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

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## ABSTRACT

The distribution data of 18 categories (including 446 species) of bryophytes in 66 islands of the Zhoushan Archipelago, China were compiled. By using the matrix temperature and the NODF metrics under six null models, we evaluated their nestedness levels and explored possible mechanisms to form nested distribution with partial Spearman correlation and the random placement model. The main results were as follows: 1) all the 18 categories of bryophytes exhibited a high degree of nestedness; 2) nestedness level was higher for mosses than liverworts, higher for acrocarpous mosses than pleurocarpous mosses, and also varied among families; 3) the nested distribution of bryophytes in the archipelago was not due to passive sampling, but mainly due to nested habitats and selective-extinction; 4) spore size might be a factor linked to selective-colonization accounting for nestedness of some bryophyte categories; and 5) nestedness level was higher for families with a high proportion of generalists than those with a high proportion of specialists, the conservation of the latter should cover more islands (patches).

## KEY WORDS

Bryophytes,  
distribution,  
habitat,  
islands,  
spore size.

## RÉSUMÉ

*Quantifier et interpréter l'imbrication des bryophytes dans l'archipel de Zhoushan, Chine.*

Les données de distribution de 18 catégories (comprenant 446 espèces) de bryophytes dans 66 îles de l'archipel de Zhoushan, en Chine, ont été compilées. En utilisant la température de la matrice et les métriques NODF sous six modèles nuls, nous avons évalué leurs niveaux d'imbrication et exploré les mécanismes possibles pour former une distribution imbriquée avec la corrélation partielle de Spearman et le modèle de placement aléatoire. Les principaux résultats sont les suivants : 1) les 18 catégories de bryophytes présentaient un degré élevé d'imbrication ; 2) le niveau d'imbrication était plus élevé pour les mousses que pour les hépatiques, plus élevé pour les mousses acrocarpiques que pour les mousses pleurocarpiques, et variait également entre les familles ; 3) la distribution imbriquée des bryophytes dans l'archipel n'était pas due à un échantillonnage passif, mais principalement à des habitats imbriqués et à une extinction sélective ; 4) la taille des spores pourrait être un facteur lié à la colonisation sélective expliquant l'imbrication de certaines catégories de bryophytes ; et 5) le niveau d'imbrication était plus élevé pour les familles avec une forte proportion de généralistes que pour celles avec une forte proportion de spécialistes, la conservation de ces dernières devrait couvrir plus d'îles (îlots).

## MOTS CLÉS

Bryophytes,  
distribution,  
habitat,  
îles,  
taille des spores.



## INTRODUCTION

Detecting distribution patterns and understanding their origin is an important aspect of ecology. Conservation of any taxa in a certain area requires data on the distributional patterns of species richness (Hokkanen *et al.* 2009).

Nestedness is one of the distribution patterns of regional biotas (Gaston & Blackburn 2000), depicting a scene in which species occurring at species-poor islands are always present in a more species-rich island (Patterson & Atmar 1986). 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 (Patterson & Atmar 1986; Atmar & Patterson 1993; Perry *et al.* 1998; Fischer & Lindenmayer 2005; Schouten *et al.* 2007; Wang *et al.* 2010; Dennis *et al.* 2012; Gao & Perry 2016). Nestedness has gradually become an important part of the theoretical framework of island biogeography and conservation biology (Patterson 1987; Lindenmayer & Fischer 2007; Whittaker & Fernández-Palacios 2007; Xu *et al.* 2017).

One of the most significant contributions of nested subset theory to conservation biology was to inform managers what size patches should be reserved in a fragmented landscape (Berglund & Jonsson 2003), which was related to the SLOSS debate. The SLOSS (a single large or several small) debate originated from the application of island biogeography theory to reserve network design (Quinn & Harrison 1988). The core question of SLOSS debate was whether a single large (SL) or (O) several small (SS) reserves, with the same combined habitat area, harbor an equal number of species and are preferable as conservational units, and thus be equally valuable for conservation purposes. The strategy of SLOSS depends on the level of species nestedness (Ovaskainen 2002). Patterson (1987) once pointed out that in a fragmented system perfectly nested by patch size, the largest patch will harbor more species than any number of small patches together. In such a system, all species of conservation concern will co-occur in the largest patch. Therefore, analyses of nestedness can provide a useful complementary tool to address the SLOSS problem in conservation biology (Patterson 1987; Wright & Reeves 1992).

There are four general hypotheses explaining nested distribution, i.e., passive sampling hypothesis (Andrén 1994; Cutler 1994; Higgins *et al.* 2006; Moore & Swihart 2007), selective extinction hypothesis (Wright *et al.* 1998; Tiselius 2016), selective colonization hypothesis (Cook & Quinn 1995) and habitat nestedness hypothesis (Calmé & Desrochers 1999; Honnay *et al.* 1999). The passive sampling hypothesis predicts that nested distribution could arise from random samples of species differing in their relative abundance (Higgins *et al.* 2006), which simply reflects a sampling effect. Therefore data should be tested for passive sampling prior to other hypotheses (Worthen *et al.* 1996; Wright *et al.* 1998). Nestedness may occur from the selective extinction of species across islands (Tiselius 2016; Xu *et al.* 2017). Most studies suggested that selective extinction causes a high level of nestedness in continental archipelagos and insular habitats (Patterson 1987, 1990;

Cutler 1991; Atmar & Patterson 1993; Wang *et al.* 2010; Xu *et al.* 2017). 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 (Patterson 1984; Simberloff & Levin 1985). The area is the main factor accounting for nestedness because species with large minimum-area requirements and small population size have higher extinction risks (Wright *et al.* 1998; Patterson & Atmar 2000; Watling & Donnelly 2006; Xu *et al.* 2017). The habitat nestedness hypothesis considers the nestedness of species assemblages as a result of nested habitats (Wright *et al.* 1998; Calmé & Desrochers 1999; Honnay *et al.* 1999; Tiselius 2016). 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 (Darlington 1957; Patterson 1987). Understanding the mechanisms that influence nestedness is important for conservation and can be used to direct management efforts (Patterson 1987). The mechanisms of nestedness varied among different taxa and in different fragmented landscapes (Matthews *et al.* 2015).

Discrepancies still exist in the effects of life-history traits on distribution. Kadmon (1995) 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 & Quinn (1995) advocated that colonization ability was important in producing nested subsets as good dispersers often exhibited a greater degree of nestedness than poor dispersers. Therefore, nested pattern and their mechanisms are likely taxon-specific.

Because nestedness is related to dispersal and colonization ability, and such ability is further determined by a combination of its biological characteristics (Dennis *et al.* 2012). The size of spores of bryophytes substantially impacted their dispersal distance and colonization rates (Zanatta *et al.* 2016, 2020), and should be a potential feature influencing the nested distribution of bryophytes because spore size exerts influences on dispersal capacity and establishment rate. However, there has been no work on the relationship between nested distribution patterns and spore size.

Simberloff & Martin (1991) once suggested that virtually all insular systems were nested to a certain degree. However, a debate is ongoing on the prevalence of nestedness among biotas, and among different landscapes and habitat conditions. After recalculation by using the NODF metric (an acronym for nestedness metric based on Overlap and Decreasing Fill), Matthews *et al.* (2015) thought that nestedness was thought to be less common than previously reported. The NODF metric allows nestedness to be calculated independently for matrix rows and matrix columns, as well as combined for the whole matrix. NODF was not sensitive to matrix size of fill, and less prone to Type I errors, thus generally considered one of the most appropriate nestedness metrics (Almeida-Neto *et al.* 2008; Morrison 2013; Gao & Perry 2016; Tiselius 2016). Therefore, further studies are still needed for the settlement of the above disputes by using the NODF metric.

Bryophytes, the amphibians of the 'Plant Kingdom', and the second largest group of higher plants next only to the angiosperms, constitute a fascinating component of biodiversity and are widely spread in almost all climatic conditions (Vanderpoorten & Goffinet 2009). Bryophytes exhibit specific eco-physiological features and life-history traits. They are poikilohydric with dominant gametophytes, often highly sensitive to habitats, and many species are capable of long-distance dispersal (He *et al.* 2016). Therefore, bryophytes represent an alternative strategy for survival in terrestrial environments, and the results obtained from studies of tracheophytes cannot be generalized to bryophytes (He *et al.* 2016). Bryophytes likely have their own distribution pattern in island systems owing to their specific eco-physiological features and life-history traits (Patiño *et al.* 2014). Although previous studies on nestedness covered a wide range of taxa, relatively few studies focused on bryophytes. Vanderpoorten *et al.* (2005) reported that bryophyte communities exhibited nestedness at a landscape scale. In boreal streamside forests, Hylander & Dynesius (2006) 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.* (2016) 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.* (2013) 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. Peintinger *et al.* (2003) detected a nested pattern of bryophyte distribution in fragmented wetland habitat islands by using the method of Wright & Reeves (1992), but no non-random pattern by using the method of Brualdi & Sanderson (1999). Tiselius (2016) used the NODF metric to evaluate the nestedness level of bryophytes in a northern Swedish archipelago and found that the nested distribution of bryophytes was attributed to the habitat filtering process. Nestedness has been generally reported in bryophytes but its mechanisms behind are still under debate. These sporadic studies have drawn attention to the nestedness of bryophytes and their mechanisms. Further studies on bryophytes in fragmented landscapes are not only important in designing refuges for bryophyte conservation, but also needed for settlement of the general disputes on nestedness.

The Zhoushan Archipelago, a typical fragmented landscape, is the largest in China, comprising 1339 continental islands with a total land area of 1371 km<sup>2</sup> (The Editorial Board of the Island Chronicles of China 2014a, b). These islands differ in area, elevation, and habitat types (Fig. 1; Appendices 1; 4). Bryophytes on the 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; and 2) to determine the mechanisms underlying the nestedness of bryophyte flora in the Zhoushan Archipelago.

## MATERIAL AND METHODS

### STUDY REGION

The Zhoushan Archipelago is located in the East China Sea (29°31'31.04"N, 121°30'123.25"E) in the northeast of Zhejiang Province (Fig. 1). The archipelago was connected to the mainland during the glacial period, and all the islands were separated from the mainland 7000-9000 years ago by the rising sea level during the Holocene (Wang & Wang 1980). The highest peak of the archipelago has an elevation of 544 m in the Taohua Island. The climate is typical of a subtropical ocean monsoon zone and is highly seasonal, the average annual temperature ranges from 16.0°C to 16.4°C. August is the hottest month with an average temperature ranging from 26.8°C to 27.2°C, while January is the coldest month with average temperatures ranging from 5.3°C to 5.7°C (Song 2001). The mean annual rainfall is *c.* 1243.5 mm (Song 2001). During the long history of human activity on the archipelago, the original old-growth broadleaved forests on some larger islands have been mostly destroyed. The larger islands are dominated by cultivated forests of *Pinus massoniana* Lamb., with relicts of secondary evergreen broad-leaved forests (The Editorial Board of the Island Chronicles of China 2014a, b). A set of 66 islands were selected representing a gradient of the area and maximal elevation (Appendix 1).

### DATA SOURCES

We didn't use quantitative sampling methods to obtain abundance data of species, only recorded species occurrence on each island, because we quantified the nestedness level of bryophytes in the archipelago by using the matrix temperature and the NODF metric based on presence/absence data of 466 species in 66 islands.

Four field collections (May 1-7, 2014; Jul. 25-Aug. 10, 2016; May 1-10, 2017; Jul. 20-Aug. 10, 2017) were conducted. Each island was surveyed twice during May and July to August. The same team of researchers visited each island with a comparable survey time taken for each inventory. On each island, we tried our best to search all different habitat types, and continued collection until no additional bryophyte species were found (Yu *et al.* 2019), which ensured us to obtain a complete species list of bryophytes for each island, and made the data comparable. A total of 446 species of bryophytes on the 66 islands were identified, which included 367 mosses and 79 liverworts. The occurrence (presence or absence) and specimen number of these species on each island were listed in Appendix 2 and Appendix 3, respectively.

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.* (2006). 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 have been listed in Appendix 4. Definitions of each habitat type are listed in Appendix 5.

Because only 79 liverworts were recorded and information of spore size for some species was unavailable, the sample size of liverworts is too small for us to further analyze the effect of spore size on nested distribution. Data of spore size for 303 moss species were available and recorded from relevant literature (Appendix 2), thus we analyzed the effect of spore size on nested distribution for mosses.

#### DATA ANALYSIS

Distribution patterns and responses to environmental factors are often taxon-specific (Patiño *et al.* 2013). Therefore, 18 categories (total bryophytes, total mosses, liverworts, acrocarpous mosses, and pleurocarpous mosses, and 13 families each with more than ten species) were incorporated into the analyses. These 13 families were Brachytheciaceae Schimp., Bryaceae Rchb., Fissidentaceae Schimp., Funariaceae Schwägr., Hypnaceae Schimp., Leskeaceae Schimp., Leucobryaceae Schimp., Mniaceae Schwägr., Polytrichaceae Schwägr., Pottiaceae Hampe, Thuidiaceae Schimp., Lejeuneaceae Rostovtzev, and Lophocoleaceae Müll. Frib. ex Vanden Berghen.

The most widely used nestedness metric is the matrix temperature (Atmar & Patterson 1993; Schouten *et al.* 2007; Meyer & Kalko 2008; Zhang *et al.* 2008; Frick *et al.* 2009; Heino *et al.* 2009; Wang *et al.* 2012, 2013, 2019; Li *et al.* 2013). The matrix temperature is the normalized sum of the squared relative distances of absences above and presences below a hypothetical isocline separating occupied from unoccupied areas of a perfectly nested matrix. The temperature varies from 0 for a perfectly nested matrix and 100 for a maximally ‘unnested’ matrix (Rodríguez-Gironés & Santamaría 2006). The NODF metric, another metric based on the overlap and decreasing fill, 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 (Almeida-Neto *et al.* 2008). The NODF varies from 100 for a perfectly nested matrix and 0 for a maximally ‘unnested’ matrix (Almeida-Neto *et al.* 2008), it has been generally considered one of the most appropriate nestedness metrics (Almeida-Neto *et al.* 2008; Morrison 2013; Gao & Perry 2016; Tiselius 2016).

We used the matrix temperature and the NODF metric to quantify the levels of nestedness for 18 bryophyte categories in the Zhoushan Archipelago, which allows comparison with previous literature. The NeD program (Strona *et al.* 2014) was used to calculate the above two metrics with presence/absence data of 466 species in 66 islands (row = species; column = islands in the matrix).

The statistical significance of any nestedness metric value has to be tested against some null hypotheses. However, which combination of metrics and null models should be used in each particular circumstance is a matter of debate (Ulrich & Gotelli 2007; Ulrich *et al.* 2009). We used the null models in the NeD program to evaluate the significance of the nestedness level of 18 bryophyte categories. Five null models are EE (maintains the total number of species occurrences in the matrix, but allows both row and column totals to vary freely), CE (assigns to each matrix cell a probability to be occupied

proportional to the corresponding row and column totals), EF (maintains observed column totals, but allows row totals to vary randomly), FE (maintains observed row totals but allows column totals to vary randomly), and FF (maintains both observed row and column totals) (Strona *et al.* 2014).

The BINMATNEST program also provides three alternative null models to assess the statistical significance of matrix temperature. Among them, the null model 3 provides the best performance in the evaluation of nestedness level of datasets, resulting in the smallest type I error (Rodríguez-Gironés & Santamaría 2006). The null model 3 was thus used to evaluate whether the 18 bryophyte categories were significantly nested for comparison with previous work. For all the other parameters, the recommended default settings of the BINMATNEST were used.

The above-observed nestedness indices were compared with the expected values of 2000 randomly generated matrices under focal null models.

The random placement model was used to determine whether passive sampling could be used to account for nested distribution patterns of bryophytes 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 (Moore & Swihart 2007):

$$S_j = S - \sum_{i=1}^s (1 - a_j)^{ni}, \quad a_j = A_j / \sum_{j=1}^n A_j;$$

$$\sigma^2 = \sum_{i=1}^s (1 - a_j)^{ni} - \sum_{i=1}^s (1 - a_j)^{2ni}$$

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 Island  $j$ , which is represented by specimen number of species  $i$  in Island  $j$ ;  $\sigma^2$  is the variance of the expected number of species in Island  $j$ .

The random placement model can be rejected if more than one-third of the observed values lie outside  $\pm$  one standard deviation of the expected values (Coleman *et al.* 1982; Moore & Swihart 2007; Wang *et al.* 2010).

In the maximally packed matrix produced by using the NeD program, the most species-rich island was placed along the top row and the most widely distributed species was placed in the leftmost column, both the other species and islands are decreasingly ordered from the most species-rich island to the least species-rich island and from the most common to the least common species, respectively. The rank of islands in the maximally packed matrix can be compared with environmental variables of the islands to evaluate their contributions to the nested pattern (Patterson & Atmar 2000). Because island area and elevation were highly correlated, to detect the independent contribution of the two island attributes on the 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 (Shipley 2000; Azeria & Kolasa 2008; Frick *et al.* 2009; Wang *et al.* 2010).



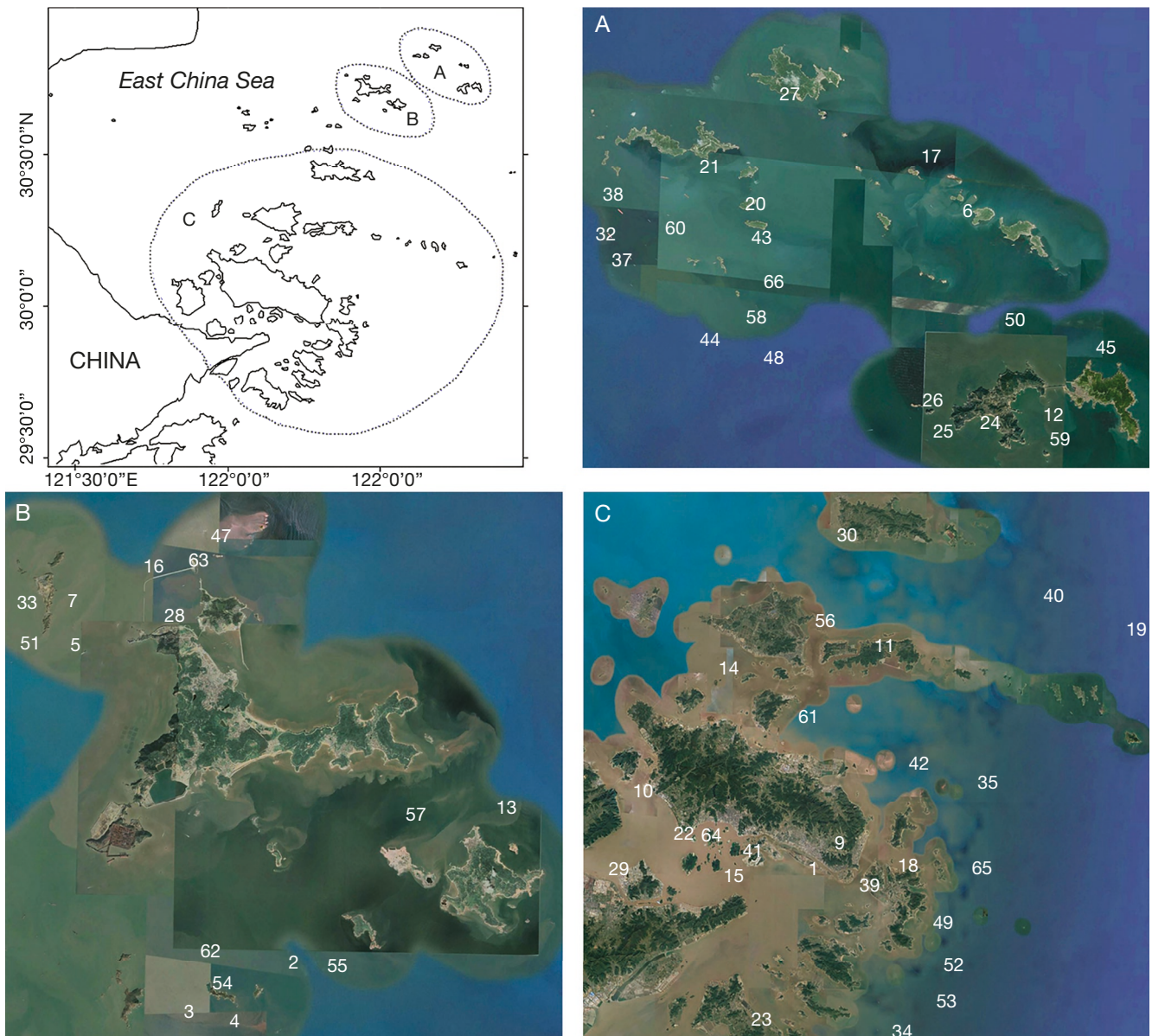


FIG. 1. — Location and map of 66 islands in the Zhoushan Archipelago (Yu *et al.* 2019).

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

To clarify the effects of spore size on the nested distribution of mosses, spearman regressions were performed to clarify the relationship between the rank of spore size (from small to large) and the rank of species in the maximally packed matrix (from left to right, or from the most common to the least

common species). Considering the availability of spore size data, only total mosses, acrocarpous mosses, pleurocarpous mosses, Bryaceae, and Pottiaceae were included in the analyses.

## RESULTS

Under null models CE, EE, FE, the distribution of all bryophyte categories in 66 islands were significantly nested by using either matrix temperature or NODF metrics, most with  $P < 0.001$ , a few with  $P < 0.01$  or  $0.05$ . Under the EF null model, except Leskeaceae, Polytrichaceae, Lejeuneaceae and Lophocoleaceae, all other 14 categories were significantly nested, most with  $P < 0.001$ . However, under the null model FF, no significant nestedness was detected for most bryophyte categories (Table 1).

TABLE 1. — Nestedness levels of different bryophyte categories in Zhoushan Archipelago. Note: **Tobs**, **Temp**, **Nobs**, **Nexp** are observed matrix temperature, expected matrix temperature, observed matrix NODF and expected matrix NODF under five null models (CE, EE, EF, FE, FF) respectively; **CE**, **EE**, **EF**, **FE**, **FF** are short for five null models in Nod program; the expected value with superscript letters **a**, **b**, and **c** indicates its difference from the observed value at  $P < 0.001$ ,  $P < 0.01$  and  $P < 0.05$ , respectively. Ratio means expected matrix temperature (under null models CE, EE, EF and FE)/observed matrix temperature.

Bryophyte categories	Number of		Temp with					Nexp with							
	species	islands	Tobs	CE	EE	EF	FE	FF	Ratio	Nobs	CE	EE	EF	FE	FF
Total bryophytes	446	66	4.882	24.417 <sup>a</sup>	44.416 <sup>a</sup>	25.927 <sup>a</sup>	20.367 <sup>a</sup>	5.471 <sup>a</sup>	5.882	41.097	18.348 <sup>a</sup>	11.66 <sup>a</sup>	16.676 <sup>a</sup>	23.473 <sup>a</sup>	40.519
Total mosses	367	66	5.013	26.575 <sup>a</sup>	47.303 <sup>a</sup>	27.364 <sup>a</sup>	22.202 <sup>a</sup>	5.697 <sup>b</sup>	6.173	43.758	19.656 <sup>a</sup>	12.577 <sup>a</sup>	18.173 <sup>a</sup>	24.589 <sup>a</sup>	42.417 <sup>a</sup>
Liverworts	79	47	7.938	18.878 <sup>a</sup>	28.504 <sup>a</sup>	18.049 <sup>a</sup>	16.678 <sup>a</sup>	7.483	2.584	29.251	15.131 <sup>a</sup>	9.222 <sup>a</sup>	14.493 <sup>a</sup>	17.324 <sup>a</sup>	30.183
Acrocarpous mosses	205	66	5.601	26.512 <sup>a</sup>	46.678 <sup>a</sup>	26.023 <sup>a</sup>	23.536 <sup>a</sup>	5.971	5.464	41.294	19.232 <sup>a</sup>	12.543 <sup>a</sup>	18.545 <sup>a</sup>	22.885 <sup>a</sup>	40.874
Pleurocarpous mosses	147	43	9.299	29.912 <sup>a</sup>	48.07 <sup>a</sup>	30.113 <sup>a</sup>	25.494 <sup>a</sup>	9.195	3.597	42.292	21.248 <sup>a</sup>	14.585 <sup>a</sup>	20.645 <sup>a</sup>	25.449 <sup>a</sup>	42.046
Brachytheciaceae	43	41	11.857	29.471 <sup>a</sup>	41.986 <sup>a</sup>	27.609 <sup>a</sup>	29.451 <sup>a</sup>	14.658 <sup>a</sup>	2.71	38.799	21.287 <sup>a</sup>	15.562 <sup>a</sup>	23.419 <sup>a</sup>	21.6 <sup>a</sup>	36.04 <sup>b</sup>
Bryaceae	45	62	7.911	31.798 <sup>a</sup>	51.533 <sup>a</sup>	24.668 <sup>a</sup>	34.544 <sup>a</sup>	8.203	4.505	55.734	27.476 <sup>a</sup>	18.105 <sup>a</sup>	35.485 <sup>a</sup>	24.788 <sup>a</sup>	57.18
Fissidentaceae	18	44	19.571	41.775 <sup>a</sup>	57.239 <sup>a</sup>	31.864 <sup>a</sup>	47.817 <sup>a</sup>	18.811	2.283	55.786	35.986 <sup>a</sup>	28.31 <sup>a</sup>	43.591 <sup>a</sup>	33.159 <sup>a</sup>	56.466
Funariaceae	11	45	22.214	42.842 <sup>a</sup>	56.13 <sup>a</sup>	31.633 <sup>a</sup>	48.454 <sup>a</sup>	21.788	2.016	50.312	38.602 <sup>a</sup>	31.422 <sup>a</sup>	42.185 <sup>a</sup>	35.835 <sup>a</sup>	50.73
Hypnaceae	25	35	9.71	33.971 <sup>a</sup>	53.026 <sup>a</sup>	27.023 <sup>a</sup>	38.589 <sup>a</sup>	8.827	3.922	68.964	33.971 <sup>a</sup>	23.176 <sup>a</sup>	44.287 <sup>a</sup>	29.687 <sup>a</sup>	70.213
Leskeaceae	13	32	24.508	35.853 <sup>c</sup>	45.689 <sup>a</sup>	26.4	41.831 <sup>a</sup>	20.113	1.527	38.042	29.722 <sup>b</sup>	22.239 <sup>a</sup>	36.319	22.888 <sup>a</sup>	42.083
Leucobryaceae	18	34	13.208	29.786 <sup>a</sup>	42.195 <sup>a</sup>	22.436 <sup>a</sup>	34.304 <sup>a</sup>	13.229	2.439	50.434	27.936 <sup>a</sup>	18.564 <sup>a</sup>	36.27 <sup>a</sup>	22.861 <sup>a</sup>	51.762
Mniaceae	12	33	11.192	31.875 <sup>a</sup>	45.104 <sup>a</sup>	17.002 <sup>b</sup>	42.813 <sup>a</sup>	11.73	3.058	63.31	34.04 <sup>a</sup>	22.233 <sup>a</sup>	56.463 <sup>c</sup>	21.099 <sup>a</sup>	63.435
Polytrichaceae	11	28	24.366	37.739 <sup>c</sup>	51.616 <sup>a</sup>	24.459	54.473 <sup>a</sup>	22.25	1.727	55.905	40.671 <sup>c</sup>	30.449 <sup>a</sup>	53.224	26.259 <sup>a</sup>	54.63
Pottiaceae	57	64	6.305	29.981 <sup>a</sup>	49.882 <sup>a</sup>	23.557 <sup>a</sup>	33.697 <sup>a</sup>	8.049 <sup>c</sup>	5.435	55.484	24.573 <sup>a</sup>	15.947 <sup>a</sup>	32.71 <sup>a</sup>	22.057 <sup>a</sup>	54.314
Thuidiaceae	13	41	9.443	31.929 <sup>a</sup>	52.391 <sup>a</sup>	18.748 <sup>a</sup>	49.918 <sup>a</sup>	11.364 <sup>c</sup>	4.049	71.895	38.8 <sup>a</sup>	25.041 <sup>a</sup>	58.198 <sup>a</sup>	25.049 <sup>a</sup>	71.781
Lejeuneaceae	13	34	18.733	30.339 <sup>b</sup>	40.298 <sup>a</sup>	20.302	37.031 <sup>a</sup>	19.018	1.706	31.266	24.294 <sup>b</sup>	15.457 <sup>a</sup>	37.47	13.229 <sup>a</sup>	32.272
Lophocoleaceae	12	34	16.854	35.026 <sup>b</sup>	50.84 <sup>a</sup>	19.928	53.265 <sup>a</sup>	18.306	2.358	58.925	46.905 <sup>c</sup>	38.054 <sup>a</sup>	58.454	32.879 <sup>a</sup>	60.491

TABLE 2. — Results tested by using the passive sampling model for 18 bryophyte categories in the Zhoushan Archipelago. Note: **Observed value**, number of islands with focal bryophyte category; **Outside value**, number of islands whose observed species richness of focal bryophyte category lie outside  $\pm$  one standard deviation of the expected species richness based on the null model proposed by Moore & Swihart (2007).

Categories	Observed value	Outside value	Outside value /observed value $\times 100$ (%)
Bryophytes	66	59	89.39
Mosses	66	58	87.88
Liverworts	47	30	63.89
Acrocarpous mosses	66	56	84.85
Pleurocarpous mosses	43	34	79.07
Brachytheciaceae	41	28	68.29
Bryaceae	62	51	82.26
Fissidentaceae	44	30	68.18
Funariaceae	45	38	84.44
Hypnaceae	35	25	71.43
Lejeuneaceae	34	23	67.65
Leskeaceae	32	23	71.88
Leucobryaceae	34	24	70.59
Lophocoleaceae	34	23	67.65
Mniaceae	33	20	60.61
Polytrichaceae	28	16	57.14
Pottiaceae	64	53	82.81
Thuidiaceae	41	22	53.66

Under the null model 3 in the BINMATNEST program, significant nested patterns were detected for all 18 categories of bryophytes (Appendix 6).

If considering the ratios of mean expected matrix temperature (under the null models CE, EE, FE and EF) to the observed temperature, mosses (6173) were more strongly nested than liverworts (2584), and acrocarpous mosses (5464) more strongly than pleurocarpous mosses (3597). Pottiaceae (5435) were the most strongly nested family, followed (in decreasing order) by Bryaceae (4505), Thuidiaceae (4049), Hypnaceae (3922), Mniaceae (3058), Brachytheciaceae (2710), Leucobryaceae (2439), Lophocoleaceae (2358), Fissidentaceae (2283), Funariaceae (2016), Polytrichaceae (1727), Lejeuneaceae (1706), and Leskeaceae (1527).

For all the 18 categories of bryophytes, more than one-third of islands whose observed species richness values lie outside  $\pm$  one standard deviation of the expected values under the null model proposed by Moore & Swihart (2007) (Table 2; Appendix 7), thus their significant nestedness levels were not due to passive sampling.

Habitat types in the 66 islands was significantly nested ( $P$ -values  $< 0.001$ ) by either matrix temperature or NODF under four null models (EE, EF, FE and CF), but not significantly by both metrics under the FF null model (Table 3).

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, total mosses, liverworts, acrocarpous mosses, pleurocarpous mosses, and eight families including Brachytheciaceae, Bryaceae, Fissidentaceae, Pottiaceae, Funariaceae, Hypnaceae, Leucobryaceae and Thuidiaceae ( $P < 0.001$ ), Mniaceae ( $P < 0.002$ ), Lejeuneaceae and Pol-



TABLE 3. — Nestedness levels of 22 habitat types among 66 islands in Zhoushan Archipelago. Note: **Tobs**, **Texp**, **Nobs**, **Nexp** are observed matrix temperature, expected matrix temperature, observed matrix NODF and expected matrix NODF under five null models (CE, EE, EF, FE, FF), respectively. The expected value with superscript letter **a** indicates its difference from the observed value at  $P < 0.001$ .

<b>Tobs</b>	<b>Texp with</b>					<b>Nobs</b>	<b>Nexp with</b>				
	<b>CE</b>	<b>EE</b>	<b>EF</b>	<b>FE</b>	<b>FF</b>		<b>CE</b>	<b>EE</b>	<b>EF</b>	<b>FE</b>	<b>FF</b>
7.421	44.051 <sup>a</sup>	70.491 <sup>a</sup>	47.180 <sup>a</sup>	34.062 <sup>a</sup>	7.342	90.259	64.158 <sup>a</sup>	52.947 <sup>a</sup>	58.994 <sup>a</sup>	70.867 <sup>a</sup>	90.533

yttrichaceae ( $P < 0.05$ ), but not for Lophocoleaceae ( $P < 0.2$ ) and Leskeaceae ( $P < 0.5$ ) (Table 4).

The ranks of island area was significantly positively correlated ( $P < 0.05$ ) with the ranks of the islands in the maximally packed matrices of 12 of the 18 bryophyte categories. No significant correlations ( $P > 0.05$ ) were found for pleurocarous mosses, Brachytheciaceae, liverworts, Funariaceae, Leskeaceae, and Lejeuneaceae. Elevation was significantly positively correlated ( $P < 0.05$ ) with the ranks of the islands in the maximally packed matrices of total bryophytes, total mosses, and pleurocarous mosses (Table 5).

The nested distribution of total mosses, acrocarpous mosses, and Pottiaceae was significantly related to spore size (Fig. 2). In Figure 2, species were ranked from the rarest to the most common in the maximally packed matrix, the species with the lowest rank has the narrowest distribution range, and the spore with the lowest rank has the smallest size. Therefore, the distribution range of the species expanded with increasing spore size for total mosses, acrocarpous mosses and Pottiaceae. No significant effect of spore size on nested distribution was detected for pleurocarpous mosses and Bryaceae in the study regions.

## DISCUSSION

Although the 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 total bryophyte and total moss 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.* (2012) reported that the observed matrix temperatures were 18.29°C, 15.58°C and 9.94°C for birds, lizards and mammals, respectively, while their corresponding expected values (under the null model 3 in the BINMATNEST program) were 48.23°C, 34.60°C and 29.53°C, respectively. The ratios of the expected matrix temperature to the observed temperature of birds, lizards, and small mammals ranged between 2.941 and 2.222, while the ratios by using the same method for total bryophyte and total moss are as high as 7.752 and 8.000, respectively (Appendix 6). Similar results were reported by Aranda *et al.* (2013) in their study of the Macaronesian flora where nestedness was higher in bryophytes than in seed plants. Bryophytes are spore-producing plants

with long-distance dispersal capacities (Patiño *et al.* 2013). We hypothesized 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 of the archipelago; and 4) the 66 islands with a range of sizes. Because overall colonization rates must be high enough to quickly compensate for any irregularity 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 (Cook & Quinn 1995). After having compared levels of nestedness among taxa with different dispersal abilities in many cases, Cook & 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.* (2013) 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 (Cook & Quinn 1995). Additionally, differences in dispersal ability among species may interact with island isolation to produce nestedness (Darlington 1957), because poor dispersers would be present only on the closest or most diverse islands, while strong dispersers would be present on most islands because of frequent colonization. Although bryophytes generally have a long-distance dispersal capacity, such capacity would vary among different species and categories with different spore sizes (Wills *et al.* 2018; Zanatta *et al.* 2020), and there still existed a dispersal restriction for bryophytes (Zanatta *et al.* 2020). This was possibly another reason accounting for a higher nestedness level of bryophytes, and the variation of nestedness level among different categories of bryophytes.

Differences in nestedness levels are likely due to difference in their responses to habitats. Generalist species with extended niche breadths often occur in different environments, and their niches tend to overlap (Bastolla *et al.* 2009). Therefore, habitat generalist species tend to have a higher level of nestedness than habitat specialist species (Neves *et al.* 2020). The species of Bryaceae and Pottiaceae are often distributed in anthropogenic habitats and many are habitat generalists (Preston *et al.* 2010; Blankenship *et al.* 2020), while epiphytic Leskeaceae and epiphyllous Lejeuneaceae contained a high proportion of habitat specialists. The nestedness level of Bryaceae and Pottiaceae was much higher than that of Leskeaceae and Lejeuneaceae, which confirmed the view of Neves *et al.* (2020) (Table 1).

TABLE 4. — Spearman correlations between the ranks of the islands in the maximally packed matrix and those of habitat types of 18 bryophyte categories in the Zhoushan Archipelago.

Categories	Correlation	Number of islands	Significance level
Total bryophytes	0.919	66	< 0.001
Total mosses	0.924	66	< 0.001
Liverworts	0.699	47	< 0.001
Acrocarpous mosses	0.906	66	< 0.001
Pleurocarpous mosses	0.761	43	< 0.001
Brachytheciaceae	0.635	41	< 0.001
Bryaceae	0.735	62	< 0.001
Fissidentaceae	0.643	44	< 0.001
Pottiaceae	0.847	64	< 0.001
Funariaceae	0.478	48	< 0.001
Hypnaceae	0.792	35	< 0.001
Leucobryaceae	0.565	32	< 0.001
Thuidiaceae	0.641	41	< 0.001
Mniaceae	0.538	33	< 0.002
Lejeuneaceae	0.397	34	< 0.05
Polytrichaceae	0.417	28	< 0.05
Lophocoleaceae	0.231	34	< 0.2
Leskaceae	0.218	32	< 0.5

The statistical significance of any nestedness index value has to be tested against some null hypothesis. The NeD program provides five null models with presence-absence matrices. Among these five null models, the FF null model tends to retain part of the structure (particularly species numbers and occurrences) of the original matrix (Cook & Quinn 1998). Hence, it might fail to detect nestedness caused by very unequal species numbers and/or site occurrences. For such matrices, other null models that contain fewer constraints might be more appropriate (Ulrich & Gotelli 2007). In the Zhoushan Archipelago, records of the 446 species on the 66 islands highly varied, from one to three islands (222 species) to 43–53 islands (four species). Meanwhile, species richness also highly varied among the 66 islands, from 3–5 species (12 islands), 212 species in the Daishan Island, to 232 species in the Zhoushan Island. Therefore, the FF null model was inappropriate and failed to detect the nestedness of bryophytes in the present study system, which was well detected under the other four null models.

Understanding the mechanisms influencing nestedness is important for conservation and can be used to direct management efforts (Patterson 1987). The passive sampling hypothesis predicts that nested distribution could arise from random samples of species differing in their relative abundance (Higgins *et al.* 2006), which simply reflects a sampling effect. Our analyses found that passive sampling played little part in forming the nested distribution of bryophytes in the Zhoushan Archipelago. According to Moore & Swihart (2007), the abundance of species in fragmented patches (or islands) was used to test the passive sampling hypothesis. In the present study, we were unable to get the abundance data of bryophytes in the 66 islands because of the high environmental complexity of the 66 islands and a relatively limited collecting time. Because each island was surveyed two times during May and July to August, and the same team of researchers visited each island, ensuring that all habitats were visited and a comparable time

TABLE 5. — Partial spearman coefficients of nestedness with area and elevation for 18 categories of bryophytes on the Zhoushan Archipelago. Note: \*,  $P < 0.05$ .

Categories (number of islands with focal taxa)	Area	Elevation
Bryophytes (66)	0.339*	0.274*
Mosses (66)	0.362*	0.271*
Liverworts (47)	0.159	0.228
Acrocarpous mosses (66)	0.344*	0.247
Pleurocarpous mosses (43)	0.226	0.322*
Pottiaceae (64)	0.343*	0.17
Bryaceae (62)	0.355*	0.053
Brachytheciaceae (41)	0.258	0.067
Hypnaceae (35)	0.376*	0.223
Funariaceae (45)	0.065	0.045
Thuidiaceae (41)	0.448*	0.002
Polytrichaceae (28)	0.391*	–0.013
Leucobryaceae (32)	0.439*	0.048
Fissidentaceae (45)	0.453*	–0.104
Leskaceae (32)	0.158	0.0172
Mniaceae (33)	0.359*	–0.005
Lejeuneaceae (33)	0.001	0.082
Lophocoleaceae (34)	0.356*	–0.064

and efforts taken for each inventory. Generally speaking, the more the specimen of a species on a given island, the high the abundance of the species. Therefore, the occurrence data of species on islands were represented by the specimen number of these species collected from each island.

Most studies suggested that selective extinction causes a high level of nestedness in continental archipelagos and insular habitats (Patterson 1987, 1990; Cutler 1991; Atmar & Patterson 1993; Wang *et al.* 2010; Xu *et al.* 2017). The area is the main factor accounting for nestedness because species with large minimum-area requirements and small population size have higher extinction risks or elimination rates in a focal island (Darlington 1957; Patterson & Atmar 2000; Watling & Donnelly 2006; Xu *et al.* 2017). The area was more important than elevation in determining the nested distribution of bryophytes in the Zhoushan Archipelago. Therefore, the nested distribution patterns of bryophytes in our system were likely 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 (Feeley 2003; Wang *et al.* 2010; Xu *et al.* 2017). 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 (Kreft *et al.* 2008).

Nested distribution may also occur if species are affiliated with different habitats and these habitats show a nested distribution across islands (Wright *et al.* 1998; Calmé & Desrochers 1999; Tiselius 2016). In the Zhoushan Archipelago, there existed a high level of nestedness for habitat types across different islands, which was consistent with the Cook & Quinn (1995) view that habitat nestedness would be stronger within continental systems, because continental archipelagos tend to exhibit a larger range of island sizes and thus may also exhibit a wider range of hydrologic environments. Meyer & Kalko

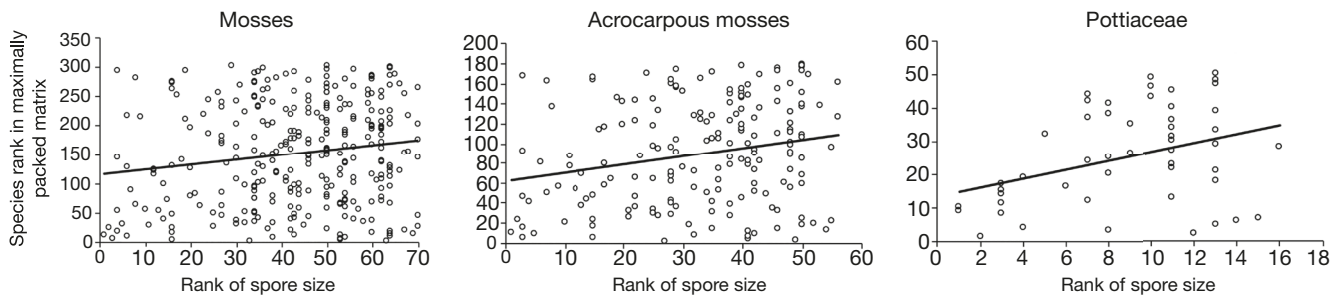


Fig. 2. — Relationship between ranks of species of total mosses, acrocarpous mosses, and Pottiaceae in their maximally packed matrices and ranks of their spore size. Note: species were ranked from the rarest to the most common in the maximally packed matrix, namely, those with the lowest rank have the narrowest distribution range, and the spore with the lowest rank has the smallest size.

(2008) 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 (Goffinet & Shaw 2000). 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 & Dynesius (2006) 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 (2016) 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 (Goffinet & Shaw 2000; Löbel & Rydin 2010). 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 the successful establishment (Löbel & Rydin 2010). We thought that dispersal by spores was not a limiting factor for bryophytes to spread onto the whole study region considering a limited geographical region of the Zhoushan Archipelago and the long-distance dispersal capacity of bryophytes by spores. Therefore, variations of spore size of bryophyte, which would result in differences in successful establishment rate, were possibly related to selective extinction (or more precisely, selective elimination). Based on our available data of spore size from 319 moss species, we found that the nested distribution of total mosses, acrocarpous mosses, and Pottiaceae was significantly influenced by spore size. That is to say, the nested distribution patterns of some bryophyte categories might partially attribute to selective elimination

because of the difference in their survival capacities concerning spore size. However, frequency of sporophyte production which could be (negatively) correlated with spore size and thus lead to unexpected results, and given that the spore sizes were mainly between 10 and 30 micrometers, i.e., really large spores were lacking, further works with larger sample covering more taxa are needed to elucidate the effect of spore size on nested distribution pattern of bryophytes.

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 (Patterson 1987). 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 (Tiselius 2016). However, bryophytes have a long-distance dispersal capacity, isolation exerted negligible effects on species richness of bryophytes in the continental islands (Patiño *et al.* 2013, 2014). In the same island system of the Zhoushan Archipelago, isolation also exerted little effect on butterfly assemblages (Xu *et al.* 2017). 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. The high level of nestedness in bryophytes in our system is mainly attributed to a combination of nested habitat types and selective extinction (or selective elimination). 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 (Fischer & Lindenmayer 2005). 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, 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.

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## APPENDICES

APPENDIX 1. — Location, area, and elevation in 66 islands of the Zhoushan Archipelago, China (Yu *et al.* 2019). [https://doi.org/10.5852/cryptogamie-algologie2022v43a6\\_s1](https://doi.org/10.5852/cryptogamie-algologie2022v43a6_s1)

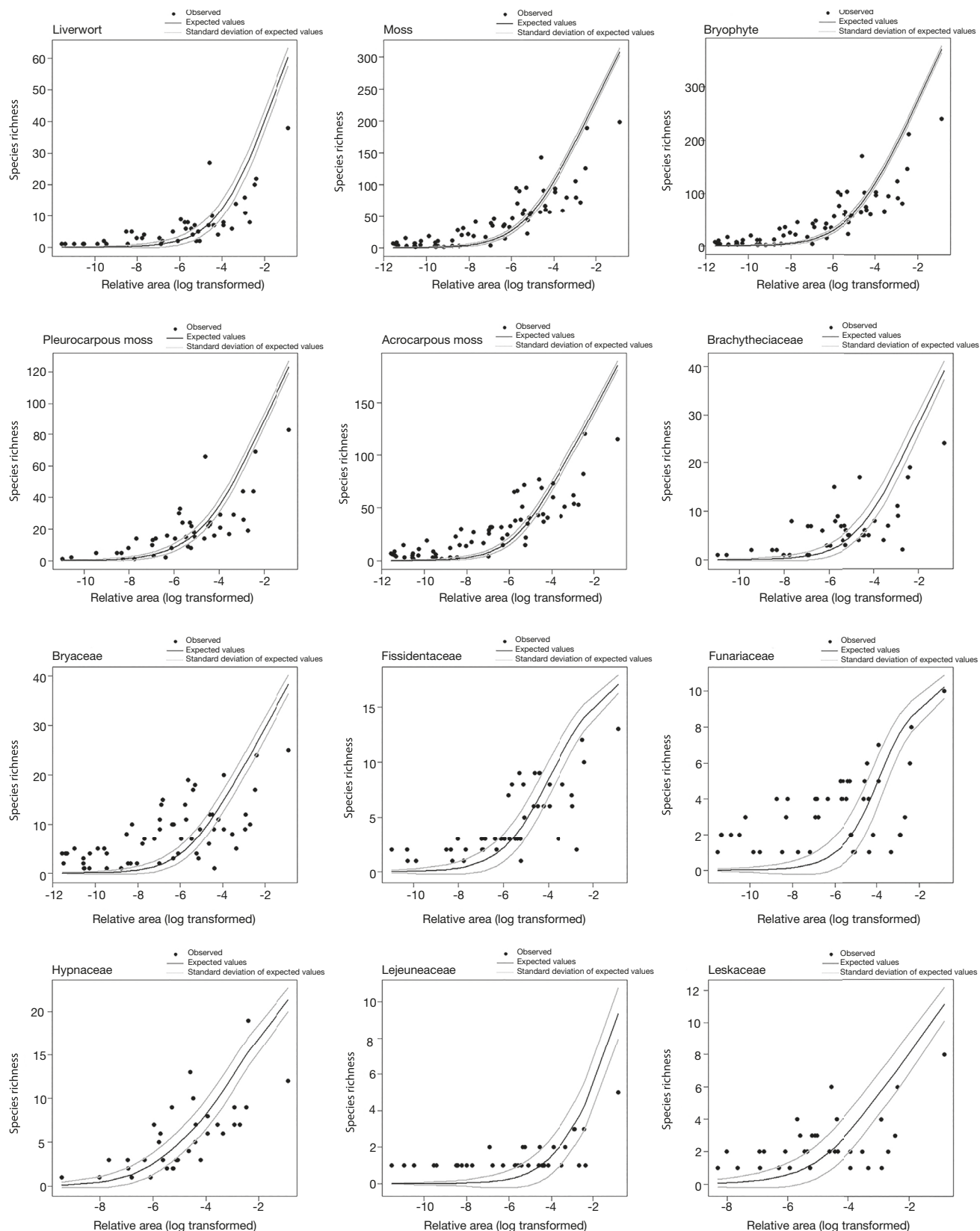
APPENDIX 2. — 446 species in 66 islands of the Zhoushan Archipelago and spore size of partial moss species. [https://doi.org/10.5852/cryptogamie-algologie2022v43a6\\_s2](https://doi.org/10.5852/cryptogamie-algologie2022v43a6_s2)

APPENDIX 3. — Specimens of 446 species in 66 islands of the Zhoushan Archipelago. [https://doi.org/10.5852/cryptogamie-algologie2022v43a6\\_s3](https://doi.org/10.5852/cryptogamie-algologie2022v43a6_s3)

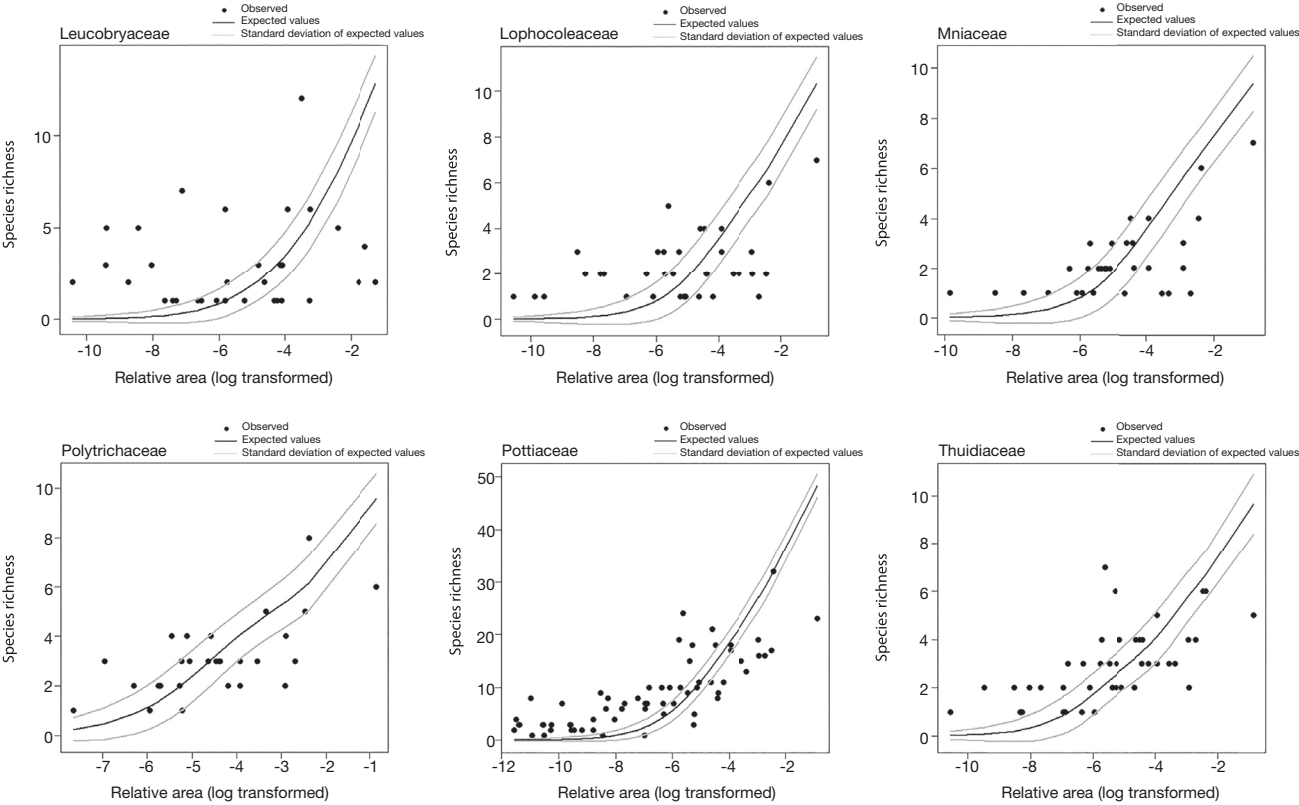
APPENDIX 4. — 22 habitat types in 66 islands of the Zhoushan Archipelago. [https://doi.org/10.5852/cryptogamie-algologie2022v43a6\\_s4](https://doi.org/10.5852/cryptogamie-algologie2022v43a6_s4)

APPENDIX 5. — Definitions of 22 habitat types in 66 islands of the Zhoushan Archipelago. [https://doi.org/10.5852/cryptogamie-algologie2022v43a6\\_s5](https://doi.org/10.5852/cryptogamie-algologie2022v43a6_s5)

APPENDIX 6. — Nestedness levels of 18 bryophyte categories in Zhoushan Archipelago under the null model 3 of the program BINMATNEST. [https://doi.org/10.5852/cryptogamie-algologie2022v43a6\\_s6](https://doi.org/10.5852/cryptogamie-algologie2022v43a6_s6)



APPENDIX 7. — The number of islands whose observed species richness of focal bryophyte category lie outside  $\pm$  one standard deviation of the expected species richness based on the null model proposed by Moore & Swihart (2007).



APPENDIX 7. — Continuation.