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Analysis of bryophyte species diversity in three northeastern provinces of China and the Korean Peninsula

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The three northeastern provinces and the Korean Peninsula are geographically and climatically diverse, and the geographical regions have continuously formed relatively unique flora. This paper collected through the national and provincial list of bryophytes, the specimens in the online herbarium, recently published bryophytes papers and bryophytes information recorded in field investigation in certain areas. Quantitative statistical analysis of plant species or taxa data was carried out by traditional methods. In order to clarify the species diversity and species genetic relationship of bryophytes in the study area, a preliminary study was conducted to explain the flora pattern and formation mechanism. There are 1,006 species of bryophytes belonging to 305 genera and 107 families in the three provinces of Northeast China, and there are 1,119 species of bryophytes belonging to 368 genera and 126 families in the Korean Peninsula. In addition, 477 new distribution records of bryophytes in the three northeastern provinces were supplemented. The dominant families and genera of bryophyte in the Korean Peninsula and the three northeastern provinces are highly similar, and the species richness of mosses and liverworts in the two study areas is dominated by families containing 2–10 species and single-species genera. According to a similarity analysis of family, genus and species, there are 541 species of bryophytes belonging to 269 genera and 102 families in the study area. The three northeastern provinces and the Korean Peninsula are rich in bryophytes, and are mainly distributed in temperate zones. Therefore, the similarity between Heilongjiang Province and Jilin Province in the three northeastern provinces is higher, while the similarity between Jilin Province, Liaoning Province and the Korean Peninsula is higher, indicating that the adjacent areas may have a common evolutionary origin or show evolutionary convergence. Compared with the Korean Peninsula, the proportion of tropical distribution and East Asian distribution in the three northeastern provinces is slightly higher. This study analyses the characteristics, similarity feature and floristic composition of bryophyte species and provides background information on bryophyte biodiversity conservation in the study area, which is highly important for the protection of bryophyte diversity and the promotion of basic data sharing.

KEYWORDS

bryophytes, northeastern provinces of China, Korean Peninsula, similarity analysis, species diversity

1 Introduction

The three Northeast provinces border the Korean Peninsula and form a unique regional geographical environment. Located in the northeast of China, bordering the Korean Peninsula, the three Northeast China provinces are rich in natural resources and strategically located. The Korean Peninsula is located in East Asia, connecting China, Russia and Japan, and has important geopolitical significance (Wang and Zhang, 2018; Li D. H, 2019). It is located in the transitional zone between the temperate and cold temperate zones and has a rich variety of ecosystem types. These ecosystems provide unique natural conditions for species diversity studies (Wang and Li, 2018; Kyoung et al., 2011). At the same time, it is the habitat of many rare and endangered species. This region is also an important channel for migratory birds in East Asia and has important biodiversity conservation value (Zhang and Wang, 2020; Yong et al., 2015). In addition, the ecosystems of the three northeastern provinces and the Korean peninsula are contiguous, and the habitats of many species cross national boundaries. Studying biodiversity in this area helps to understand the dynamic changes of transboundary ecosystems and is an international consensus (Liu and Jin, 2019; Margules and Pressey, 2000). Bryophyte evolution constitutes a key step in the evolution of land plants, and the importance of these plants in regulating ecosystems and conserving biodiversity is increasingly recognized (Chen et al., 2013; Lubna et al., 2024). Bryophytes face greater and more serious threats than other plants because they are small and diverse, more difficult to collect and classify in the field than other plants (Xing et al., 2022), and extremely sensitive to environmental changes (Shi and Wang, 2021). The protection of bryophytes is currently a weak link in biodiversity conservation (Zhou, 2000). The species list is used to measure the background information of a natural geographical area or administrative unit (Lu et al., 2021; Zhang, 2001). It is very important to update it in time for biodiversity conservation research, management and detection (Ma, 2015). In recent years, the new records and new distribution of bryophytes in the study area have been published one after another, but the complete list of bryophytes in the area is old, and it is urgent to conduct a comprehensive analysis and systematic integration of the current research data.

The collection of bryophytes in the northeastern provinces of China began in the middle of the 19th century and can be roughly divided into three stages. Before the 20th century, bryophytes collection records were generated mainly by European scholars. From the beginning of the 20th century to the middle of the 20th century, Russian scholars and Japanese scholars, became the main record collectors. In 1949, Kong Xianwu and Chen Fenghuai et al. first researched moss collection in China and obtained numerous results in their research (Xu et al., 2023). Gao Qian published the *Annals of Moss Plants in Northeast China* in 1977, which recorded 45 families, 153 genera and 433 species of the Flora Muscorum Chinae Boreali-Orientalis (Gao, 1977). In 1981, he also published the *Flora Hepaticarum Chinae Boreali-Orientalis*, which recorded 185 species of moss in 32 families and 55 genera in the three northeastern provinces of China (Gao, 1981). Li Xingjiang and Wu Pengcheng et al. published *Flora Bryophytprum Sinicopum* (Volumes 1–10) from 1994 to 2011, which recorded 56 families, 198 genera and 621 species of bryophytes in the three northeastern provinces of China (Gao, 1994, 1996; Li, 2000, 2006; Wu and Jia, 2011; Wu, 2002; Hu and Wang, 2005; Wu and Jia, 2004; Gao, 2003; Gao and Wu, 2008). The above monographs focus on bryophytes in northeastern China, and some provincial studies have focused on bryophytes specifically in the three northeastern provinces. For example, Zhang Shumei et al. recorded 502 species of bryophytes in 83 families and 205 genera in Liaoning Province in 2022 (Zhang et al., 2022). In addition, the research focuses on the important geographical mountains in the study area. For example, in 2000, Guo Shuiliang et al. investigated the bryophytes on Changbai Mountain and reported that there were 469 species of bryophytes in 179 genera of 65 families, including approximately 44 wild medicinal bryophytes (Guo and Cao, 2000). In 2013, Feng Chao investigated volcanic bryophytes in Wudalianchi, Heilongjiang Province, and recorded 286 species of bryophytes in 47 families and 128 genera (Feng, 2013). In 2019, Li Juan conducted a survey of bryophytes on the periglacial geomorphology of Gushihe in Laodudingzi, a mountainous region of eastern Liaoning Province, and reported that there were 59 species of bryophytes in 26 families and 46 genera (Li J, 2019). In 2022, Song Yuling et al. investigated and studied mosses in the Changshan Islands, Dalian, and recorded 96 species of mosses in 14 families and 38 genera (Song et al., 2022).

Within the Korean Peninsula, the environment of North Korea is relatively isolated; foreign exchanges are not frequent, and the economy is relatively underdeveloped (Lankov, 2013). Therefore, based on the current literature, significantly more bryophyte-related studies have been conducted in South Korea than in North Korea. The collection of bryophytes on the Korean Peninsula can be traced back to the early 20th century. Fauri collected bryophytes there in 1901 and from 1906 to 1907 (Lee and Choi, 2012). By the end of the 20th century, studies related to bryophytes had gradually increased in abundance. In 1997, Yamada and Choe (1997) investigated liverworts and hornworts throughout the entire Korean Peninsula and reported 236 species in 35 families and 75 genera, including 232 species in 33 families and 72 genera of liverworts and 4 species in 2 families and 3 genera of hornworts. This study on the liverworts and hornworts on the Korean Peninsula was relatively comprehensive. Since then, in the 21st century, the research area of bryophytes has been studied in more detail, and newly recorded species are discovered constantly. In 2011, Yoon et al. (2011b) reported four new species in South Korea. In September of the same year, 37 families, 96 genera and 158 species of Tokuyama moss were recorded (Yoon et al., 2011a). In 2018, Yim and Hyun (2018) recorded 63 species of bryophytes in 30 families, 49 genera and 30 families on Jeju Island. In 2019, Kwon et al. (2019) reported a new species from South Korea. In 2020, Bum et al. (2020) recorded 68 families, 143 genera and 274 species of bryophytes on Taibai Mountain, including 167 species of moss in 39 families and 93 genera and 107 species of liverworts in 29 families and 50 genera. In November of the same year, Kim et al. (2020) updated the list of Korean moss plants and recorded 775 species of 56 families and 250 genera. In 2021, Bum et al. (2021) recorded 57 families, 106 genera and 204 species of Yashan bryophytes, including 115 species of

moss in 33 families and 67 genera and 89 species of liverworts in 24 families and 39 genera. In recent years, new records of bryophyte groups in the study area have been continuously published, but the local chronicles and lists are separated by years. Based on the above situation, the three northeastern provinces and the Korean peninsula are currently missing the latest comprehensive bryophyte list.

The three northeastern provinces and the Korean peninsula have unique geographical, historical, cultural, economic and political characteristics. These characteristics make the region an important object for the study of development and cooperation in Northeast Asia. The origin and development of biodiversity are closely related to adjacent areas. The comprehensive comparison of several regional floras can better explain the relationship and characteristics of species composition between different regions. In this paper, a list of bryophytes in the three northeastern provinces and the Korean peninsula was compiled. By analysing the species, distribution and diversity characteristics of bryophytes in the three northeastern provinces and the Korean Peninsula, diversity differences and genetic relationship far and near of the bryophyte flora in the two regions were discussed, which provided background information for the conservation of bryophyte biodiversity in the study area. In addition, the study of species diversity in the three northeastern provinces and the Korean Peninsula as a research area not only helps to reveal the ecological laws and biodiversity characteristics of the region, but also provides a scientific basis for cross-border ecological protection, response to climate change and regional sustainable development. This research has important significance for international cooperation and can promote ecological security and ecological civilisation building in Northeast Asia.

2 Materials and methods

2.1 Data sources

The main sources of species list and geographical distribution datasets are: *Bryophyte Flora* and related books, mainly including: Flora *Hepaticarum Chinae Boreali-Orientalis*; *Flora Muscorum Chinae Boreali-Orientalis*; *Flora Bryophytprum Sinicopum* (Volumes 1–10). Major online databases, such as the National Specimen Information Infrastructure (http://www.nsii.org.cn/, accessed on 20 September 2023), the Global Biodiversity Information Facility (http://www.gbif.org, accessed on 30 December 2023), World Flora Online (http://www.worldfloraonline.org, accessed on 30 December 2023), iplant (http://www.iplant.cn/, accessed on 20 July 2023), the National Plant Specimen Resource Center (https://www.cvh.ac.cn/, accessed on 20 October 2023), and the Catalogue of Life China (http://www.sp2000.org.cn/, accessed on 31 December 2023). Relevant literature, such as the China National Knowledge Infrastructure (https://www.cnki.net/, accessed on 31 March 2024), VIP (http://www.cqvip.com/, accessed on 19 November 2023), WangfangData (https://www.wanfangdata.com.cn/, accessed on 10 November 2023), Baidu Scholar (https://xueshu.baidu.com/, accessed on 26 November 2023), RISS (https://www.riss.kr/index.do, accessed on 25 November 2023), on the bryophytes of the three northeastern provinces of China and the Korean peninsula (including journal articles, dissertations and conference papers, a total of 41 articles). In the field herbarium, the bryophyte specimens from Northeast Forestry University (NEFU) and Northeast Agricultural University (NEAU) were not sorted digitally online. Field investigation. From 2019 to 2021, a total of 400 specimens were collected in the Xiaoxing'anling area of Heilongjiang Province and are currently stored in the NEFU herbarium.

2.2 Data processing

The species list was constructed as follows. WPS software (Kingsoft Office Software, 2023) was used to determine the collected species information, habitat, distribution, etc. The specific names of the bryophytes on the Korean Peninsula were obtained from Mapcarta (https://mapcarta.com, accessed on 17 December 2023). TNRS (Taxonomic Name Resolution) (https://tnrs.biendata.org/, accessed on 1 March 2024) was used to check the Latin name spelling of the collected species. When a Latin species name could not be verified, it was used to reference the Missouri Botanical Garden Tropicos (https://www.tropicos.org/, accessed on 25 December 2023), which removed duplicate and invalid species. According to the classification of the CoLChina system integration, the final list of names was formed. Species that were not included in CoLChina were pulled instead from iplant, WFO (https://www.worldfloraonline.org/, accessed on 30 December 2023), published literature or classifications, or other reliable sources of original records. The complete names were verified via NYBG access (http://sweetgum.nybg.org/science/ih/, accessed on 20 December 2023) (Supplementary Table S3).

2.3 Data analysis

2.3.1 Species similarity analysis

In the study of flora, the species similarity coefficient is usually used as the quantitative index of similarity between two regions. The application of the species similarity coefficient not only can help clearly determine the degree of floristic correlation between two (or more) regions but also provides theoretical significance for floristic division and the study of the geographical attributes of the flora in transitional regions. To clarify the distance between the bryophyte species in the three northeastern provinces of China and between the species in these provinces and those on the Korean Peninsula, this paper discusses and analyses the species similarity coefficient. The specific formula is as follows:

$$J = c/(a + b - c) \quad (1)$$

In Formula 1, a represents the number of species in area A, b represents the number of species in area B, and c represents the number of species common to both areas A and B. (The similarity coefficient is between 0 and 1, and the closer

the value is to 1, the higher the degree of similarity between the two regions is).

2.3.2 Floristic analysis

The number of characteristics of plants in families or genera that are abundant among the vegetation or plant communities in a given region are essential for the study of the floristic properties of the plants. By counting and analysing the numbers of dominant families, genera and species, the species characteristics, richness and relationships with other flora can be better understood. This study focused on the specific distribution of bryophytes in the three northeastern provinces of China and the Korean Peninsula.

There is no specific floristic type classification for bryophytes; thus, at present, the most popular references used are Mr. Wu Zhengyi's "Distribution Types of Seed Plant Genera in China" (Wu, 1991) and "Distribution Types of Seed Plant Families in the World" (Wu et al., 2003), which use the GBIF and related records to determine the specific floristic types of each bryophyte in the three northeastern provinces of China and the Korean Peninsula. The components of the bryophyte flora in these areas were subsequently analysed via floristic genealogy, which refers to the proportions of various floristic components in a specific floristic region, reflecting those proportions in a broader region and/or the contributions of the components to the overall floristic composition (Liu et al., 2024).

The ratio of floristic components (FER) is calculated as follows:

$$FER = (FEi/T) \times 100\,\% \quad (2)$$

In Formula 2, FEi represents the number of species of the ith floristic component of a fauna (i=1, 2,3…), and T represents the total number of species of each component.

3 Results

3.1 Differences in bryophyte composition between the three northeastern provinces of China and the Korean Peninsula

There were 1006 species of bryophytes in 107 families and 305 genera (including 63 varieties, 15 subspecies and 3 variants) in the three northeastern provinces of China, including 668 species of mosses in 220 genera of 64 families (47 varieties, 7 subspecies and 1 variant) 252 species of liverworts in 81 genera of 40 families (16 varieties, 8 subspecies and 2 variants), and 5 species of hornworts in 3 families and 4 genera (Supplementary Table S1). There were 126 families, 368 genera and 1,119 species (23 varieties, 7 subspecies and 1 variant) of bryophytes on the Korean Peninsula, including 771 species of mosses in 74 families, 260 genera (19 varieties, 4 subspecies and 1 variant), 311 species of liverworts in 50 families, 103 genera (4 varieties, 3 subspecies), and 6 species of hornworts in 3 families, 5 genera (Supplementary Table S2). The species richness of bryophytes in the study area and the actual sampling points (Figure 1).

3.1.1 Composition of the families

Families were divided into four groups according to the number of species they contained: families with only 1 species, families with 2–10 species, families with 11–20 species, and families with more than 20 species (Table 1). In terms of the composition of the moss and liverwort families, the Korean Peninsula and the three northeastern provinces of China were dominated by families containing 2–10 species. The number of genera and species of moss plants accounted for 44.59% and 43.75%, respectively, and the number of genera and species of liverwort plants accounted for 40.82% and 47.5%. In terms of the composition of the hornwort families, the Korean Peninsula was dominated by families with 2–10 species, accounting for 66.67%, but the three northeastern provinces of China had the highest proportion of families with single species, accounting for 66.67%.

3.1.2 Dominance of the families

Analysis of the dominant families of bryophytes on the Korean Peninsula and in the three northeastern provinces of China (Figures 2A, B) revealed that there were 5 dominant families of bryophytes sharedbetween the two regions, and the similarity was 0.5. However, three families, Sphagnaceae, Bryaceae and Amblystegiaceae, were dominant families in only the three northeastern provinces of China, with a total of 105 species. Two families, Fissidentaceae and Pylaisiaceae, were the dominant families among Korean mosses, with a total of 61 species. There were 3 dominant families of liverworts shared between the Korean Peninsula and the northeastern provinces of China, and the similarity was 0.25. However, one family, Cephaloziaceae, containing 16 species, was dominant in only the three northeastern provinces of China and not on the Korean Peninsula. There were four dominant families on the Korean Peninsula but not in the three northeastern provinces of China, namely, Lejeuneaceae, Plagiochilaceae, Anastrophyllaceae and Jungermanniaceae. A total of 78 species were included in the analysis.

3.1.3 Composition of the genera

The genera were divided into four groups according to the number of species contained in the genus: genera with only 1 species, genera with 2–5 species, genera with 6–10 species, and genera with more than 10 species (Table 2). In terms of the composition of the three taxa and genera of bryophytes, the Korean Peninsula and the three northeastern provinces of China had the highest proportions of genera with a single species. The number of genera and species accounted for 47.31% and 43.18% in moss plants, 51.46% and 48.15% in liverwort plants, and 80.00% and 75.00% in hornwort plants.

3.1.4 Dominance of the genera

According to the analysis of the dominant genera of bryophytes on the Korean Peninsula and in the three northeastern provinces of China (Figures 3A, B), there were 6 dominant genera shared between the bryophytes on the Korean Peninsula and those in the three northeastern provinces of China, and the similarity was 0.75. However, one genus, *Plagiomnium*, with 15 species, was the dominant genus of moss in only the three northeastern provinces of China. In addition, only one genus, *Fissidens*, containing 30

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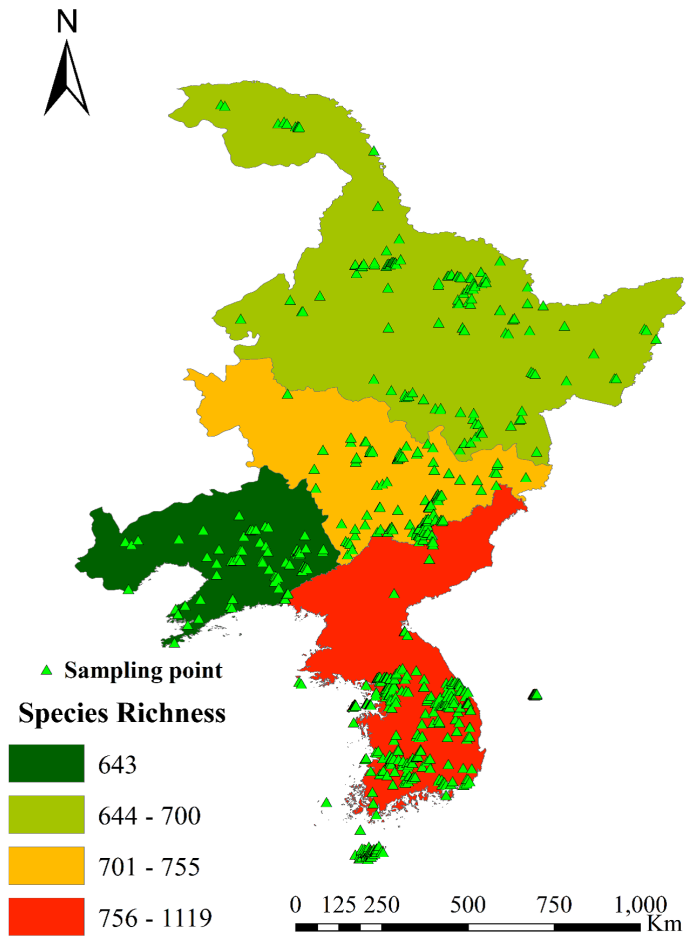

FIGURE 1
Species distribution of bryophytes in three provinces of Northeast China and Korean Peninsula.

species, was the dominant genus among Korean mosses. There were 4 dominant genera of liverworts shared between the Korean Peninsula and the northeastern provinces of China, and the similarity was 0.36. Three genera, *Riccia*, *Chiloscyphus* and *Cephalozia*, with a total of 31 species, were the dominant genera in only the three northeastern provinces of China. Four genera, *Plagiochila*, *Radula*, *Lejeunea* and *Cololejeunea*, containing 51 species in total, were dominant only on the Korean Peninsula.

TABLE 1 Composition of the species within families.

Bryophytes	Group (number of species)	Korean Peninsula	Proportion (%)	Three northeastern provinces of China	Proportion (%)
Mosses	1	17	22.97	14	17.19
	2–10	33	44.59	28	43.75
	11–20	10	13.51	11	17.19
	>20	14	18.92	11	17.19
Liverworts	1	17	34.69	11	27.5
	2–10	20	40.82	19	47.5
	11–20	10	20.41	7	17.5
	>20	2	4.08	3	7.5
Hornworts	1	1	33.33	2	66.67
	2–10	2	66.67	1	33.33

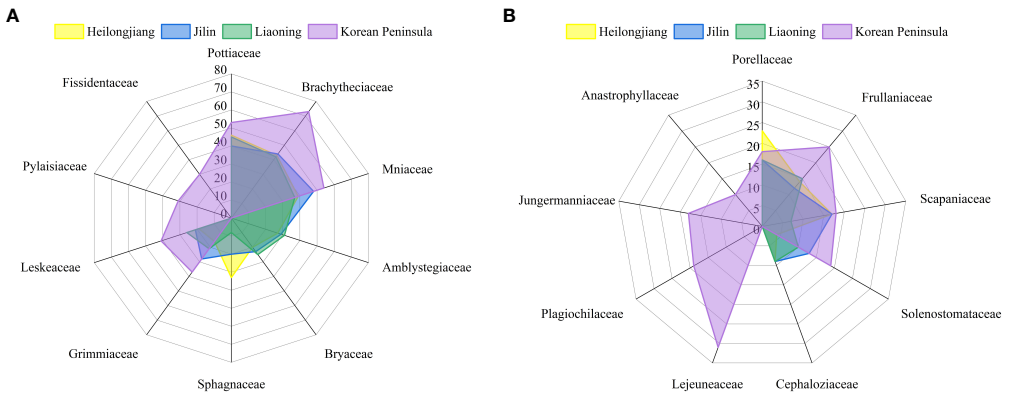

FIGURE 2
Comparison of the dominant bryophyte families in the three northeastern provinces of China and on the Korean Peninsula: **(A)** mosses; **(B)** liverworts and hornworts.

3.2 Similarity of bryophytes between the three northeastern provinces of China and the Korean Peninsula

3.2.1 The similarity of families

At the family level (Figures 4, 5), there were 24 families of bryophytes on the Korean Peninsula but not in the three northeastern provinces of China. There were 17 species of moss in 12 families and 14 genera, accounting for 16.22% of the total family, 5.38% of the total genus and 2.14% of the total species of the Korean Peninsula. These included Sematophyllacea, Rhizogoniaceae, Racopilaceae, Cryphaeaceae, Hookeriaceae, Oedipodiaceae, flowers and leaves Calymperaceae, Daltoniaceae, Symphyodontaceae, Pterigynandraceae, Myuriaceae, and Pterobryaceae. The liverworts and hornworts included 12 families, 16 genera and 18 species, accounting for 23.08% of the total families, 14.81% of the total genera and 5.56% of the total species of liverworts and hornworts in Korea. These included Acrobolbaceae, Jubulaceae, Neotrichocoleaceae, Calyculariaceae, Moerckiaceae and Pleuroziaceae, Wiesnerellaceae, Treubiaceae, Haplomitriaceae, Mastigophoraceae, and Harpanthaceae. The hornworts were all Dendrocerotaceae.

There were 4 families of bryophytes in the three northeastern provinces of China that were not distributed on the Korean Peninsula. The mosses were Schistostegaceae and Habrodontaceae, which were distributed in Jilin Province and Liaoning Province, respectively, and contained 2 families, 2 genera and 2 species, accounting for 3.12% of the total families, 0.90% of the total genera and 0.27% of the total species in the provinces. The liverworts and hornworts were Saccogynaceae and Phymatocerotaceae, which were distributed in Jilin Province and contained 2 families, 2 genera and 2 species, accounting for 4.65% of the total family number, 2.35% of the total genus number and 0.71% of the total species number of liverworts and hornworts.

3.2.2 The similarity of genera

At the genus level (Figures 6A, B), there were 99 genera of bryophytes in Korea that were not distributed in the three

TABLE 2 Composition of species within genera.

Bryophytes	Group (number of species)	Korean Peninsula	Proportion (%)	Three northeastern provinces of China	Proportion (%)
Mosses	1	123	47.31	95	43.18
	2–5	102	39.38	94	42.73
	6–10	22	8.49	19	8.64
	>10	13	5.02	12	5.45
Liverworts	1	53	51.46	39	48.15
	2–5	36	34.95	28	34.57
	6–10	8	7.77	9	11.11
	>10	6	5.83	5	6.17
Hornworts	1	4	80.00	3	75.00
	2-5	1	20.00	1	25.00

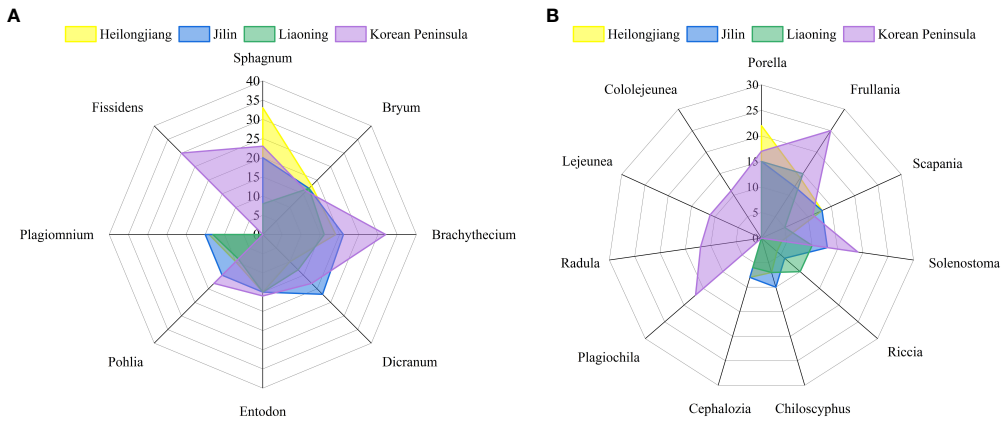

FIGURE 3
Comparison of the dominant bryophyte genera between the three northeastern provinces of China and the Korean Peninsula: **(A)** mosses; **(B)** liverworts and hornworts.

northeastern provinces. The Bryophytes included *Pseudoleskea*, *Hylocomiopsis*, *Orthoamblystegium*, *Bryohaplocladium*, *Rigodiadelphus*, *Homaliadelphus*, *Glossadelphus*, *Vesicularia*, *Ectropothecium*, *Oxyrrhynchium*, *Sciurohypnum*, *Steerecleus*, *Schwetschkea*, *Pseudocampylium*, *Sasaokaea*, *Sakuraia*, *Isotheciastrum*, *Dolichomitra*, *Dolichomitriopsis*, *Tripterocladium*, *Taxithelium*, *Sematophyllum*, *Orthomnion*, and *Epipterygium*, which in total included 83 species in 65 genera, accounting for 25% of the total number of moss genera on the Korean Peninsula and 10.44% of the total species. The liverworts and hornworts included *Cryptolophocolea*, *Tetralophozia*, *Gymnocolea*, *Hattoria*, *Xenochila*, *Delavayella*, *Jamesoniella*, *Crossogyna*, *Kurzia*, *Alobiellopsis*, *Acrobolbus*, *Cheilolejeunea*, *Microlejeunea*, *Tuzibeanthus*, *Ptychanthus*, *Lopholejeunea*, *Acanthocoleus*, *Jubula*,

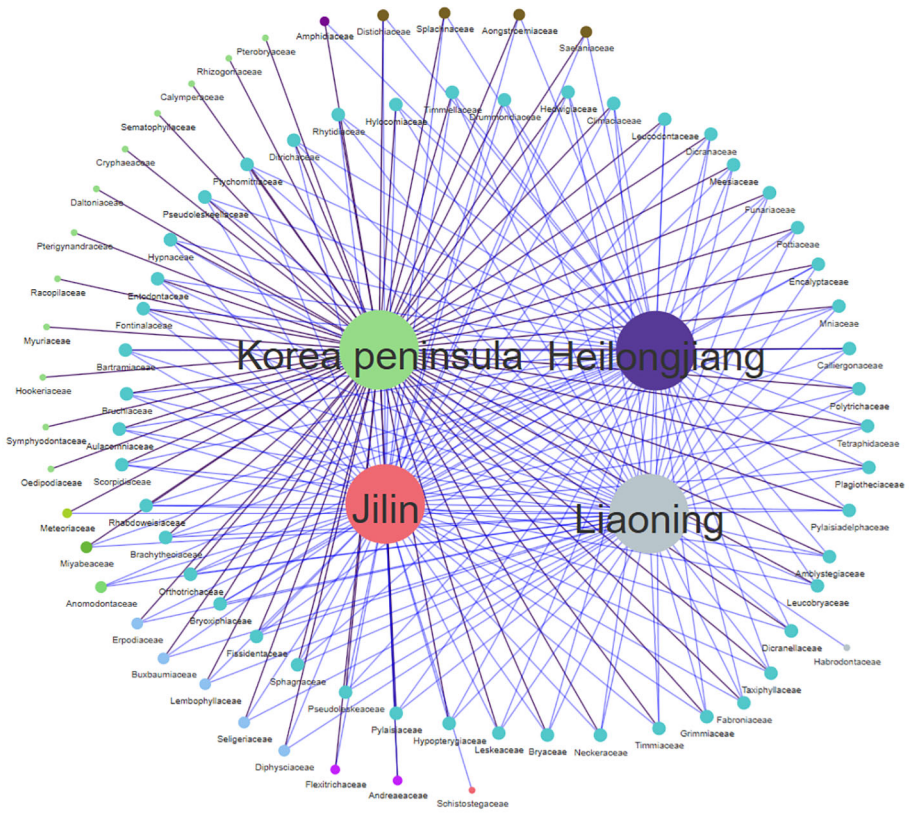

FIGURE 4
Diversity of moss families in the three northeastern provinces of China and the Korean Peninsula.

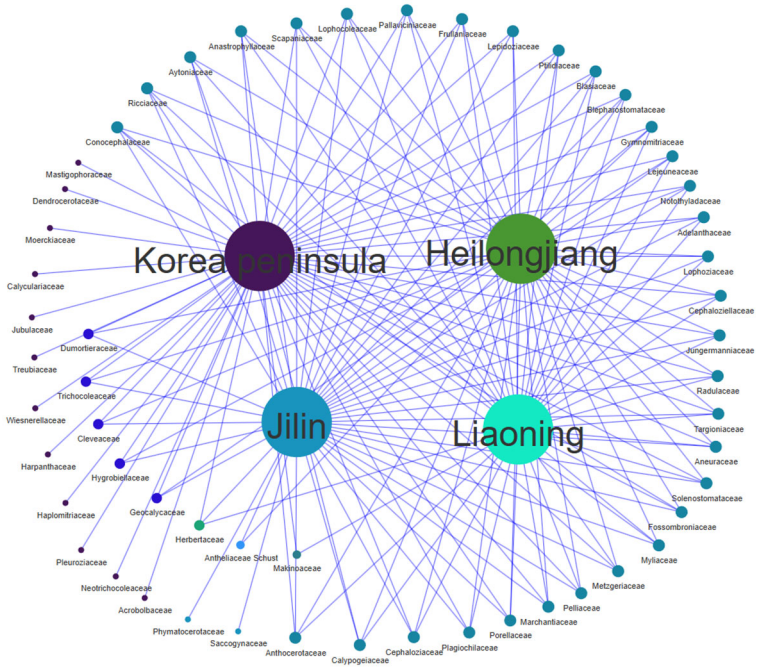

FIGURE 5
Diversity of liverwort and hornwort families in the three northeastern provinces of China and the Korean Peninsula.

Nipponolejeunea, *Neohattoria*, *Saccularia*, *Trichocoleopsis*, *Neotrichocolea*, *Calycularia*, *Folioceros* and *Megaceros*, which in total contained 34 genera and 40 species, accounting for 37.04% of the total genera and 14.13% of the total species.

There were 36 genera of bryophytes in the three northeastern provinces of China that were not distributed on the Korean Peninsula. There were 25 genera of moss, of which *Cinclidotus* was found only in Heilongjiang. There were five genera, *Schistostega*, *Entosthodon*, *Fleischerobryum*, *Cyrtohypnum*, and *Psilopilum*, which were distributed only in Jilin Province. There were six genera, *Oreas*, *Gyroweisia*, *Stegonia*, *Erythrodontium*, *Habrodon* and *Floribundaria*, which were distributed only in Liaoning. There were 11 genera of liverworts and hornworts, and only 3 genera are distributed in Jilin, *Apomarsupella*, *Saccogyna* and *Phymatoceros*. There were only 2 genera in Liaoning, *Schiffneria* and *Pleurocladula*.

3.2.3 The similarity of species

At the species level (Figures 7A, B), a total of 578 species of bryophytes from the Korean Peninsula were not distributed in the three northeastern provinces of China. Among them were 365 species of mosses, accounting for 45.91% of the total species of mosses on the Korean Peninsula, including *Anomodon sieboldii* (Dozy & Molk.) Granzow, *Vesicularia flaccida* (Sull. & Lesq.) Z. Iwats., *Pylaisia condensata* A. Jaeger (Mitt.), *Anacamptodon fortunei* (Mitt.),

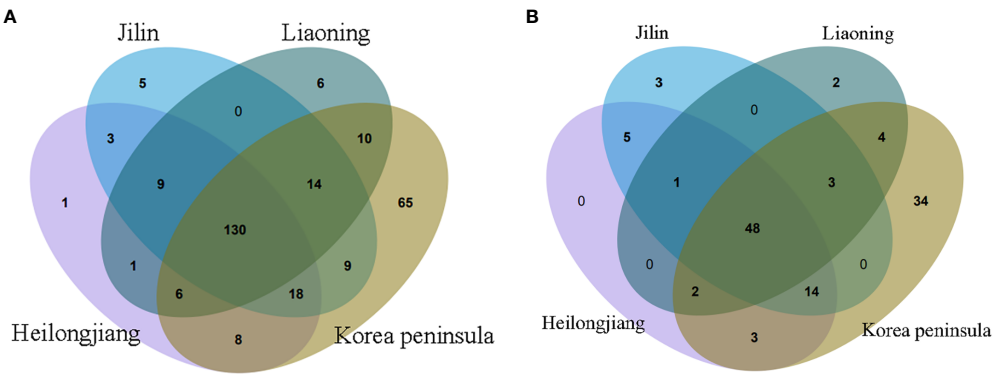

FIGURE 6
Diversity of bryophytes genera in the three northeastern provinces of China and the Korean Peninsula: **(A)** mosses; **(B)** liverworts and hornworts.

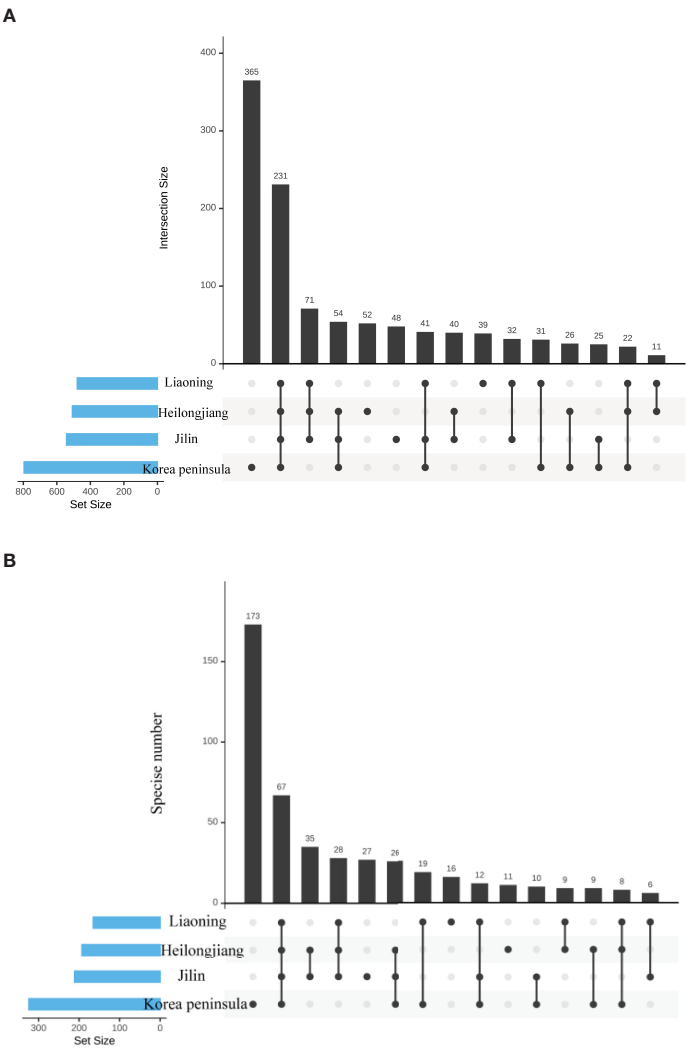

FIGURE 7
Diversity of bryophyte species in the three northeastern provinces of China and on the Korean Peninsula: **(A)** mosses; **(B)** liverworts and hornworts.

Myurella tenerrima (Brid.) Lindb., and *Ctenidium hastile* (Mitt.) Lindb. There were 173 species of liverworts and hornworts, such as *Plagiochila shangaica* Steph., *Mesoptychia chichibuensis* (Inoue) L. Soderstr. & Va whisa., and *Bazzania pompeana* (Sande Lac.) Mitt., which accounted for 53.77% of the total number of Korean liverwort species. The species included *Phaeoceros carolinianus* (Michx.) Prosk., *Megaceros flagellaris* (Mitt.) Steph., and *Folioceros fuciformis* D. C. Bhardwaj (Mont.), representing 50% of the total species.

There were 425 species of bryophytes in the three northeastern provinces of China that were not distributed on the Korean Peninsula. There were 293 species of moss, 174 of which were distributed in Heilongjiang Province, including *Splachnum vasculosum* Hedw., *Brachythecium glaciale* Schimp., and *Brachythecium glaciale* Schimp. There were 191 species in Jilin Province, including *Lewinskya rupestris* (Schleich.ex Schwagr.) F. Lara, Garilleti & Goffinet, *Anacamptodon amblystegioides* Cardot, and *Racomitrium microcarpum* Brid. There were 153 species in Liaoning Province, including *Hygrohypnum alpestre* (Hedw.) Loeske, *Homomallium plagiangium* (Mull. Hal.) Broth., and *Floribundaria floribunda* (Dozy & Molk.) M. Fleisch., accounting for 40.53% of the total moss species in the three northeastern provinces of China. There were 132 species of liverworts and hornworts, accounting for 46.76% and 40% of the liverworts and hornworts, respectively, in the three northeastern provinces of China. Among them, there were 83 species of liverworts in Heilongjiang Province, including *Riccardia flagellifrons* C. Gao, *Herbertus fragilis* (Steph.) Herzog, and *Marsupella alpina* (Gottsche ex Husn.) Bernet), but no hornworts. In Jilin Province, there were 95 species of liverworts and hornworts, including *Lophozia guttulata* (Lindb. & Arnell) A. Evans, *Nardia leptocaulis* C. Gao, and *Riccardia changbaishanensis* C. Gao, and one species of hornwort, *Phymatoceros bulbiculosus* (Brot.) Stotler, W. T. Doyle & Crand. – Stotl. In Liaoning Province, there were 58 species of liverworts and hornworts, including *Frullania aoshimensis* Horik., *Riccia liaoningensis* C. Gao & K. C. Chang, and *Mannia triandra* (Scop.) Grolle), and one species of hornwort, *Notothylas japonica* Horik.

The species similarity of mosses between the three provinces of Northeast China and the Korean Peninsula was 0.39, with Jilin Province exhibiting the highest similarity to the Korean Peninsula

at 0.36. For liverworts, the similarity between the three northeastern provinces and the Korean Peninsula was 0.33, with Liaoning and Jilin Provinces showing closer resemblance to the liverwort composition of the Korean Peninsula, both at 0.28. Regarding hornworts, the overall similarity between the three northeastern provinces and the Korean Peninsula was 0.38; however, Heilongjiang Province displayed a notably higher similarity of 0.50, attributed to the fact that all three hornwort species recorded in Heilongjiang are also found on the Korean Peninsula. The overall bryophyte similarity between the three northeastern provinces and the Korean Peninsula was 0.38. Geographically, Jilin and Liaoning Provinces exhibited greater similarity to the Korean Peninsula compared to Heilongjiang, with a similarity value of 0.33, significantly higher than that of Heilongjiang. This indicates that the bryophyte species composition in Jilin and Liaoning Provinces is more closely aligned with that of the Korean Peninsula (Table 3).

3.3 Differences in lichen floristic composition between the three northeastern provinces of China and the Korean Peninsula

The bryophyte flora of the Korean Peninsula contains 11 geographical components, whereas the bryophyte flora of the three northeastern provinces contained 10 geographical components (Table 4). The bryophyte flora of the three northeastern provinces of China and the Korean Peninsula were mainly temperate components, followed by a tropical distribution and strong East Asian characteristics (Figure 8). In the temperate zone, the proportions of moss, liverwort and hornwort in the three north-eastern provinces of China were 71.07% and 69.71%, respectively, which were much higher than those on the Korean Peninsula. Owing to geographical location, the tropical and East Asian components of the Korean Peninsula were greater than those of the three northeastern provinces of China, the proportions of tropical liverwort and hornwort were 31.45%, and the proportions of East Asian moss, liverwort and hornwort were 31.48% and 18.56%, respectively. The bryophyte flora of the three north-eastern provinces of China and the Korean Peninsula had strong characteristics of temperate components, which was consistent with the geographical location of this region in the northern part of northeast Asia across the southeastern Korean Strait and Japan, reflecting the close relationship between flora in this region and the Changbai Mountain flora; thus, the temperate components were relatively high. Moreover, the bryophyte flora of the three northeastern provinces of China and the Korean Peninsula were also affected by tropical components. Although the tropical components had less influence than the temperate components, the bryophyte flora of the three northeastern provinces of China and the Korean Peninsula mainly intersected with temperate and tropical properties, and the bryophyte flora of the three northeastern provinces of China and the Korean Peninsula were in transition from north to south. This finding was also consistent with the location of the three northeastern provinces in China's temperate monsoon zone and the more complex location of the Korean Peninsula in the subtropical, warm temperate and medium temperate climate zones.

4 Discussion

4.1 Characteristics of bryophyte species composition

The bryophyte composition of the three northeastern provinces of China and the Korean Peninsula is rich. It is attributed to its unique geographical location, climatic conditions, complex topography, historical evolution and ecosystem integrity. These factors not only provide diverse habitats for bryophytes, but also promote the differentiation, migration and adaptation of species. Bryophytes of Korean Peninsula accounted for 63.32% of the families, 29.15% of the genera and 6.18% of the species in the world, and those of the three northeastern provinces of China accounted for 53.77% of the families, 24.26% of the genera and 5.56% of the species in the world. As a waterborne plant, the influence of temperature and precipitation on the

TABLE 3 Similarities in bryophyte species between the three northeastern provinces of China and the Korean Peninsula.

Bryophytes	District	Common species	Similarity coefficient
Mosses	Three Northeastern provinces – Korean Peninsula	430	0.39
	Heilongjiang – Korean Peninsula	333	0.34
	Jilin – Korean Peninsula	351	0.36
	Liaoning – Korean Peninsula	325	0.34
Liverworts	Three Northeastern provinces – Korean Peninsula	148	0.33
	Heilongjiang – Korean Peninsula	107	0.27
	Jilin – Korean Peninsula	115	0.28
	Liaoning – Korean Peninsula	106	0.28
Hornworts	Three Northeastern provinces – Korean Peninsula	3	0.38
	Heilongjiang – Korean Peninsula	3	0.50

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TABLE 4 Comparison of bryophyte flora between in the three northeastern provinces of China and the Korean Peninsula.

Floristic component	Mosses		Liverworts		Hornworts	
	Northeast	Korean Peninsula	Northeast	Korean Peninsula	Northeast	Korean Peninsula
North temperate	55.79	43.65	55.39	31.18	60.00	33.33
Pantropical	2.08	3.57	2.60	3.53	20.00	50.00
East Asia-North America	6.08	5.42	4.09	6.73	—	—
Old World tropical	—	0.66	—	—	—	—
Old World temperate	3.12	2.51	2.23	2.88	—	—
Tropical Asian (India-Malaysian distribution)	6.82	3.97	8.92	7.69	—	—
Temperate Asian	12.17	10.05	11.90	10.26	20.00	—
East Asian	6.82	24.87	5.20	25.32	—	—
Tropical Asia – Tropical Oceania	0.45	1.85	0.37	2.56	—	16.67
Tropical Asia – Tropical America	0.30	1.46	2.23	2.24	—	—
Tropical Asia – Tropical Africa	0.59	0.79	2.23	1.60	—	—

growth of bryophytes is more significant than that of other environmental factors (Bates et al., 2010). Affected by the humid climate resulting from being surrounded by the sea on three sides, bryophytes are more abundant on the Korean Peninsula than in the three northeastern provinces of China. In addition, the complex topography, the role of glacial refuges in historical evolution, the advantages of biogeographic intersections, less human interference, and diverse habitat types are all factors that make the species richness of the Korean Peninsula higher than that of the three northeastern provinces. These factors jointly contribute to the Korean Peninsula being a hot spot of bryophyte diversity. In contrast, the diversity of bryophytes in the three provinces of Northeast China is relatively low due to the cold climate, relatively single terrain features, and the influence of human activities. In the future, more intensive investigations of bryophytes in the three provinces of Northeast China may further reveal their potential diversity.

Families and genera are two commonly used taxonomic units that reflect the relationships of species at different levels. As a higher taxonomic unit, a family reflects a wider range of phylogenetic relationships among species. Moreover, in the geographical division of flora, a family, as an indicator of greater division, can provide a general overview of floristic characteristics in a specific space and reveal the connections between a specific floristic region and other floristic regions, helping to explore floristic origins, etc. (Li N, 2019). The classification of the size of a family or genus into different grades for statistical analysis is also a necessary analytical method in

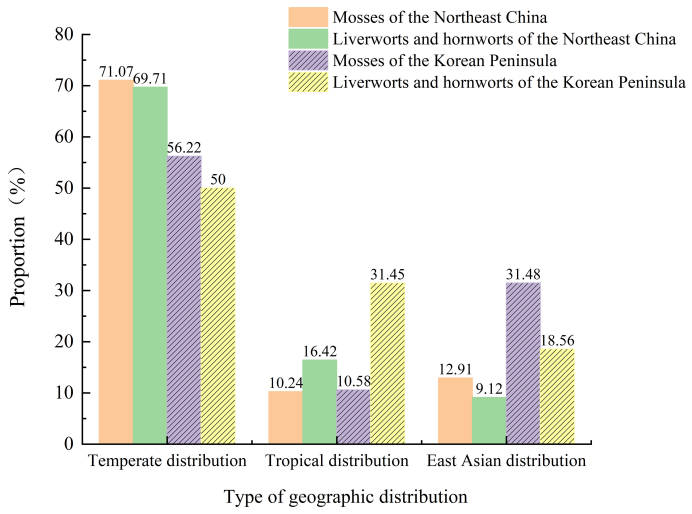

FIGURE 8
Proportions of different components of bryophytes in the three northeastern provinces of China and the Korean Peninsula.

the study of flora or diversity and has been widely used in related research in China.

In terms of family composition, the moss and liverworts of the three northeastern provinces of China and the Korean Peninsula were composed mainly of families containing 1 genus and families containing 2 to 10 species. On the Korean Peninsula, there were mosses from 33 families containing 1 genus, accounting for 44.59%, and 33 families containing 2 to 10 species, accounting for 44.59%. There were liverworts of 27 families with 1 genus, accounting for 55.1%, and 20 families with 2–10 species, accounting for 40.82%. In the three northeastern provinces of China, there were 30 families of mosses with 1 genus (35.14%) and 28 families with 2–10 species (40.82%). Among the liverworts, 20 families contained 1 genus, accounting for 55.10%, and 19 families contained 2–10 species, accounting for 40.82%. There were slight differences in family composition between the two regions of hornworts. In the Korean Peninsula, families containing 2–10 species and families containing 2–5 genera were dominant, accounting for 66.67%, whereas in the three northeastern provinces of China, families containing 1 species and families containing 1 genus were dominant, accounting for 66.67%.

In terms of genus composition, the bryophytes in the three northeastern provinces of China and the Korean Peninsula are dominated by genera containing 1 species. Among the bryophytes of the Korean Peninsula, the mosses of 122 genera contained 1 species, accounting for 46.92%, the liverworts of 53 genera contained 1 species, accounting for 51.46%, and the hornworts of 4 genera contained 1 species, accounting for 80%. Among the bryophytes in the three northeastern provinces of China, 95 genera contained 1 species of moss, accounting for 43.18%; 39 genera contained 1 species of liverworts, accounting for 48.15%; and 3 genera contained 1 species of hornworts, accounting for 75%. At present, it has been proposed that a single family or a single genus represents two directions of species evolution and that newly evolved species or a few residual species constitute the ultimate evolution of an ancient genus (Zhang, 2016). Combined with the results of this study, it is speculated that there may be more newly evolved species or a few residual species in the three northeastern provinces of China and on the Korean Peninsula.

4.2 Dominant bryophyte genera

The bryophyte flora of the Korean Peninsula and the three northeastern provinces reflects the characteristics of temperate forests in East Asia, and this region where the bryophyte flora exists is a key area for studying the origin and evolution of East Asian flora. This area is the distribution centre of many bryophytes, with high bryophyte species diversity, providing important materials for studying the distribution pattern of species. The study of dominant families and genera not only helps to improve the classification system of bryophytes, but also reveals the evolutionary history of bryophytes by studying the evolutionary relationship of dominant families and genera. Moreover, such research not only helps to understand the structure and function of regional ecosystems, but also provides a scientific basis for biodiversity conservation and sustainable use (Wang et al., 2020).

Owing to factors such as temperature and geographical location, there were some differences between the dominant families and dominant genera in the three northeastern provinces of China and on the Korean Peninsula. Amblystegiaceae and Cephaloziaceae were the dominant families in the three northeastern provinces of China but not on the Korean Peninsula. Among them, Amblystegiaceae was distributed mainly in the cold temperate zone, and Maimaitimin Sulaiman et al. reported that Amblystegiaceae is also a dominant family in Xinjiang (Mymytimin and Wang, 1999). Fissidentaceae, Pylaisiaceae, Lejeuneaceae, Anastrophyllaceae and Jungermanniaceae were the dominant families in the Korean Peninsula but not in the three northeastern provinces of China. Zhou Xuping et al. reported that Fissidentaceae in Niangniangshan National Wetland Park in Liupanshui, located in subtropical areas, was also a dominant family (Zhou XP et al., 2022). Bai Populus, Li Fei et al. reported that Lejeuneaceae was also a dominant family in Qianjiangyuan National Park, which is also located in the subtropical zone, and in the Shaluo area of Chishui, Guizhou (Bai, 2021; Li et al., 2022). Quan Dongli et al. reported that Jungermanniaceae was also a dominant family in Xishuangbanna, which is located in subtropical Yunnan Province (Quan et al., 2021). Brachytheciaceae and Grimmiaceae, which had a large number of species, were the dominant families in both regions. They have low requirements for growth and can grow in a variety of environments, which also reflects the diversity and complexity of habitats and flora in the study area.

Similarly, there were differences in the dominant bryophyte genera between the Korean Peninsula and the three northeastern provinces of China. *Plagiomnium*, *Riccia*, *Chiloscyphus* and Cephalozia are the dominant genera in the three northeastern provinces but not on the Korean Peninsula. Among them, *Plagiomnium* was also a dominant genus in the Yudaokou area of the Hunshandake Sandy Land in Inner Mongolia, which has a similar climate type (Deng, 2023). Five genera were dominant on the Korean Peninsula but not in the three northeastern provinces of China, namely, *Fissidens*, *Plagiochila*, *Radula*, *Lejeunea* and *Cololejeunea*, which were mostly composed of some tropical genera. Among them, *Fissidens* was also found by He Lin et al. to be a dominant genus in the source area of the Chishui River in Guizhou (He et al., 2020). Jiang Ya et al. reported that *Plagiochila* was the dominant genus in the Jinping Watershed National Nature Reserve in Yunnan (Jiang et al., 2018). Tan Hongying et al. reported that *Lejeunea* was the dominant genus in Ahahu National Wetland Park in Guiyang (Tan et al., 2023). Bryophytes that were in dominant families or dominant genera in the Korean Peninsula were also in dominant families or dominant genera in southern China, which is also in the subtropical region; however, they were not in dominant families or dominant genera in the three northeastern provinces, which fully reflects the differences caused by the growth of bryophytes in different regions. The Korean Peninsula is surrounded by the sea on three sides (east to the Sea of Japan (East Sea) and west to the Yellow Sea). It is significantly affected by the marine climate, such as the climate is humid, and the precipitation is abundant, especially in the southern region. This

humid environment is highly suitable for the growth of bryophytes, as they are heavily dependent on water. Additionally, the climate of the Korean Peninsula is relatively mild, with winters not as cold as those in the three northeastern provinces of China, and summers being warm and humid. Such climatic conditions provide a longer growing season and a more favourable habitat for bryophytes. As a result, there are notable differences in species distribution and dominant groups between the two regions.

4.3 Similarity and floristic composition of bryophytes

There were more bryophytes distributed in Jilin Province than in Liaoning Province and Heilongjiang Province, which may be due to the unique geographical location and diverse geomorphologic types in the Changbai Mountain area. Changbai Mountain is situated in the transitional zone between the temperate and cold-temperate regions of East Asia. This unique location endows it with characteristics of both climatic zones, creating an ideal habitat for species with diverse ecological requirements. Moreover, the area exhibits distinct vertical climate and vegetation zones, ranging from the foothills to the summit. This vertical stratification offers a variety of habitats, supporting a wide range of species adapted to different environmental conditions. Moreover, the warm and humid environment of the Korean Peninsula is more suitable for the growth of bryophytes, so many bryophytes here are not distributed in the three northeastern provinces of China.

Liaoning Province is the only province of the three northeastern provinces of China that is both coastal and borderline, with a sea area (continental shelf) of approximately 150,000 square kilometres (Zhou LY et al., 2022). According to the comparative analysis of provincial similarity, Heilongjiang Province and Jilin Province, which are probably both inland provinces, are more similar in terms of bryophyte composition, and their species similarity value is 0.61. Both Jilin Province and Liaoning Province border the Korean Peninsula, so within the scope of the three northeast provinces, these two provinces have the largest similarity values with the Korean Peninsula, both of which are 0.33. The Changbai Mountain and the Xingan Mountains among the different geographical unit species, indicating that the bryophyte compositions of the two regions were the most similar. The species similarity value was 0.39.

The three northeastern provinces of China and the Korean Peninsula have diverse geographical distributions. In the two study areas, moss, liverwort and hornwort are distributed mainly in temperate zones, among which those in the three northeastern provinces of China account for a slightly greater proportion, 71.07% and 69.71%, respectively, while those on the Korean Peninsula accounted for 56.22% and 50%. In terms of the tropical distribution and East Asian distribution, the proportions of moss, liverwort and hornwort on the Korean Peninsula are greater than those in the three northeastern provinces of China. This is due to the complex terrain of the Korean peninsula, with mountains, hills, plains and coastlines intertwined. In particular, mountainous areas such as the Taibai Mountains and the Jingang Mountains have formed diverse microhabitats, providing rich habitats for bryophytes. Although the three northeastern provinces also have mountains, such as Changbai Mountain and Greater Khingan Mountains, the overall terrain is dominated by plains (such as Songnen Plain and Liaohe Plain) and the habitat type is relatively monotonous, limiting the diversity of bryophytes. In addition, the Korean Peninsula lies at the heart of the East Asian flora and is an important channel for species exchange between China, Japan and the Russian Far East. This geographical location allows the Korean Peninsula to bring together bryophyte species from different regions. However, although the three northeastern provinces also lie within the East Asian flora, their northern borders with Siberia and the cold climate limit the migration and exchange of species.

5 Conclusions

The Korean Peninsula is very similar to the three northeastern provinces (especially Jilin and Liaoning) in terms of bryophyte diversity. The ecosystems of the Korean Peninsula, Jilin Province and Liaoning Province are highly continuous, especially the temperate forest and wetland ecosystems. This continuity facilitates the migration and dispersal of bryophytes. The composition of bryophytes on the Korean Peninsula is more diverse. The Korean peninsula and the three northeastern provinces are located in the core area of East Asian flora and are an important channel for species exchange between China, Japan and the Russian Far East. This geographical location allows the two places to share many bryophyte species. The southern part of the Korean peninsula is influenced by the marine climate, which further increases the diversity of bryophytes. The formation of these similarities and differences is influenced by many factors, such as geographical proximity, climatic conditions, topography, historical development and biogeographical overlap. Studying these factors not only helps to understand the distribution patterns and evolutionary history of bryophytes, but also provides an important basis for regional biodiversity conservation and transboundary cooperation. Future research should further explore the ecological functions and conservation strategies of bryophytes in response to the challenges of global environmental change.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Author contributions

CY: Conceptualization, Writing – original draft, Writing – review & editing. RL: Data curation, Methodology, Resources, Software, Writing – original draft, Writing – review & editing. JC: Investigation, Validation, Writing – original draft, Writing – review & editing. HW: Conceptualization, Supervision, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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The author(s) declare that no Generative AI was used in the creation of this manuscript.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2025.1540547/full#supplementary-material

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