Turf	North temperate	
	<i>Campylopus laxitextus</i>	Dicranaceae	Cushion	East Asian-Tropical Asian-Australian-Oceanian	
	<i>Campulopus subulatus</i>	Dicranaceae	Cushion	North temperate	
	<i>Fissidens guangdongensis</i>	Fissidentaceae	Turf	Tropical Asian	
	<i>Fissidens crispulus</i>	Fissidentaceae	Turf	Palaeotropical	
	<i>Leucobryum humillimum</i>	Leucobryaceae	Weft	East Asian Tropical Asian	
	<i>Duthiella speciosissima</i>	Trachypodaceae	Weft	East Asian	
	<i>Taxithelium oblongifolium</i>	Sematophyllaceae	Mat	East Asian Tropical Asian	
	<i>Sematophyllum phoenicium</i>	Sematophyllaceae	Mat	Palaeotropical	
	<i>Pseudotaxiphyllum pohliaecarpum</i>	Hypnaceae	Mat	East Asian-Tropical Asian-Australian-Oceanian	
	500	<i>Brothera leana</i>	Dicranaceae	Turf	North temperate
		<i>Campylopus gracilis</i>	Dicranaceae	Cushion	North temperate
		<i>Campylopus umbellatus</i>	Dicranaceae	Cushion	East Asian-Tropical Asian-Australian-Oceanian
		<i>Dicranodontium didymodon</i>	Dicranaceae	Cushion	Endemic to China
<i>Leucobryum bowringii</i>		Leucobryaceae	Weft	Pantropical	
<i>Leucobryum boninense</i>		Leucobryaceae	Weft	East Asian	
<i>Octoblepharum albidum</i>		Leucobryaceae	Cushion	Pantropical	
<i>Fissidens guangdongensis</i>		Fissidentaceae	Turf	Tropical Asian	
<i>Sematophyllum subhumile</i>		Sematophyllaceae	Mat	East Asian-Tropical Asian-Australian-Oceanian	
<i>Sematophyllum subpinnatum</i>		Sematophyllaceae	Mat	Pantropical	
<i>Papillidiopsis macrosticta</i>		Sematophyllaceae	Cushion	East Asian	
<i>Pseudotaxiphyllum pohliaecarpum</i>		Hypnaceae	Mat	East Asian-Tropical Asian-Australian-Oceanian	
700		<i>Campulopus ericoides</i>	Dicranaceae	Cushion	Tropical Asian
		<i>Leucobryum scabrum</i>	Leucobryaceae	Weft	East Asian
	<i>Leucobryum juniperoideum</i>	Leucobryaceae	Weft	North temperate	
	<i>Hyoplia involuta</i>	Pottiaceae	Turf	Pantropical	
	<i>Pohlia nutans</i>	Bryaceae	Turf	Cosmopolitan	
	<i>Thuidium pristocalyx</i>	Thuidiaceae	Mat	Palaeotropical	
	<i>Claopodium assurgens</i>	Thuidiaceae	Mat	East Asian-Tropical Asian-Australian-Oceanian	
	<i>Hypnum plumaeformae</i> var. <i>minus</i>	Hypnaceae	Weft	East Asian	
	<i>Pseudotaxiphyllum densum</i>	Hypnaceae	Mat	East Asian	
	<i>Pogonatum neesii</i>	Polytrichaceae	Turf	East Asian-Tropical Asian-Australian-Oceanian	
	900	<i>Campylopus umbellatus</i>	Dicranaceae	Cushion	East Asian-Tropical Asian-Australian-Oceanian
		<i>Fissidens crispulus</i>	Fissidentaceae	Turf	Palaeotropical
		<i>Hyoplia javanica</i>	Pottiaceae	Turf	Tropical Asian
		<i>Pseudosymbplepharis angustata</i>	Pottiaceae	Cushion	Palaeotropical
<i>Archidium ohioense</i>		Archidiaceae	Turf	Pantropical	
<i>Anomobryum julaceum</i>		Bryaceae	Cushion	Cosmopolitan	
<i>Plagiomnium vesicatum</i>		Mniaceae	Mat	Pantropical	
<i>Pterobryopsis crassicaulis</i>		Pterobryaceae	Mat	Tropical Asian	
<i>Chrysocladium retrorsum</i>		Meteoriaceae	Weft	East Asian Tropical Asian	
<i>Thuidium glaucinoides</i>		Thuidiaceae	Mat	Tropical Asian	
<i>Brachythecium garovaglioides</i>		Brachytheciaceae	Weft	East Asian	
<i>Brachythecium buchananii</i>		Brachytheciaceae	Weft	East Asian Tropical Asian	
<i>Sematophyllum subpinnatum</i>		Sematophyllaceae	Mat	Pantropical	
<i>Hypnum plumaeforme</i>		Hypnaceae	Weft	East Asian Tropical Asian	
<i>Hypnum callichroum</i>	Hypnaceae	Weft	North temperate		

Appendix B

Table A2. Composition and distribution of terrestrial mosses along the altitudinal gradient ($n = 6$).

Site No.	Transect No.	Altitude (m asl)	Total Number of Species	Cover (%)	Thickness (mm)
1	1	100	10	17.0	3.1
	2	110	6	14.5	2.8
	3	120	8	13.6	3.8
2	1	290	10	10.2	3.5
	2	306	7	10.8	3.2
	3	315	6	10.2	3.0
3	1	490	7	15.8	3.1
	2	505	8	10.7	3.3
	3	512	6	10.3	4.0
4	1	690	7	7.3	4.5
	2	705	3	7.0	6.0
	3	720	5	7.3	4.7
5	1	890	6	23.5	8.1
	2	900	10	25.0	10.0
	3	912	7	23.0	7.7

Appendix C

Table A3. Phytogeographical elements of terrestrial mosses on Tai Mo Shan.

Patterns	Moss Species (% Total)
1. Cosmopolitan	2 (3.8%)
2. Pantropical	8 (15.1%)
3. Paleotropical	5 (9.4%)
4. Tropical Asian	6 (11.3%)
5. East Asian–Tropical Asian–Australian–Oceanian	8 (15.1%)
6. East Asian	9 (17.0%)
7. East Asian–Tropical Asian	6 (11.3%)
8. Northern temperate	8 (15.1%)
9. Endemic to China	1 (1.9%)
Total	53

Appendix D.

Table A4. Canonical correlation coefficients for canonical variable sets for biotic and environmental variables.

Canonical Variable Sets	Canonical Correlation Coefficient	Canonical Variance Explained (%)	F	df	p
1	0.985	84.9	8.542	15	0.000
2	0.922	14.6	3.533	8	0.015
3	0.355	0.4	0.432	3	0.735

Appendix E.

Table A5. Canonical loadings for biotic and environmental variables.

	Set 1	Set 2	Set 3
Biotic variables			
Species richness	0.267	0.617	0.741
Cover	0.961	0.274	−0.030
Thickness	0.846	−0.514	0.143
Environmental variables			
Air temperature	−0.621	0.658	−0.085
Dew point	−0.800	0.486	−0.088
Relative humidity	0.352	−0.736	0.051
Rainfall	0.733	−0.623	0.082
pH	0.069	0.389	0.067
Ground cover	−0.232	0.878	−0.035
Canopy closure	−0.453	0.845	−0.086
Wind speed	0.498	−0.738	−0.029
Altitude	0.566	−0.750	0.048

Appendix F.

Table A6. Proportion (%) of variance explained.

Canonical Variable Sets	Set 1 by Self	Set 1 by Set 2	Set 2 by Self	Set 2 by Set 1
1	57.0	55.3	28.0	27.2
2	24.0	20.4	48.2	41.0
3	19.0	2.4	0.4	0.1

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