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

CURRENT STATUS: UNDER REVIEW

Jing Yu
Shanghai Normal University

Dandan Li
Shanghai Normal University

Lin Shen
Shanghai Normal University

Busheng Zhuo
Shanghai Normal University

Shuiliang Guo  gsg@shnu.edu.cn
Shanghai Normal University

Corresponding Author
ORCiD: 0000-0001-5666-6045

DOI:
10.21203/rs.2.16293/v1

SUBJECT AREAS
Terrestrial Ecology

KEYWORDS
BINMATNEST, matrix temperature, NODF, null model, selective colonization hypothesis, selective extinction hypothesis, passive sampling hypothesis, habitat nestedness hypothesis
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 complied 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 km$^2$ [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 Leskaceae, 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 $j$ ($j = 1, 2, 3, \ldots n$, $n =$ number of islands) $S_j$ could be calculated as follows [79]:
\[ S_j = S - \sum_{i=1}^{n_i} (1 - a_j) \alpha_i; \quad a_j = \frac{A_j}{\sum_{j=1}^{n} A_j}; \quad \sigma^2 = \sum_{i=1}^{n_i} (1 - a_j)^2 \]

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 \( j \); \( n_i \) is the total occurrence number of species \( i \) in the focal islands; \( \sigma^2 \) 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.

Funding

This study was supported by the National Nature Science Foundation of China (Bryophyte diversity and biogeography of the coastal island along Zhejiang and Fujie Provinces, China, No. 31570208) and Shanghai Engineering Research Centre of Plant Germplasm Resources (No. 17DZ2252700). The fund of the National Nature Science Foundation of China supported the design, sample collection, analysis, and interpretation of data as well as writing the manuscript. The fund of Shanghai Engineering Research Centre of Plant Germplasm Resources supported partial sample collection.

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.

Acknowledgments

We thank Wei Wei, Xiaoying Ma, Cheng Zang, Lichang Yan, Jinrong Cai, and Qi Wang, Shanghai Normal University, for collecting specimens. Thanks are also due to Prof. Tong Cao, Shanghai Normal University, for identifying bryophyte specimens, and to Prof. Rod Seppelt, Bundall, Queensland, Australia, for improving the English text.

References

1. Gaston KJ, Blackburn TM. Pattern and Process in Macroecology. Blackwell Science, Oxford, 2000.

2. Patterson BD, Atmar W. Nested subsets and the structure of insular mammalian faunas and archipelagos. Biol J Linn Soc. 1986; 28(1-2): 65–82.

3. Atmar W, Patterson BD. The measure of order and disorder in the distribution of species in fragmented habitat. Oecologia. 1993; 96(3): 373–382.

4. Perry G, Rodda G, Fritts T, Sharp T. The lizard fauna of Guam's fringing islets: island biogeography, phylogenetic history, and conservation implications. Global Ecol Biogeogr Lett. 1998; 7(5): 353–365.

5. Fischer J, Lindenmayer DB. Perfectly nested or significantly nested—an important difference for conservation management. Oikos. 2005; 109(3): 485–494.

6. Schouten MA, Verweij PA, Barendregt A, Kleukers RJM, de Ruiter PC. Nested assemblages of Orthoptera species in the Netherlands: the importance of habitat features and life-history traits. J Biogeogr. 2007; 34(11): 1938–1946.

7. Wang YP, Bao YX, Yu MJ, Xu GF, Ding P. Nestedness for different reasons: the distributions of birds, lizards and small mammals on islands of an inundated lake.
Divers Distrib. 2010; 16(5): 862–873.

8. Dennis RL, Hardy PB, Dapporto L. Nestedness in island faunas: novel insights into island biogeography through butterfly community profiles of colonization ability and migration capacity. J Biogeogr. 2012; 39(8): 1412–1426.

9. Gao D, Perry G. Detecting the small island effect and nestedness of herpetofauna of the West Indies. Ecol Evol. 2016; 6(15): 5390-5403.

10. He XL, He KS, Hyvönen J. Will bryophytes survive in a warming world?. Perspectives in Plant Ecology. Evol Syst. 2016; 19: 49–60.

11. Vanderpoorten A, Sotiaux A, Engels P. A GIS-based survey for the conservation of bryophytes at the landscape scale. Biol Conserv. 2005; 121(2): 189–194.

12. Hylander K, Dynesius M. Causes of the large variation in bryophyte species richness and composition among boreal streamside forests. J Veg Sci. 2006; 17(3): 333–346.

13. Mateo RG, Broennimann O, Normand S, Petitpierre B, Araújo MB, Svenning JC, Baselga A, Fernández-González F, Gómez-Rubio V, Muñoz J, Suarez GM, Luoto M, Guisan A, Vanderpoorten A. The mossy north: an inverse latitudinal diversity gradient in European bryophytes. Sci Rep. 2016; 6: 25546.

14. Aranda SC, Gabriel R, Borges PA, Santos AM, Hortal J, Baselga A, Lobo JM. How do different dispersal modes shape the species-area relationship? Evidence for between-group coherence in the Macaronesian flora. Global Ecol Biogeogr. 2013; 22(4): 483–493.

15. Tiselius AK. Island biogeography of young land uplift islands viewed through the lens of bryophytes in a northern Swedish archipelago. Umeå University, Faculty of Science and Technology, Department of Ecology and Environmental Sciences, 2016.

16. Kadmon R. Nested species subsets and geographic isolation: a case study. Ecology. 1995; 76(2): 458–465.
17. Cook RR, Quinn JF. The influence of colonization in nested species subsets. Oecologia. 1995; 102(4): 413-424.

18. Simberloff D, Martin JL. Nestedness of insular avifaunas: simple summary statistics masking complex species patterns. Ornis Fennica. 1991; 68(4): 178-192.

19. Matthews TJ, Cottey-Jones HEW, Whittaker RJ. Quantifying and interpreting nestedness in habitat islands: a synthetic analysis of multiple datasets. Divers Distrib. 2015; 21(4): 392-404.

20. Zanatta F, Patiño J, Lebeau F, Massinon M, Hylander K, de Haan M, Ballings P, Degreef J, Vanderpoorten A. Measuring spore settling velocity for an improved assessment of dispersal rates in mosses. Ann Bot. 2016; 118(2): 197-206.

21. The Editorial Board of the Island Chronicles of China. The Island Chronicles of China (Vol. Zhejiang no. 1) - the northern part of Zhoushan Archipelago. Beijing: Ocean Press, 2014. [In Chinese]

22. The Editorial Board of the Island Chronicles of China. The Island Chronicles of China (Vol. Zhejiang no. 2) - the southern part of Zhoushan Archipelago. Beijing: Ocean Press, 2014. [In Chinese]

23. Wang YP, Wang X, Ding P. Nestedness of snake assemblages on islands of an inundated lake. Curr Zool. 2012; 58(6): 828-836.

24. Patiño J, Bisang L, Hedenäs L, Dirkse G, Bjarnason ÁH, Ah-Peng C, Vanderpoorten A. Baker's law and the island syndromes in bryophytes. J Ecol. 2013; 101(5): 1245-1255.

25. Wills AJ, Cranfield RJ, Ward BJ, Tunsell VL. Cryptogam Recolonization after Wildfire: Leaders and Laggards in Assemblages? Fire Ecol. 2018; 14(1): 65-84.

26. Patterson BD. The principle of nested subsets and its implications for biological conservation. Conserv Biol. 1987; 1(4): 323-334.
27. Andrén H. Can one use nested subset pattern to reject the random sample hypothesis? Examples from boreal bird communities. Oikos. 1994; 70(3): 489-491.

28. Cutler AH. Nested biotas and biological conservation: metrics, mechanisms, and meaning of nestedness. Landscape Urban Plan. 1994; 28(1): 73-82.

29. Higgins CL, Willig MR, Strauss RE. The role of stochastic processes in producing nested patterns of species distributions. Oikos. 2006; 114(1): 159-167.

30. Wright DH, Patterson BD, Mikkelsen GM, Cutler A, Atmar W. A comparative analysis of nested subset patterns of species composition. Oecologia. 1998; 113(1): 1-20.

31. Darlington Junior PJ. Zoogeography: the geographical distribution of animals. Wiley, New York, 1957.

32. Calmé S, Desrochers A. Nested bird and microhabitat assemblages in a peatland archipelago. Oecologia. 1999; 118(3): 361-370.

33. Honnay O, Hermy M, Coppin P. Nested plant communities in deciduous forest fragments: species relaxation or nested habitats?. Oikos. 1999; 84(1): 119-129.

34. Worthen WB, Carswell ML, Kelly KA. Nested subset structure of larval mycophagous fly assemblages: nestedness in a non-island system. Oecologia. 1996; 107(2): 257-264.

35. Patterson BD. On the temporal development of nested subset patterns of species composition. Oikos. 1990; 59: 330-342.

36. Cutler AH. Nested faunas and extinction in fragmented habitats. Conserv Biol. 1991; 5(4): 496-504.

37. Patterson BD. Mammalian extinction and biogeography in the Southern Rocky Mountains. In: Nitecki MH. (ed) Extinctions. University of Chicago Press, Chicago, 1984, pp 247-293.

38. Simberloff D, Levin B. Predictable sequences of species loss with decreasing island
area-land birds in two archipelagos. New Zeal J Ecol. 1985; 8(1): 11–20.

39. Patterson BD, Atmar W. Analyzing species composition in fragments. In: Rheinwakl D ed. Isolated Vertebrate Communities in the Trop, Proceedings of the 4th International Symposium, Bonn. Bonn. Zool. Monogr. 2000; 46: 93–108.

40. Watling JI, Donnelly MA. Fragments as islands: a synthesis of faunal responses to habitat patchiness. Conserv Biol. 2006; 20(4): 1016–1025.

41. Feeley K. Analysis of avian communities in Lake Guri, Venezuela, using multiple assembly rule models. Oecologia. 2003; 137(1): 104–113.

42. Kreft H, Jetz W, Mutke J, Kier G, Barthlott W. Global diversity of island floras from a macroecological perspective. Ecol Lett. 2008; 11(2): 116–127.

43. Meyer CF, Kalko EK. Bat assemblages on Neotropical land-bridge islands: nested subsets and null model analyses of species co-occurrence patterns. Divers Distrib. 2008; 14(4): 644–654.

44. Goffinet B, Shaw AJ. Bryophyte Biology. Cambridge University Press, UK, 2010.

45. During HJ. Ecological classification of bryophytes and lichens. In: Bates JW & Farmer AM eds, Bryophytes and lichens in a changing environment. Oxford: Clarendon Press, 1992, 1–31.

46. Löbel S, Rydin H. Trade-offs and habitat constraints in the establishment of epiphytic bryophytes. Funct Ecol. 2010; 24(4): 887–897.

47. Patiño J, Weigelt P, Guilhaumon F, Kreft H, Triantis KA, Naranjo-Cigala A, Sólymos P, Vanderpoorten A. Differences in species-area relationships among the major lineages of land plants: a macroecological perspective. Global Ecol Biogeogr. 2014; 23(11): 1275–1283.

48. Patiño J, Guilhaumon F, Whittaker RJ, Triantis KA, Gradstein SR, Hedenäs L, González-Mancebo JM, Vanderpoorten A. Accounting for data heterogeneity in patterns of
biodiversity: an application of linear mixed effect models to the oceanic Island Biogeography of spore-producing plants. Ecography. 2013; 36(8): 904–913.

49. Wang JT, Wang PX. The relationship between sea level rising and climate change on east of China. Chinese J Geogr. 1980; 35: 299–313. [In Chinese]

50. Song YM. Hydrological characteristics of Zhoushan islands. J China Hydrol. 2001; 21: 59–62. [In Chinese]

51. Yu J, Shen L, Li DD, Guo SL. Determinants of bryophyte species richness on the Zhoushan Archipelago, China. Basic Appl Ecol. 2019; 37: 38–50.

52. Gao C. Flora Bryophytorum Sinicorum, Vol. 1. Beijing: Science Press, 1994; 1-368. [In Chinese]

53. Gao C. Flora Bryophytorum Sinicorum, Vol. 2. Beijing: Science Press, 1996; 1-293. [In Chinese]

54. Li XJ. Flora Bryophytorum Sinicorum, Vol. 3. Beijing: Science Press, 2000; 1–157. [In Chinese]

55. Li XJ. Flora Bryophytorum Sinicorum, Vol. 4. Beijing: Science Press, 2006; 1–263. [In Chinese]

56. Wu PC, Jia Y. Flora Bryophytorum Sinicorum, Vol. 8. Beijing: Science Press, 2004; 1–482. [In Chinese]

57. Wu PC, Jia Y. Flora Bryophytorum Sinicorum, Vol. 5. Beijing: Science Press, 2011; 1–263. [In Chinese]

58. Wu PC. Flora Bryophytorum Sinicorum, Vol. 6. Beijing: Science Press, 2002; 1–290. [In Chinese]

59. Hu RL, Wang YF. Flora Bryophytorum Sinicorum, Vol. 7. Beijing: Science Press, 2005; 1–287. [In Chinese]

60. Noguchi A. Illustrated Moss Flora of Japan. Part 1: 1–242. Hattori Botanical
61. Noguchi A. Illustrated Moss Flora of Japan. Part 2: 243-491. Hattori Botanical Laboratory, Nichinan, 1988.

62. Noguchi A. Illustrated Moss Flora of Japan. Part 3: 493-742. Hattori Botanical Laboratory, Nichinan, 1989.

63. Noguchi A. Illustrated Moss Flora of Japan. Part 4: 743-1012. Hattori Botanical Laboratory, Nichinan, 1991.

64. Noguchi A. Illustrated Moss Flora of Japan. Part 5: 1013-1253. Hattori Botanical Laboratory, Nichinan, 1994.

65. Zander RH, Eckel PM. General of the Pottiaceae: mosses of harsh environments. Buffalo Soc Nat Sci, Búfalo, NY. 1993; 32: 1-378.

66. Yu J. Studies of spores of Chinese mosses-morphology, phylogeny and ecological adaptation. Ph.D thesis of Institute of Applied Ecology, Chinese Academy of Sciences. Shengyang, 2001.

67. Triantis KA, Vardinoyannis K, Tsolaki EP, Botsaris I, Lika K, Mylonas M. Re-approaching the small island effect. J Biogeogr. 2006; 33(5): 914-923.

68. Rodríguez-Gironés MA, Santamaría L. A new algorithm to calculate the nestedness temperature of presence-absence matrices. J Biogeogr. 2006; 33(5): 924-935.

69. Zhang JC, Wang YP, Jiang PP, Li P, Yu MJ, Ding P. Nested analysis of passeriform bird assemblages in the Thousand Island Lake region. Biodivers. 2008; 16(4): 321-331.

70. Frick WF, Hayes JP, Heady III PA. Nestedness of desert bat assemblages: species composition patterns in insular and terrestrial landscapes. Oecologia. 2009; 158(4): 687-697.

71. Heino J, Mykrä H, Muotka T. Temporal variability of nestedness and idiosyncratic species in stream insect assemblages. Divers Distrib. 2009; 15(2): 198-206.
72. Li ZT, Lu Z, Shu XL, Jiang GW, Xu L, Zhou F. Nestedness of bird assemblages in the karst forest fragments of southwestern Guangxi, China. Chinese Birds. 2013; 4(2): 170-183.

73. Wang T, Sun T, Xiao YY, Liu Y, Li CH, Chen DF, Li H. Nested distribution patterns of fish assemblages in Daya Bay. Chinese J Zool. 2019; 54: 327-338.

74. Ulrich W, Gotelli NJ. Null model analysis of species nestedness patterns. Ecology. 2007; 88(7): 1824-1831.

75. Ulrich W, Almeida-Neto M, Gotelli NJ. A consumer’s guide to nestedness analysis. Oikos. 2009; 118(1): 3-17.

76. Almeida-Neto M, Guimarães P, Guimarães Jr PR, Loyola RD, Ulrich W. A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. Oikos. 2008; 117(8): 1227-1239.

77. Morrison LW. Nestedness in insular floras: spatiotemporal variation and underlying mechanisms. J Plant Ecol. 2013; 6(6): 480-488.

78. Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O’Hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H. Vegan: Community Ecology Package. R package version 2.0-10, URL http://CRAN.R-project.org/package=vegan, 2013.

79. Moore JE, Swihart RK. Toward ecologically explicit null models of nestedness. Oecologia. 2007; 152(4): 763-777.

80. Coleman BD, Mares MA, Willig MR, Hsieh YH. Randomness, area, and species richness. Ecology. 1982; 63(4): 1121-1133.

81. Shipley B. Cause and Correlation in Biology: A User’s Guide to Path Analysis, Structural Equations, and Causal Inference. Cambridge University Press, Cambridge, 2000.

82. Azeria ET, Kolasa J. Nestedness, niche metrics and temporal dynamics of a
metacommunity in a dynamic natural model system. Oikos. 2008; 117(7): 1006-1019.

83. R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available online at https://www.R-project.org/, 2018.

Tables

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

| Groups            | Number of species | Number of islands | $T_{obs}$ | $T_{exp}$ | $T_{obs}/T_{exp}$ | $N_{obs}$ |
|-------------------|-------------------|-------------------|-----------|-----------|-------------------|-----------|
| Bryophytes        | 446               | 66                | 2.934***  | 22.743    | 0.129             | 41.097*   |
| Mosses            | 367               | 66                | 3.210***  | 25.726    | 0.125             | 43.928*   |
| Liverworts        | 79                | 47                | 3.190***  | 14.650    | 0.218             | 29.251*   |
| Acrocarpous mosses| 205               | 66                | 3.439***  | 24.892    | 0.138             | 41.294*   |
| Pleurocarpous mosses | 147           | 43                | 5.956***  | 14.691    | 0.405             | 42.292*   |
| Brachytheciaceae  | 43                | 38                | 7.794**   | 27.245    | 0.286             | 38.799*   |
| Bryaceae          | 44                | 62                | 4.941***  | 26.491    | 0.187             | 55.734*   |
| Fissidentaceae    | 18                | 44                | 13.098*** | 32.655    | 0.401             | 55.786*   |
| Funariaceae       | 11                | 45                | 12.838*** | 33.573    | 0.382             | 50.312*   |
| Hypnaceae         | 25                | 34                | 3.984***  | 22.123    | 0.180             | 56.344*   |
| Leskaceae         | 13                | 32                | 8.619***  | 21.350    | 0.404             | 38.042*   |
| Leucobryaceae     | 18                | 32                | 4.558***  | 14.056    | 0.324             | 50.434*   |
| Mniaceae          | 11                | 33                | 1.819***  | 17.871    | 0.102             | 63.310*   |
| Polytrichaceae    | 11                | 28                | 6.964**   | 22.017    | 0.316             | 64.157*   |
| Pottiaceae        | 57                | 64                | 4.786***  | 23.545    | 0.203             | 60.193*   |
| Thuidiaceae       | 13                | 41                | 2.708**   | 18.138    | 0.149             | 71.895*   |
| Lejeuneaceae      | 13                | 34                | 3.737***  | 10.994    | 0.340             | 31.266*   |
| Lophocoleaceae    | 12                | 34                | 5.718***  | 18.248    | 0.313             | 44.990*   |

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 | < 0.001            |
| 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.
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.
Relationship between nested ranks of moss distribution and their spore sizes

Supplementary Files

This is a list of supplementary files associated with the primary manuscript. Click to download.

Additional file 1- Figure S2 spore size and island number.jpg
Additional file 1- Figure S1 Location and map.jpg
Additional file 1- Table S1. Location, area and elevation.docx
Additional file 1- Table S2. 22 habitat types in 66 islands.xlsx
Additional file 1- Table S3 446 species and spore size.xlsx