

Quantifying and interpreting nestedness of bryophytes in the Zhoushan Archipelago, China

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Abstract

Background: Detecting nestedness distribution and understanding their origin are important for biological conservation. Although previous studies on nestedness covered a wide range of taxa, discrepancies still exist on the prevalence of nestedness among biotas, and on the mechanisms to form nested distribution. Because bryophytes are poikilohydric, highly sensitive to habitats, and have a long-distance dispersal capacity, together with the fact that continental islands highly varied in area, elevation and habitat types, bryophytes on continental archipelago are thus an ideal system for the settlement of relevant disputes on nested distribution. However, few studies have been conducted on nestedness of bryophytes. To quantify nestedness level of different bryophyte categories on continental islands and possible mechanisms, we compiled a presence/absence matrix of 446 species of bryophytes in 66 islands of the Zhoushan Archipelago, China. We also recorded spore sizes of 319 moss species based on available literature. By using the matrix temperature and the NODF metrics, as well as a conservative null model, we evaluated the nestedness levels of 18 bryophyte categories. We further explored possible mechanisms to form nested distribution by using partial Spearman rank correlations based on island area, elevation, habitat types and spore size of moss species. Results : We found that all 18 categories of bryophytes exhibited a high degree of nestedness. Nestedness level was higher for mosses than liverworts, higher for acrocarpous mosses than pleurocarpous mosses and varied among different bryophyte 13 families. The nested distribution of bryophytes in the archipelago was not due to passive sampling, but mainly due to nested habitats and selective-extinction. Spore size might be a factor linked to selective-colonization accounting for nestedness of some moss categories. Conclusions : Nested habitats, selective-extinction, and partial selective-colonization resulted in a high level of nestedness for bryophytes in continental islands. Although the nestedness of bryophyte distribution in the Zhoushan Archipelago was statistically significant, such a nestedness was not perfect. Conservation of bryophytes should not only focus on the species-richest islands.

Background

Detecting distribution patterns and understanding their origin is an important aspect of ecology. Nestedness is one of the distribution patterns of regional biotas [1]. Species assemblages are nested if the species present at species-poor islands are a subset of those present at species-rich islands [2]. Numerous studies have investigated nestedness and underlying processes in a wide range of taxa on both islands and fragmented habitats, and nestedness was considered as common for biotas throughout the world [2-9].

Bryophytes exhibit specific eco-physiological features and life-history traits. They are poikilohydric, highly sensitive to habitats, and have a long-distance dispersal capacity [10]. Although previous studies on nestedness covered a wide range of taxa, few focused on bryophytes. Vanderpoorten et al. [11] reported that bryophyte communities exhibited nestedness at the landscape scale. In boreal streamside forests, Hylander and Dynesius [12] found that species composition was significantly nested for bryophytes. They detected a strong positive correlation of nestedness of bryophytes with species richness of vascular

plants. Mateo et al. [13] examined the spatial variation of species richness in European bryophytes and found that liverworts exhibited a higher level of nestedness than mosses. Aranda et al. [14] found that nestedness was higher in bryophytes than in seed plants in the macaronesian flora. They suggested that the higher dispersal capacity resulted in more similar and compositionally nested island floras. Tiselius [15] used NODF metric to evaluate the level of nestedness of bryophytes in a northern Swedish archipelago and found that the nested distribution of bryophytes was attributed to habitat filtering process. The above sporadic studies have drawn attention to nestedness of bryophytes and their mechanisms.

Discrepancies still exist in the effects of life-history traits on distribution. Kadmon [16] reported that wind-dispersing plant species showed no evidence of nested occurrence, while species lacking a long-distance dispersal capacity showed a strong pattern of nestedness. However, Cook and Quinn [17] advocated that colonization ability was important in producing nested subsets as good dispersers often exhibited a greater degree of nestedness than poor dispersers. Simberloff and Martin [18] once suggested that virtually all insular systems were nested to a certain degree. However, debate is ongoing on the prevalence of nestedness among biotas and different landscapes and habitat conditions. The metrics of nestedness applied in much of the previous work have been criticized as inappropriate. After recalculation by using the NODF metric, nestedness was thought to be less common than previously reported [19]. Therefore, further studies, especially on special biota such as bryophytes, are still needed for settlement of the above disputes.

Because nestedness was related to dispersal and colonization ability, and such ability was further determined by a combination of its biological characteristics [8], spore size should be a potential feature influencing the nested distribution of bryophytes because spore size exerted influences on dispersal capacity and establishment rate [20]. However, there has been no work on the relationship between the distribution pattern of bryophytes and spore size.

The Zhoushan Archipelago is the largest archipelago in China, comprising 1339 continental islands with a total land area of 1371 km² [21, 22]. These islands differ in area, elevation, and habitat types (Additional file 1: Figure S1, Tables S1, S2). Bryophytes on this archipelago are thus an ideal system to provide new evidence for the settlement of relevant disputes on the prevalence of nested distribution and the mechanisms to form nested distribution patterns. Our objectives were: 1) to quantify the level of nestedness of bryophytes; (2) to determine the mechanisms underlying the nestedness of bryophyte flora in the Zhoushan Archipelago.

Results

Nestedness levels for different bryophyte groups

Nestedness metrics for 18 bryophyte categories were all significantly lower than the means of randomly generated matrices under corresponding null models, all with *P*-values < 0.001 by using the BINMATNEST,

and with P -values < 0.01 by using the NODF (except for Lejeuneaceae, $P < 0.05$). Therefore, the species compositions of the 18 bryophyte categories had a significantly nested structure among these continental islands. If considering the ratio of matrix temperature to the corresponding mean temperature generated by using Null model 3, the nestedness level was higher for mosses than liverworts, higher for acrocarpous mosses than pleurocarpous mosses. According to nestedness level from high to low, the 13 families were ranked as Mniaceae, Thuidiaceae, Hypnaceae, Bryaceae, Pottiaceae, Brachytheciaceae, Lophocoleaceae, Polytrichaceae, Leucobryaceae, Lejeuneaceae, Funariaceae, Fissidentaceae, and Leskaceae (Table 1, Fig.1).

Mechanisms determining nestedness

Effects of passive sampling on nested distribution of bryophytes

As more as 56 (for Total bryophytes), 55 (for Total mosses), and 33 (for liverworts) observed data points lay outside one standard deviation of the expected curve produced from the random placement model, accounting for more than 84.0 %, 83%, and 66% of the total observed data points for Total bryophytes, Total mosses, and liverworts, respectively (Fig. 2). Therefore, the nested distribution patterns of the three categories of bryophytes in the study region were not due to passive sampling.

Effects of habitat types on nested distribution of bryophytes

The observed matrix temperature for the presence/absence matrix of habitat types was 8.597, while the expected value based on Null model 3 was 47.398, the former being significantly lower than the latter ($P < 0.001$). Therefore, there existed a high level of nestedness of habitat types among the 66 islands.

Significantly positive Spearman correlations were detected between the ranks of the islands in the maximally packed matrix of species distribution and those of habitat types for Total bryophytes ($r = 0.919$, $n = 66$, $P < 0.001$), Total mosses ($r = 0.924$, $n = 66$, $P < 0.001$), liverworts ($r = 0.699$, $n = 47$, $P < 0.001$), acrocarpous mosses ($r = 0.906$, $n = 66$, $P < 0.001$), and Pleurocarpous mosses ($r = 0.761$, $n = 43$, $P < 0.001$), as well as for all other 13 families except Lophocoleaceae ($r = 0.231$, $n = 34$, $P < 0.2$) and Leskaceae ($r = 0.218$, $n = 32$, $P < 0.5$) (Table 2).

Effects of island attributes on nested distributions of bryophytes

Island area exerted a significantly positive effect ($P < 0.05$) on nested distribution of the 18 bryophyte categories except pleurocarous mosses, Bryachytheciaceae, liverworts, Funariaceae, Leskaceae, and Lejeuneaceae. Elevation exerted a significantly positive effect ($P < 0.05$) on the nestedness of Total bryophytes, Total mosses, and pleurocarpous mosses, and a slightly positive effect ($P < 0.2$) on liverworts, acrocarpous mosses, and Hypnaceae (Table 3).

Effects of spore size on nested distributions of bryophytes

The nested distribution of Total mosses, acrocarpous mosses, and Pottiaceae was significantly and positively related to spore size (Fig. 3). Because the species were reversely ranked according to their places in the maximally packed matrix of their distribution, the species in front of the rank has a narrow distribution range. The distribution range of the species expanded with increasing spore size for Total mosses, acrocarpous mosses and Pottiaceae (Additional file 1: Figure S2). No significant effects of spore sizes on nested distribution were detected for pleurocarpous mosses and Bryaceae in the study regions.

Discussion

Nestedness level of bryophyte distribution

Although nested distribution of a wide range of biotas has been detected, very few studies have been conducted on bryophytes. Our study is among the first to evaluate the level of nestedness of bryophyte distribution on Asian continental islands. Having compared the results of some other biotas with ours, we found that bryophytes on continental islands have a higher level of nestedness in their distribution. For example, in the study of nestedness of birds, lizards, and small mammals on islands of an inundated lake, Wang et al. [23] reported that the observed nestedness temperatures were 18.29, 15.58 and 9.94 for birds, lizards and mammals, respectively, while their corresponding expected values based on Null mode 3 were 48.23, 34.60 and 29.53, respectively. Similar results were reported by Aranda et al. [14] in their study of the macaronesian flora that nestedness was higher in bryophytes than in seed plants.

Bryophytes are spore-producing plants with long-distance dispersal capacities [24]. We thought that the high level of nestedness for bryophytes in the Zhoushan Archipelago was possibly due to (1) their strong dispersal abilities, (2) no species of bryophytes endemic to the archipelago, (3) a comparatively narrow geographical range, and (4) a range of island sizes of the 66 island. Because overall colonization rates must be high enough to quickly compensate for any irregularities in species distribution that might be created by local extinction, colonization-generated patterns of nestedness should be expected in the species exhibiting strong dispersal abilities [17]. After having compared levels of nestedness among taxa with different dispersal abilities in many cases they analyzed, Cook and Quinn (1995) found that taxa with a comparatively higher level of nestedness had stronger dispersal ability and endemic species typically reduced the overall level of nestedness in many cases. Aranda et al. [14] also thought that higher dispersal capacity or the higher frequency of long-distance dispersal in bryophytes results in more similar and compositionally nested island bryophyte floras. It was understandable that the biotas of proximate islands exhibit a higher level of nestedness than those of distant islands [17]. The 66 islands highly varied in area size, together with variation in dispersal capacity among different bryophyte species, which were possibly another reason accounting for a high level of nestedness for bryophytes in the Zhoushan Archipelago [17]. Besides, although bryophytes have a long-distance dispersal capacity, such capacity would vary among different species and categories [25]. Because taxa with a comparatively higher level of nestedness had stronger dispersal ability [17], the variation in their dispersal capacity, coupled with a range of isolation degrees of islands, would result in different levels of nestedness.

Mechanisms determining nested distributions of bryophytes

Understanding the mechanisms influencing nestedness is important for conservation and can be used to direct management efforts [26]. There existed four general hypotheses explaining nested distribution: (1) passive sampling hypothesis [27–29], (2) selective extinction hypothesis [30], (3) selective colonization hypothesis [17, 31] and (4) habitat nestedness hypothesis [32, 33].

The passive sampling hypothesis predicts that nested distribution could arise from random samples of species differing in their relative abundance [29], which simply reflects a sampling effect. Therefore data should be tested for passive sampling prior to other hypotheses [30, 34]. Our analyses found that passive sampling played little part in forming nested distribution of bryophytes in the Zhoushan archipelago.

Nestedness may occur from the selective extinction of species across islands [15]. Most studies suggested that selective extinction causes a high level of nestedness in continental archipelagos and insular habitats [3, 7, 26, 35, 36]. According to the selective -extinction hypothesis, in systems experiencing species loss, species would disappear from sites in a predictable sequence and thus lead to nestedness [37, 38]. Area is the main factor accounting for nestedness because species with large minimum-area requirements and small population size have higher extinction risks [30, 39, 40]. Among the three analyzed island environmental factors, area was the first essential attribute of island determining the nested distribution of bryophytes in the Zhoushan archipelago. Therefore, the nested distribution patterns of bryophytes in our system were attributed to, or at least partially to selective-extinction for bryophytes. Such a mechanism of area-related extinction to explain nestedness has also been reported for other biotas [7, 41]. Besides area, elevation also exerted a significant effect on nestedness of Total bryophytes, Total mosses, liverworts, pleurocarpous mosses and slightly significant effects on that of acrocarpous mosses. The effect of elevation on nestedness was likely due to habitat diversity increasing with elevation [42].

Nested species distribution may also occur if species are affiliated with different habitats and the habitats show a nested distribution across islands [15, 30, 32, 33]. In the Zhoushan archipelago, there existed a high level of nestedness for habitat types across different islands, which was consistent with the viewpoint by Cook and Quinn [17] that habitat nestedness would be stronger within continental systems because continental archipelagos tended to exhibit a larger range of island sizes and thus may also exhibit a wider range of hydrologic environments. Meyer and Kalko [43] pointed out that nested habitat distribution may produce nested subsets if many species are habitat specialists. Bryophytes are more sensitive to habitats than vascular plants, and many are habitat specialists [44]. Therefore, significantly positive Spearman correlations were detected between the ranks of the islands in the maximally packed matrix of species distribution and those of habitat types for almost all eighteen bryophyte categories. The nested distribution of bryophytes in our system was closely related to the nested habitats. Habitat nestedness hypothesis thus well explained the formation of nested distribution of bryophytes in the Zhoushan archipelago. Hylander and Dynesius [12] also found that the nested distribution of bryophytes in boreal streamside forests was mainly due to nested habitats. Additionally, bryophyte colonization on the islands of the archipelago was strongly controlled by the availability of suitable habitats. For habitats that were scarce on the islands, there existed a strong filtering effect with

sharply decreased presence probabilities for species associated with those habitats. In a northern Swedish archipelago, Tiselius [15] also found that the nested distribution of bryophytes was attributed to the habitat filtering process.

In bryophytes, there existed an influential trade-off concerning the production of a few, large spores or of many, small spores that control establishment rate vs. dispersal ability [45, 46]. Species with larger spores have a higher probability to survive in a harsher habitat, thus possibly in a wider region, or occurred in more islands. Large spores have a low dispersal capacity but better chances of successful establishment [46]. We thought that dispersal by spores was not a limiting factor for bryophytes to spread onto the whole study region considering the limited geographical region of the Zhoushan Archipelago and long-distance dispersal capacity of bryophytes by spores. Therefore, variations of spore sizes of bryophyte, which would result in differences in successful establishment rate, were possibly related to selective-colonization. Based on our available data of spore sizes from 319 moss species, we found that the nested distribution of Total mosses, acrocarpous mosses, and Pottiaceae was significantly influenced by spore sizes. That is to say, the nested distribution patterns of some bryophyte categories might partially attribute to selective-colonization because of the difference in their colonization capacities concerning spore sizes.

The selective colonization hypothesis is that habitat isolation would create nested subsets through a dispersal limitation because species with different dispersal capacities vary in their ability to colonize distant sites [26, 31]. When species show different dispersal capacities, the process of differential colonization across a gradient of island isolation will cause a nested pattern in which the more isolated islands have sampled only the subset of species with high dispersal capacity [15]. However, bryophytes have a long-distance dispersal capacity, isolation exerted negligible effects on SR of bryophytes in the continental islands (*SR*) [47, 48]. Therefore, selective colonization concerning dispersal capacity might not be a major factor in the formation of nested distribution patterns of bryophyte categories in our system. Therefore, the high level of nestedness in bryophytes in our system mainly attributed to a combination of nested habitat types and selective-extinction. Selective colonization concerning spore size played somewhat effects on the formation of nestedness for some bryophyte taxa in the Zhoushan archipelago.

A high level of nestedness indicates that conservation focus should be on the most species-rich islands. However, there was a difference between a perfect nested system and a statistically significant nested system [5]. In the Zhoushan archipelago, there existed a statistically significant nestedness for bryophytes, and bryophytes were richest in the Zhoushan Island (the largest island within the archipelago), with 232 species in total. However, among 446 species in the Zhoushan archipelago, there still nearly half of the species were absent from the largest island. The nestedness was far from a perfect level for bryophytes in the archipelago. The high proportion of species absent in the species-richest island also indicated that other islands should not be neglected in the conservation of bryophytes. Additionally, the levels of nestedness varied among bryophyte families on continental islands. For families with lower

levels of nestedness, such as Leskeaceae, Fissidentaceae, and Funariaceae, their biological conservation should cover more islands than other families with high levels of nestedness.

Conclusions

There existed a high level of nestedness for 18 categories of bryophytes in the Zhoushan archipelago. The nestedness level was higher for mosses than liverworts, higher for acrocarpous mosses than pleurocarpous mosses. Thirteen families varied in their nestedness levels to some extent. The nested distribution of bryophytes was not due to passive sampling, but mainly due to a combination of nested habitats and selective-extinction. Selective colonization concerning spore size also exerted somewhat effects on nestedness of some groups of bryophytes. For Total mosses, acrocarpous mosses, and Pottiaceae, spore size concerning establishment rate was likely a causal factor structuring nested distribution patterns. Though there was a statistically significant nestedness for bryophytes in our system, such nestedness was not perfect. Conservation of bryophytes should not only focus on the species-richest island.

Methods

Study region

The present paper is part of a series dealing with the flora, ecology and biogeography of bryophytes in the Zhoushan Archipelago, China. The study region covers 66 islands of the Archipelago (Additional file 1: Figure S1).

The previous paper presented background information about the study region, and the sampling method [51].

Data sources

The occurrences of 446 species of bryophytes on the 66 islands were reported by our previous paper, which included 367 mosses (11 species of Polytrichaceae, 149 pleurocarpous mosses, 207 acrocarpous mosses), and 79 liverworts [51] (Additional file 1: Table S3).

Spore sizes of 319 moss species were available and recorded from relevant literature [52–66]. Habitat types are not equally distributed among the 66 islands. Different habitat types exhibit different capacities in maintaining species richness and species groups. We enumerated the habitat types presented on each island following the approach suggested by Triantis et al. [67]. Habitat types on each island were recorded mainly based on our observations *in situ* and the documents of the Editorial Board of the Island Chronicles of China (2014a, b), which included low herbosa (< 30 cm in height), high herbosa (> 30 cm in height), low broad-leaved forest (Diameter at breast height, DBH < 10 cm), middle broad-leaved forest (20 cm > DBH ≥ 10 cm), high broad-leaved forest (DBH > 20 cm), low coniferous forest (DBH < 10 m), middle coniferous forest (20 cm > DBH ≥ 10 cm), high coniferous forest (DBH > 20 cm), flower bed and pot, soil

road, vehicle road, cottage in use, abandoned cottage, paddy field, vegetable field, nursery and orchard, mountain stream, pond and reservoir, stone step, cemetery, and dock (Additional file 1: Table S2).

Data analysis

Distribution patterns and their responses to environmental factors are often taxon-specific [47]. Therefore, eighteen categories (Total bryophytes, Total mosses, liverworts, acrocarpous mosses, and pleurocarpous mosses, and thirteen families each with more than ten species) were incorporated into the analyses.

We used the matrix temperature and the NODF metric to quantify the levels of nestedness of 18 bryophyte group categories in the Zhoushan Archipelago, which allows comparison with previous literature.

The program BINMATNEST [68] had been widely used in the early studies of nestedness to produce “matrix temperature” to evaluate the level of nestedness [6, 23, 43, 69–71, 72-73]. “Matrix temperature” indicates the level of order or disorder of the matrix. The temperature varies from 0 for a perfectly nested matrix and 100 for a maximally ‘unnested’ matrix [68]. The BINMATNEST also provides three alternative null models to assess the statistical significance of matrix temperature. Among them, Null model 3 (keeping row sums and column sums fixed) provides the best performance in the evaluation of nestedness level of datasets, resulting in the smallest type I error [7, 43, 68, 74, 75]. The null model 3 was thus used to evaluate whether the 18 bryophyte categories were significantly nested. For all the other parameters, the recommended default settings of the BINMATNEST were used [68].

The NODF metric allows nestedness to be calculated independently for matrix rows (i.e. nestedness amongst islands) and matrix columns (i.e. nestedness amongst species incidences), as well as combined for the whole matrix, which was generally considered one of the most appropriate nestedness metrics [9, 15, 76, 77]. To determine whether the observed NODF metric was significantly different from the value expected for a random matrix, the default null model (also keeping row sums and column sums fixed) was used [78]. The NODF metric varies from 100 for a perfectly nested matrix and 0 for a maximally ‘unnested’ matrix [76].

The random placement model was used to determine whether passive sampling could be used to account for nested distribution patterns of Total bryophytes, Total mosses, and liverworts in the Zhoushan Archipelago. According to the random placement model, the expected number of species in Island j ($j = 1, 2, 3, \dots, n$, $n =$ number of islands) S_j could be calculated as follows [79]:

$$S_j = S - \sum_{i=1}^n (1 - a_j)^{ni}; \quad a_j = \frac{A_j}{\sum_{j=1}^n A_j}; \quad \sigma^2 = \sum_{i=1}^n (1 - a_j)^{ni} - \sum_{i=1}^n (1 - a_j)^{2ni}$$

Where S is the total number of species in focal islands; a_j is the relative area of Island j ; A_j is the area of island j ; ni is the total occurrence number of species i in the focal islands; σ^2 is the variance of the expected number of species in Island j .

The hypothesis of random distribution should be rejected if more than one-third of the points lie outside one standard deviation of the expected curve [7, 79, 80].

The order in which islands and species are sorted by BINMATNEST can be compared with environmental variables or biological traits of the species to evaluate their contributions to the nested pattern (Patterson & Armar, 2000). Because island area and elevation were highly correlated, to detect the independent contribution of the two island attributes on nested distribution of bryophytes, partial Spearman rank correlation between the island rank in the maximally packed matrix of bryophyte distribution and the rank of focal island attribute were calculated [7, 70, 81, 82].

To clarify the value of the habitat nestedness hypothesis in explaining the nested distribution of bryophytes, the BINMATNEST was used to quantify the level of habitat nestedness by calculating the matrix temperature of the presence/absence matrix of habitat types, and to provide the island rank of the maximally packed matrix of habitat type presence/absence distribution. The spearman rank correlation between the island rank of the maximally packed matrix of bryophyte presence/absence distribution and that to habitat types was calculated.

To clarify the effects of spore sizes on nested distribution of mosses, linear regressions were performed to clarify the relationship between spore size and nestedness rank of species. Considering the availability of spore size data, only Total mosses, acrocarpous mosses, pleurocarpous mosses, Bryaceae, and Pottiaceae, which involved 319 moss species, were included in the analyses. The species were reversely ranked according to their places in the maximally packed matrix of their distribution.

NODF metric was calculated and maximally nested presence-absence matrices were visualized by using vegan 2.0-10 package [78] within the R statistical framework v3.2.0 [83].

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Availability of data and material

All the datasets that used and analyzed for this study are included in the article and its Additional files. Raw datasets are available from the corresponding author on reasonable request.

Competing interests

The authors declare that they have no competing interests.

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Author contributions:

SLG and JY conceived the ideas, collected and analyzed the data, and led the writing; DDL LS and BSZ participated in the collection of the data. All authors have read and approved the final manuscript.

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Tables

Table 1. Nestedness levels of different bryophyte groupings in Zhoushan Archipelago

Groups	Number of species	Number of islands	T_{obs}	T_{exp}	T_{obs} / T_{exp}	N_{obs}	N_{exp}
Bryophytes	446	66	2.934***	22.743	0.129	41.097**	23.456
Mosses	367	66	3.210***	25.726	0.125	43.928**	24.640
Liverworts	79	47	3.190***	14.650	0.218	29.251**	18.173
Acrocarpous mosses	205	66	3.439***	24.892	0.138	41.294**	23.802
Pleurocarpous mosses	147	43	5.956***	14.691	0.405	42.292**	24.355
Brachytheciaceae	43	38	7.794***	27.245	0.286	38.799**	23.628
Bryaceae	44	62	4.941***	26.491	0.187	55.734**	31.914
Fissidentaceae	18	44	13.098***	32.655	0.401	55.786**	36.484
Funariaceae	11	45	12.838***	33.573	0.382	50.312**	35.586
Hypnaceae	25	34	3.984***	22.123	0.180	66.344**	34.432
Leskaceae	13	32	8.619***	21.350	0.404	38.042**	27.067
Leucobryaceae	18	32	4.558***	14.056	0.324	50.434**	29.378
Mniaceae	11	33	1.819***	17.871	0.102	63.310**	34.388
Polytrichaceae	11	28	6.964***	22.017	0.316	64.157**	38.140
Pottiaceae	57	64	4.786***	23.545	0.203	60.193**	40.078
Thuidiaceae	13	41	2.708***	18.138	0.149	71.895**	40.075
Lejeuneaceae	13	34	3.737***	10.994	0.340	31.266*	20.370
Lophocoleaceae	12	34	5.718***	18.248	0.313	44.990**	28.860

Note: T_{obs} , T_{exp} , N_{obs} , N_{exp} are observed matrix temperature, expected matrix temperature, observed matrix NODF and expected matrix NODF, respectively; ***: $P < 0.001$, ** $P < 0.01$, * $P < 0.05$

Table 2. Spearman correlations between the ranks of the islands in the maximally packed matrix of species distribution and those of habitat types for 18 categories of bryophytes in the Zhoushan Archipelago.

Categories	correlation	n	Significance level	Categories	correlation	n	Significance level
Total bryophytes	0.919	66	< 0.001	Funariaceae	0.478	45	< 0.001
Total mosses	0.924	66	< 0.001	Hypnaceae	0.792	35	< 0.001
Liverworts	0.699	47	< 0.001	Leucobryaceae	0.565	32	< 0.001
Acrocarpous mosses	0.906	66	< 0.001	Thuidiaceae	0.641	41	< 0.001
Pleurocarpous mosses	0.761	43	< 0.001	Mniaceae	0.538	33	< 0.002
Brachytheciaceae	0.635	41	< 0.001	Lejeuneaceae	0.397	34	< 0.05
Bryaceae	0.735	62	< 0.001	Polytrichaceae	0.417	28	< 0.05
Fissidentaceae	0.643	44	< 0.001	Lophocoleaceae	0.231	34	< 0.2
Pottiaceae	0.847	64	< 0.001	Leskaceae	0.218	32	< 0.5

Table 3. Partial spearman coefficients of nestedness with area and elevation

for 18 categories of bryophytes on the Zhoushan archipelago

Categories (number of island with focal taxa)	Area	Elevation	Categories (number of island with focal taxa)	Area	Elevation
Bryophytes (66)	0.339**	0.274**	Funariaceae (45)	0.065	0.045
Mosses (66)	0.362**	0.271**	Thuidiaceae (41)	0.448**	0.002
Liverworts (47)	0.159	0.228*	Polytrichaceae (28)	0.391**	-0.013
Acrocarpousmosses (66)	0.344**	0.247*	Leucobryaceae (32)	0.439*	0.048
Pleurocarpous mosses (43)	0.226*	0.322**	Fissidentaceae (45)	0.453**	-0.104
Pottiaceae (64)	0.343**	0.170	Leskaceae (32)	0.158	0.0172
Bryaceae (62)	0.355**	0.053	Mniaceae (33)	0.359**	-0.005
Brachytheciaceae (41)	0.258*	0.067	Lejeuneaceae (33)	0.001	0.082
Hypnaceae (35)	0.376**	0.223*	Lophocoleaceae (34)	0.356**	-0.064

Note: **: $P < 0.05$, *: $P < 0.2$

Figures

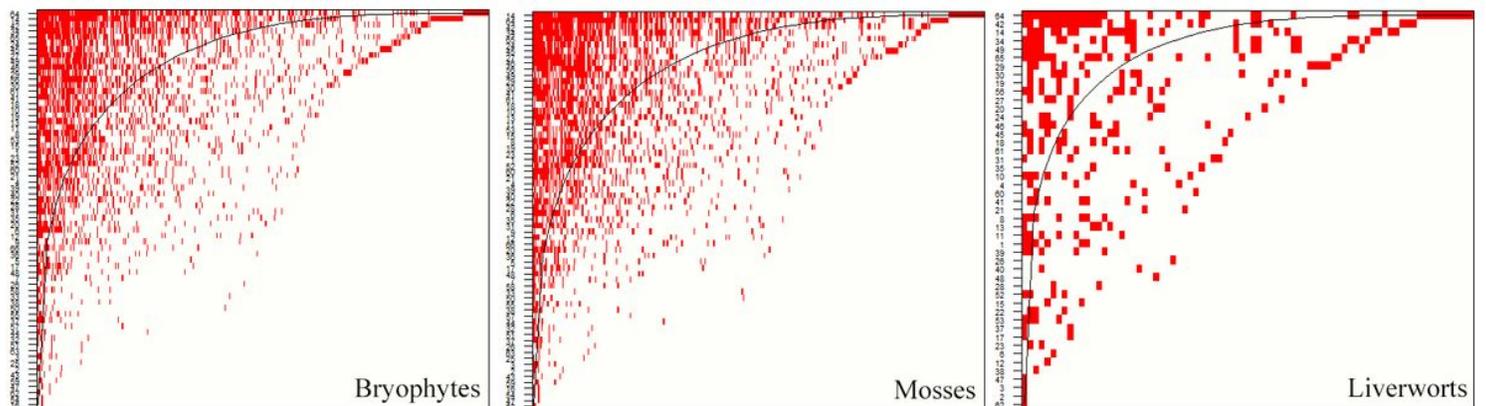


Figure 1

Maximally nested presence-absence matrix of Total bryophytes, Total mosses and liverworts from 66 islands of the Zhoushan archipelago. Note: x-axis is for species, y-axis for islands. No species number were marked because of too many species to be showed. Shadow is for presence, and blank for absence.

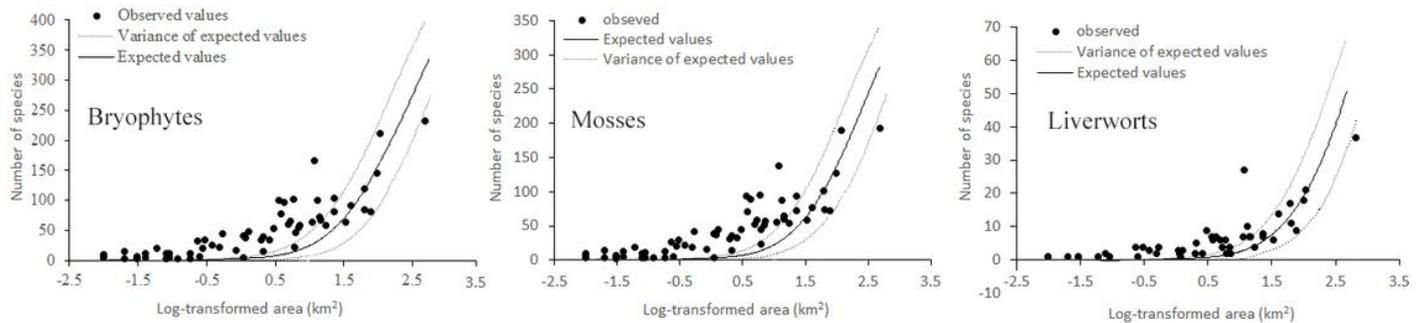


Figure 2

Comparison of observed data with expected value under the random placement models for bryophytes, mosses and liverworts in the Zhoushan archipelago

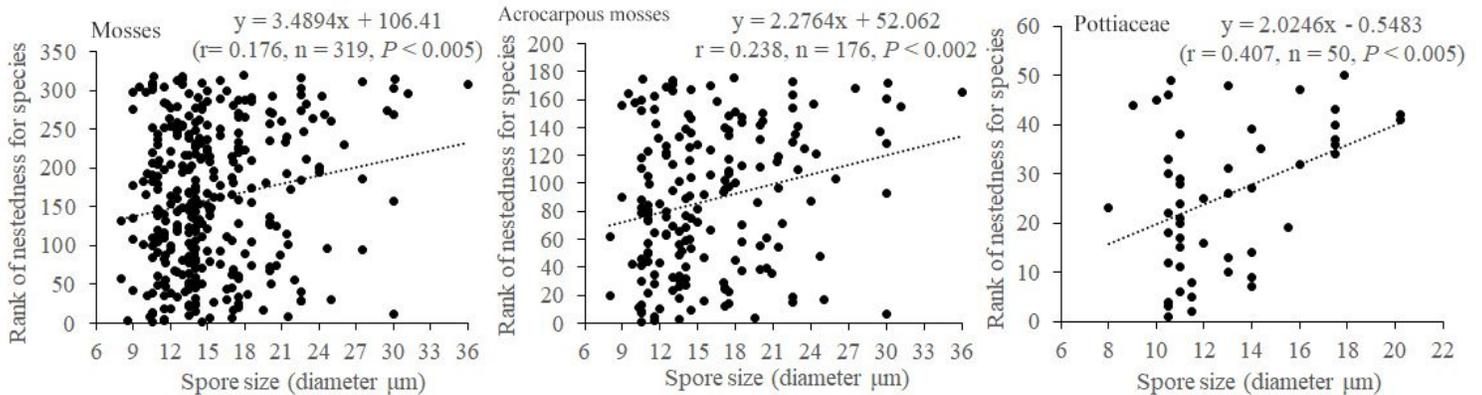


Figure 3

Relationship between nested ranks of moss distribution and their spore sizes

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