Science of the Total Environment 664 (2019) 334–346

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Spatial pattern of plant diversity in a group of uninhabited islands from the perspectives of island and site scales

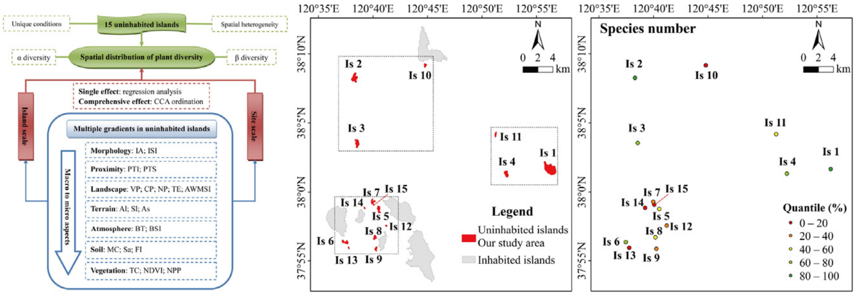
Yuan Chi [a,*], Jingkuan Sun [b], Zhanyong Fu [b,c], Zuolun Xie [d]

[a] First Institute of Oceanography, Ministry of Natural Resources, Qingdao, Shandong Province 266061, PR China
[b] Shandong Key Laboratory of Eco-Environmental Science for Yellow River Delta, Binzhou University, Binzhou, Shandong Province 256600, PR China
[c] School of Chemical and Environmental Engineering, China University of Mining and Technology, Beijing 100083, PR China
[d] State Key Laboratory of Estuarine and Coastal Research, East China Normal University, Shanghai 200062, PR China

HIGHLIGHTS

- Plant diversity on uninhabited islands in North China was analyzed at island and site scales.
- The gradients included morphology, proximity, landscape, terrain, atmosphere, soil, and vegetation.
- The plant diversity showed distinct spatial heterogeneity at the dual scales in the study area.
- Island area, vegetation condition, and terrain complexity contributed the most at island scale.
- Most of gradient factors influenced the species composition and distribution at site scale.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 7 December 2018
Received in revised form 26 January 2019
Accepted 26 January 2019
Available online 29 January 2019

Editor: Elena Paoletti

Keywords:
Uninhabited islands
Plant diversity
Spatial pattern
Multiple gradients
Island scale
Site scale

ABSTRACT

Uninhabited islands are important for providing isolated habitats for unique biological resources, and revealing the spatial pattern of plant diversity is of great significance for the island biodiversity conservation. A total of 15 uninhabited islands in Miaodao Archipelago, a group of typical uninhabited islands in North China, were selected as the study area. The multiple gradients at island and site scales were identified and quantified based on field investigation and remote sensing methods, and seven "from macro to micro" aspects, including morphology, proximity, landscape, terrain, atmosphere, soil, and vegetation, were selected to cover all aspects of factors influencing the plant diversity. Then, the single and comprehensive effects of the multiple gradients on the spatial pattern of plant diversity at the dual scales were analyzed using methods of regression analysis and canonical correspondence analysis ordination. Results indicated that 130 plant species were recorded. The species accumulation curves proved the sufficiency of the numbers of sampling sites and islands to represent the overall characteristics of plant diversity. The species composition on the uninhabited islands possessed common characteristics with the neighboring inhabited islands and mainland, meanwhile, showed unique features on the dominant species. The α diversity showed distinct spatial heterogeneities at the dual scales; the β diversity indicated the great difference of species composition within an island and among different islands. At island scale, island area, vegetation condition, and terrain complexity contributed the most to the spatial pattern of plant diversity. At site scale, biodiversity indices changed irregularly along the multiple gradient factors, yet all aspects of

---

* Corresponding author at: First Institute of Oceanography, Ministry of Natural Resources, No. 6, Xianxialing Road, Qingdao, Shandong Province 266061, PR China.
E-mail address: chiyuan@fio.org.cn (Y. Chi).

https://doi.org/10.1016/j.scitotenv.2019.01.352

gradients showed significant effects on the species composition and distribution. The island area played a fundamental role in determining the α diversity at island scale and generating the β diversity within an island, however, was not significantly correlated with the diversity at site scale.

1. Introduction

Uninhabited islands are islands without registered inhabitants living on them (Zhou, 2014). Compared with inhabited islands, most of the uninhabited islands generally possess smaller areas, farer distances to the mainland, and less human activities (Nam et al., 2010; Zhang et al., 2012; Chi et al., 2017a). Island ecosystems are always vulnerable to external disturbances due to the special position, limited areas, and isolated space (Eldridge et al., 2014; Morgan and Werner, 2014; Taramelli et al., 2015; Chi et al., 2015, 2017a; Xie et al., 2018; Gil et al., 2018). Thus, the ecosystems of uninhabited islands are more vulnerable to the disturbances, which mainly refer to natural disturbances, such as drought, storm surge, and seawater intrusion (Yang and Ying, 1997; Reaser et al., 2007; China Islands Compiling Committee, 2013; Chi et al., 2015). The islands provide isolated habitats for unique biological resources, and are always recognized as “biodiversity hotspots” with small areas but a disproportionate amount of the biodiversity (Whittaker and Fernández-Palacios, 2007; Maunder et al., 2008; Weigelt et al., 2013; Eldridge et al., 2014; Borges et al., 2018). The maintenance for plant diversity is the one of the core ecological functions of islands (Maunder et al., 2008; Nogué et al., 2017). The plant diversity on the uninhabited islands is especially valuable due to the little anthropogenic influences. These islands provide not only the important habitats for rare species, but also the natural laboratory for the study on biogeography and conservation biology (Nam et al., 2010; Chi et al., 2016; Nogué et al., 2017; Patiño et al., 2017). Meanwhile, plant diversity, which involves ecological structures, functions, and processes, is of great significance for the stability of the uninhabited island ecosystem (Hooper et al., 2005; Tilman et al., 2006; Chi et al., 2016; Chen et al., 2018). It is important to reveal the composition of the plant species and the spatial pattern of the plant diversity on the uninhabited islands, for grasping the fundamental characteristics of the island ecosystem and providing reference for island biodiversity conservation. However, current studies focusing on the plant diversity on the uninhabited islands are still insufficient.

The spatial pattern of plant diversity on the uninhabited islands is influenced by various ecological factors. The multiple gradients are naturally generated and should be artificially identified from the complicated ecological characteristics of the uninhabited islands. In a macro view, the morphology of the islands, which mainly refers to the island area and shape, is the most unique feature for the uninhabited islands, and it provides the carrier and delimits the extent for the plant community (MacArchur and Wilson, 1963, 1967; Weigelt et al., 2016; Whittaker et al., 2017; Chi et al., 2018). The proximities to the mainland, the inhabited islands, and the sea indicate the isolation of the uninhabited islands and the influences from the sea (Peng et al., 2014; Chi et al., 2016; Whittaker et al., 2017). In an intermediate view, landscape and terrain gradients take effects. The landscape gradient indicates the land cover composition and configuration, and it influences the plant diversity via the effects on the regional species pool and dispersal limitations (Janišová et al., 2014). Bedrock islands, which constitute the majority of the uninhabited islands in China, always possess complex terrain condition; the terrain condition influences the plant diversity by altering the microclimate (Panitsa et al., 2006; Chi et al., 2016; Boscutti et al., 2018). In a micro view, the atmosphere, soil factors, and vegetation growth condition directly represent different habitat conditions for the plant diversity (Hu and Xu, 2018; Jactel et al., 2018; Li et al., 2018). The aforementioned gradients cover different “from macro to micro” aspects of factors influencing the spatial pattern of plant diversity on the uninhabited islands. Furthermore, scale effects exist in the ecological characteristics of an archipelago, that is, the multiple gradients and plant diversity pattern may vary across different scales, which received few studies (Sfenthourakis and Panitsa, 2012; Chi et al., 2018; Ibanez et al., 2018). The multiple gradients can be identified and quantified at island and site scales, and they influence the spatial pattern of plant diversity at the dual scales. How the spatial pattern of plant diversity varies under the multiple gradients at the dual scales is urgent to be explored.

Therefore, the spatial pattern of plant diversity on the uninhabited islands was focused on, and a total of 15 uninhabited islands in Miaodao Archipelago, a group of typical uninhabited islands in North China, were selected as the study area. The multiple gradients at the dual scales were measured based on field investigation and remote sensing methods, and seven “from macro to micro” aspects, including morphology, proximity, landscape, terrain, atmosphere, soil, and vegetation, were selected to cover all aspects of factors influencing the plant diversity pattern. Then, the single and comprehensive effects of the multiple gradients on the spatial pattern of plant diversity at the dual scales were analyzed using methods of regression analysis and canonical correspondence analysis (CCA) ordination (Fig. 1).

We aimed to solve the following scientific questions in this study: How the plant diversity on the uninhabited islands varied under the multiple gradients at island and site scales? Which gradient factors contributed the most to the spatial pattern of plant diversity? We proposed the following hypotheses: First, The plant species compositions possessed differences between the uninhabited islands and the neighboring areas (the inhabited islands and the mainland), as well as among different uninhabited islands, due to the differences in natural and anthropogenic conditions. Second, the α and β diversities exhibited spatial heterogeneities within the studied uninhabited islands at different scales. Third, the spatial pattern of plant diversity was determined by multiple gradients, and the influences of the multiple gradients varied across island and site scales.

2. Materials and methods

2.1. Study area and data source

2.1.1. Study area

Miaodao Archipelago is located in the junction of the Bohai and Yellow Seas, and it is at the north of Shandong Peninsula in North China (Fig. 2a). The archipelago is composed of 10 inhabited islands, which possess large areas, and numerous uninhabited islands, which are small in areas. The inhabited islands carry the majority of human activity in the archipelago, whereas the uninhabited islands are much less influenced by human activities due to their small areas, distinct isolation, and steep terrain. However, some infrastructures were constructed in certain areas on parts of the uninhabited islands for the developments of tourism and aquaculture in recent years, which may result in anthropogenic influences on the plant diversity through occupying the habitat, splitting the natural landscape, generating the pollutants, and introducing alien species (Chi et al., 2016, 2017a, 2017b, 2018).

The uninhabited islands with vegetation coverage were used as our study objects. There are still many uninhabited islands that are uncovered in Miaodao Archipelago, and these islands are composed of bare

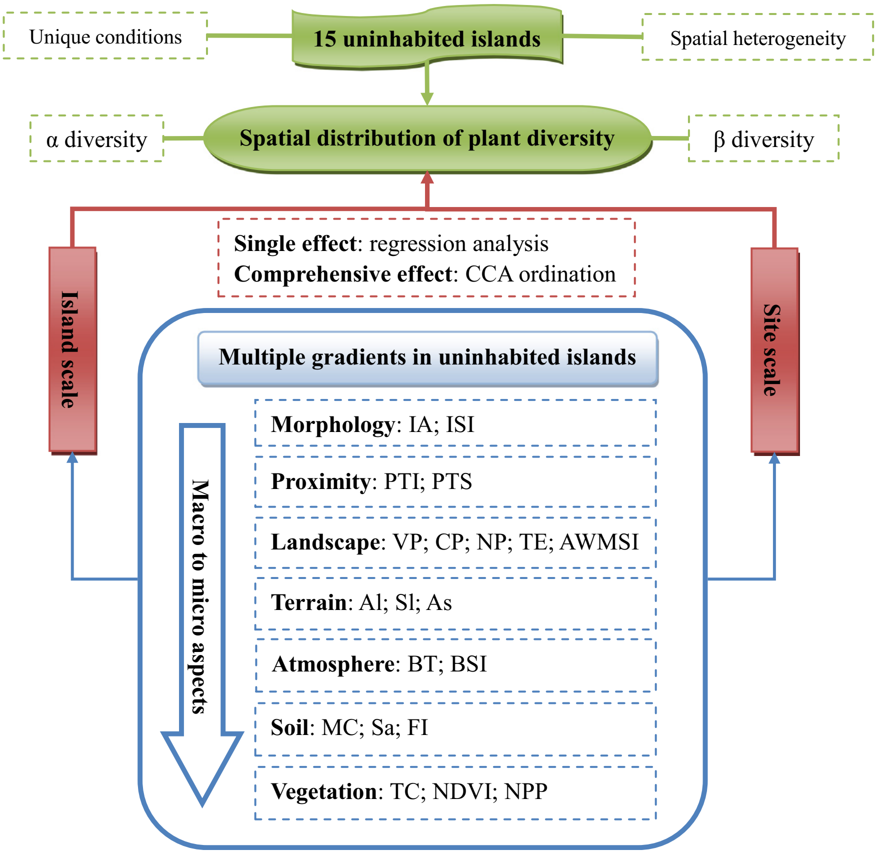


Fig. 1. Framework of spatial pattern of plant diversity from the perspectives of the dual scales: IA: island area; ISI: island shape index; PTI: proximity to the inhabited islands and the mainland; PTS: proximity to the sea; VP: vegetation proportion; CP: construction proportion; NP: number of patches; TE: total edge; AWMSI: area weighted mean shape index; Al: altitude; Sl: slope; As: aspect; BT: brightness temperature; BSI: bare soil index; MC: moisture content; Sa: salinity; FI: fertility index; TC: total coverage; NDVI: normal difference vegetation index; NPP: net primary productivity.

rock without vegetation and were not considered in this study. A total of 15 uninhabited islands were selected, and they were named as Is 1–Is 15 in a descending order of their areas (Fig. 2a). Great differences in areas, shapes, distances to the mainland exist among different islands. These islands are bedrock islands with eroded hills as the main topographic type, and the terrain conditions are complicated. Furthermore, human activity intensity, although in a low level as a whole, possesses spatial heterogeneity on different islands and in different positions within an island. All these conditions contribute to the multiple gradient effects on the spatial pattern of plant diversity at island and site scales.

2.1.2. Data source

(1) Field investigation and sampling

Field investigation and sampling were conducted in June 2018. The uninhabited islands have no routine sailings, and the docks on them are mostly simple and in disrepair, resulting in bad traffic conditions. A boat with small draft was used to reach the islands. The sampling sites were set based on the island area, vegetation area, plant community, representativeness and accessibility. Specifically, more sampling sites were set on islands with larger island and vegetation areas, as well as more various plant community types. In the process of field work, the sampling sites were set to represent the ecological characteristics of the surrounding areas, and the actual positions of the sampling sites were adjusted according to the accessibility condition in the premise of steep terrain. Finally, a total of 62 sampling sites were set (Fig. 2b, c, and d). The latitude and longitude of each sampling site were measured using a handheld GPS device. The altitude (Al), slope (Sl), and aspect (As) were measured using an electronic compass. The community types were recorded. They could be roughly divided into tree, shrub, and herb communities. In detail, tree community consisted of *Celtis bungeana*, *Robinia pseudoacacia*, *Pinus thunbergii*, *Ulmus pumila*, and *Ailanthus altissima* communities; the tree species has a low number, however, various understory shrub and herb species exist. Shrub and herb communities possess various types; the former includes *Grewia biloba*, *Flueggea suffruticosa*, and *Cudrania tricuspidata* communities; and the latter includes *Artemisia lavandulaefolia*, *Carex lanceolata*, and *Phragmites australis* communities. Plant data, including abundance, coverage, and height of species in tree, shrub, and herb layers, were investigated. The surface (0–20 cm) soil samples were collected, and moisture content (MC), salinity (Sa), total nitrogen (TN), available phosphorus (AP), available potassium (AK), and organic matter (OM) were measured in a laboratory.

(2) Remote sensing

A set of remote sensing data with the date in accordance with the field investigation were acquired from satellites LANDSAT 8 and SPOT 6. Radiometric calibration, image clipping, and band fusion were conducted using ENVI 5.3 and ArcGIS 10.0. The top of atmosphere (TOA) radiance and reflectance of each band in LANDSAT 8 data were obtained for the calculations of ecological indices. The fused image with red-green-blue color was obtained based on SPOT 6 data. Based on the fused image, the outlines of the 15 uninhabited islands were drawn. Then, the land cover types were divided into vegetation area, bare land, building land, and traffic land using visual interpretation method. They were generated for the calculations of factors in landscape gradient. The vegetation areas denote forest, shrub, and grassland; the bare lands indicate the natural lands without vegetation coverage, and consist of bare rock in the shore areas and uncovered land

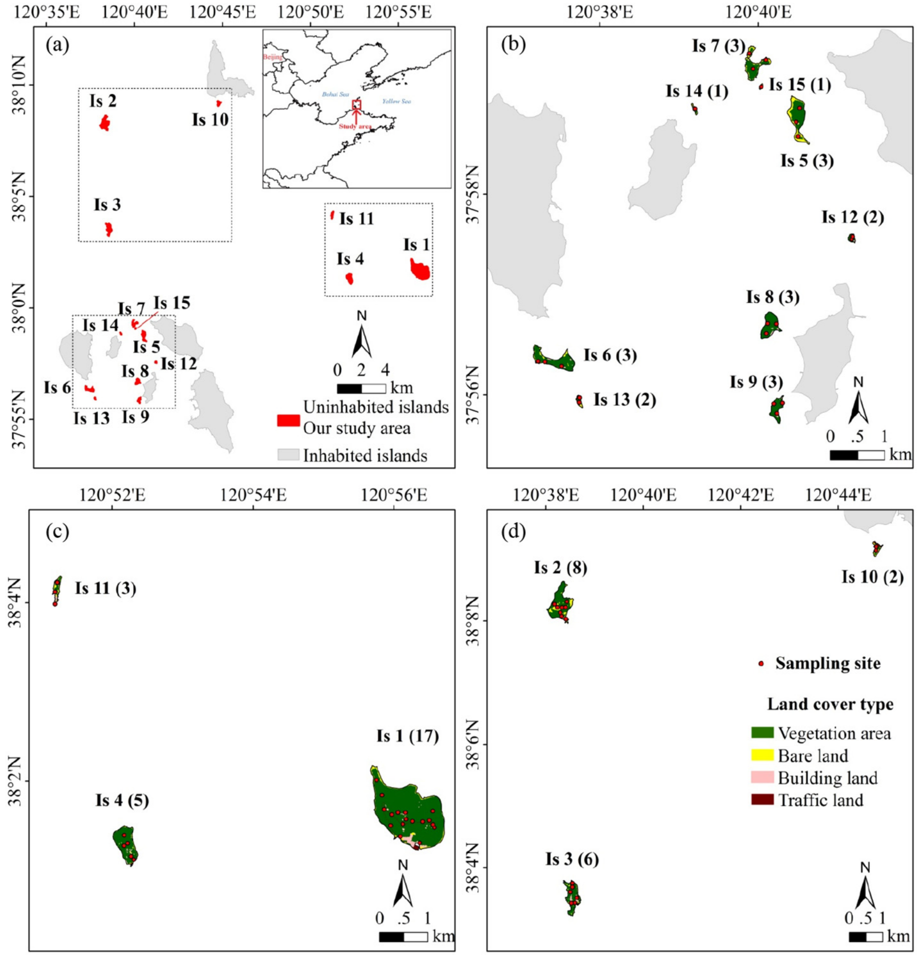


Fig. 2. Location (a), island composition (a), sampling sites (b, c, and d), and land cover types (b, c, and d) of the study area: Is 1: Dazhushan Island; Is 2: Gaoshan Island; Is 3: Houji Island; Is 4: Xiaozhushan Island; Is 5: Tanglang Island; Is 6: Nantuozi Island; Is 7: Danglang Island; Is: 8: Yangtuozi Island; Is 9: Niutuozi Island; Is 10: Tuozi Island; Is 11: Cheyou Island; Is 12: Shaobing Island; Is 13: Yulin Island; Is 14: Lijuba Island; Is 15: Xiedao Island. The number in the bracket after the island name indicates the number of sampling sites on this island.

in the inner island; the building lands refer to the building areas for tourism and aquaculture; and the traffic lands are composed of docks and roads (Fig. 2b, c, and d).

2.2. Spatial distribution of plant diversity

2.2.1. Species statistics

Shrub and herb species were used to represent the plant diversity on the uninhabited islands considering the low number of tree species. The term “species” refers to the “species, subspecies, and variety” in the study. The species on all and each of the uninhabited islands were analyzed and the species list was shown in Table S1 in the Supplementary data. The important value (IV), which was frequently used in the measurement of biodiversity indices and the determination of the dominant species, was adopted (Zhang, 2004; Fang et al., 2009; Chi et al., 2016). It was calculated based on the abundance, coverage, and height using the following equation:

$$IV_{s,i} = \left(\frac{Ab_{s,i}}{Ab_s} + \frac{Co_{s,i}}{Co_s} + \frac{He_{s,i}}{He_s}\right)/3, \tag{1}$$

where $IV_{s,i}$, $Ab_{s,i}$, $Co_{s,i}$, and $He_{s,i}$ are the IV, abundance, coverage, and height of species i in sampling site s, respectively; and Ab_s, Co_s, and He_s are the total abundance, total coverage, and total height in sample site s, respectively. On all of the uninhabited islands, the species with the highest 10 IVs were considered the dominant species; on each of the uninhabited islands, the species with the highest three IVs were considered the dominant species on this island.

Then, species accumulation curves were adopted to identify the representativeness of our recorded species for the study area (Gotelli and Colwell, 2001; Chi et al., 2016). The species accumulation curves for number of species versus numbers of sampling sites and uninhabited islands were generated by randomly and repeatedly sampling all of the record species using the software Estimate S 9.1 (Colwell, 1997).

2.2.2. α diversity

The α diversity was analyzed at island and site scales. Three indices, namely, species number (N), Shannon Wiener index (H′), and Pielou index (E), were used to measure the α diversity. The N directly refers to species richness and was used for the island scale. It was measured for each island and the N map was generated at island scale. The H′ and E reflect species complexity and evenness, respectively; they were adopted for the site scale and calculated using the following equations (Chi et al., 2016):

$$\mathrm{H}'_s = -\sum_{i=1}^{n} IV_{s,i}\mathrm{Ln}IV_{s,i}, \tag{2}$$

$$\mathrm{E}_s = \mathrm{H}'_s/\mathrm{Ln}(\mathrm{N}_s), \tag{3}$$

where N_s, H'_s, and E_s are the species number, Shannon–Wiener index, and Pielou index, respectively, of sampling site s. The two indices were calculated for each site and their maps were generated at site scale.

2.2.3. β diversity

Whittaker (W) and Jaccard (J) indices were adopted to represent the β diversity within an island and among different islands, respectively. The W was used to represent the difference of species composition across all sampling sites contained in an island; and the J aimed to reveal the species diversity variance between each two islands. The two indices were calculated using the following equations (Mac Nally et al., 2004; Magurran, 2004):

$$W = N_c/N_m - 1, \tag{4}$$

$$J = a/(a+b+c), \tag{5}$$

where N_c and N_m are cumulative N value and mean N value among all sampling sites of an island; a indicates the number of species shared by the two islands; b and c refer to the numbers of species only observed on each one of the two islands. The W was calculated for each of the islands; and the J was calculated for each combination of two islands in all the islands. Then, to explore the driving factors of the W and J indices, the relationships of the W with the island area (IA) and proximity to the inhabited islands and the mainland (PTI), as well as the J with area difference and mutual distance among islands, were analyzed.

2.3. Multiple gradient effects on the spatial pattern of plant diversity

2.3.1. Multiple gradient factors

The multiple gradients are naturally generated at island and site scales due to the unique ecological conditions of the uninhabited islands, and they were identified and classified as seven “from macro to micro” aspects.

(1) Morphology

The morphology denotes the area and shape of an uninhabited island. The IA is the most basic parameter for an island and it determines the space and carrying capacity for population, as well as various ecological processes (MacArchur and Wilson, 1963, 1967; Chi et al., 2018). The island shape affects the spatial extent of plant community and influences the continuity of its spatial distribution. It was represented by an island shape index (ISI) using the following equation (Peng et al., 2014):

$$ISI = P/\left(2 \times \sqrt{\pi \times IA}\right), \tag{6}$$

where P is the island perimeter. ISI = 1 indicates that the island shape shows a circle, and ISI increases with the increase in the complexity of the island shape. The IA and ISI were used as the morphology gradient factors, and they were derived based on the outlines of the uninhabited islands.

(2) Proximity

The proximity refers to the spatial distances to geographical objects that are important to the plant diversity on the uninhabited islands. The inhabited islands and the neighboring mainland provide species source and sink for the uninhabited islands (Whittaker et al., 2017). The PTI indicates the isolation of the uninhabited island, which greatly influence the species migration (MacArchur and Wilson, 1963, 1967; Peng et al., 2014). The sea is also an important geographical object. The seawater intrusion contaminates underground water, generates soil sanilization, and then affects plant growth (Moujabber et al., 2006; Fan et al., 2012); the sea wind restrains plant height, causes abnormal crown, and occasionally destroys plants (Niu et al., 2015). The positions closer to the sea are more influenced by the sea compared to the positions in the inner island (Chi et al., 2016). Thus, PTI and proximity to the sea (PTS) were considered the proximity gradient factors. Based on the *Euclidean Distance* tool in ArcGIS 10.0, the PTIs were obtained by inputting the positions of the barycenters of the uninhabited islands and the extents of the inhabited islands and the mainland, and the PTSs were obtained by inputting the positions of the sampling sites and the extent of the sea.

(3) Landscape

Landscape is regarded as an area that contains a mosaic of different natural and artificial land covers (Ndubisi, 2014; Chi et al., 2018). It affects the plant diversity by changing the composition and configuration of the land covers (Fu et al., 2011; Lam et al., 2018). The composition was represented by proportions of vegetation (VP) and construction areas (CP), which are natural and artificial land cover types, respectively. The construction areas are the sum of building and traffic lands. The landscape configuration was measured by common landscape indices, namely, number of patches (NP), total edge (TE), and area weighted mean shape index (AWMSI), which represent the landscape fragmentation, edge effect, and shape complexity, respectively (Chi et al., 2018). Therefore, five factors were selected in the landscape gradient, and they were obtained based on the land cover data.

(4) Terrain

The terrain gradient denotes the Al, Sl, and As, which were found to be important factors influencing the island plant diversity (Chown et al., 1998; Panitsa et al., 2006; Whittaker et al., 2017). The data for Al, Sl, and As were obtained by field work. The original As values increase clockwise from 0° to 360°, and they were standardized using the equation in the study of Chi et al. (2016). The standardized As values increase when the aspects turn to the south.

(5) Atmosphere

Atmosphere gradient refers to the heat and aridity conditions of the land surface. They are important physical parameters for the plant diversity (Chown et al., 1998; Ávila et al., 2019). The extent of the study area is in a small scale with heterogeneous temperature and precipitation, which have little effects in the spatial patterns of plant diversity within the study area. However, differences in heat and aridity conditions of the island surface still exit, and brightness temperature (BT) and bare soil index (BSI) were adopted to represent the heat and aridity gradients, respectively. They were obtained through band calculations based on the LANDSAT 8 data. The BT was calculated using the TOA radiance and the metadata (USGS, 2018); the BSI was calculated using the following equations (Hu and Xu, 2018):

$$BSI = \frac{(Re_6 + Re_4) - (Re_5 + Re_2)}{(Re_6 + Re_4) + (Re_5 + Re_2)}, \tag{7}$$

where Re_x is the TOA reflectance of band *x*.

(6) Soil

Soil factors are closely related to plant community (He et al., 2011; Li et al., 2018). Soil MC, Sa, and fertility are key factors for plant growth on bedrock islands (Chi et al., 2016). The soil factors were obtained by field sampling and laboratory measurement. The fertility was represented using a fertility index (FI) using the equation in the study of Chi et al. (2018).

(7) Vegetation

Vegetation gradient denotes the vegetation growth condition, and total coverage (TC), normalized difference vegetation index (NDVI), and net primary productivity (NPP) were used as the vegetation gradient factors. The relationship between plant diversity and productivity is a key issue in ecology research (Jactel et al., 2018; Schulze et al., 2018). The TC was measured through field work; the NDVI was obtained through band calculation based on the LANDSAT 8 data; and the NPP was estimated using the Carnegie–Ames–Stanford approach based on the LANDSAT 8 and meteorological data (Potter et al., 1993).

Table 1
Dominant species on all the uninhabited islands in Miaodao Archipelago.

Rank	Species	Genus	Family
1	*Artemisia lavandulaefolia*	*Artemisia*	Compositae
2	*Chenopodium album*	*Chenopodium*	Chenopodiaceae
3	*Flueggea suffruticosa*	*Flueggea*	Euphorbiaceae
4	*Grewia biloba*	*Grewia*	Tiliaceae
5	*Cudrania tricuspidata*	*Cudrania*	Moraceae
6	*Miscanthus sinensis*	*Miscanthus*	Gramineae
7	*Elymus dahuricus*	*Elymus*	Gramineae
8	*Dendranthema lavandulifolium*	*Dendranthema*	Compositae
9	*Phragmites australis*	*Phragmites*	Gramineae
10	*Caragana leveillei*	*Caragana*	Leguminosae

The dominant species were determined by their IVs and ranked following a descending order of IVs.

The archipelagic geological age and configuration information were also proven to be the important factors for the variation of species diversity among islands in large spatial scales (Chown et al., 1998; Ávila et al., 2019). All the islands in Miaodao Archipelago possessed the same geological background, and their formation and changes were consistent across the geological periods. At the beginning of Holocene, the configuration of Miaodao Archipelago was formed generally as it is now. Thus, the geological age and configuration information are the same among the studied islands and were not considered in the multiple gradients.

2.3.2. Multiple gradient effects at the dual scales

(1) Multiple gradient factors at the dual scales.

The multiple gradients involved seven aspects and consisted of 20 gradient factors. These factors influenced the spatial pattern of plant diversity at both island and site scales. For the 20 gradient factors, the IA, ISI, and PTI could be calculated only at island scale, and their values at site scale were assigned according to the island where the sampling sites were located. The PTS, Al, Sl, As, BT, BSI, MC, Sa, FI, TC, NDVI, and NPP could be calculated only at site scale, and their values at island scale were obtained using the average values of the sampling sites on the island. The VP, CP, NP, TE, and AWMSI can be calculated at the both scales. At island scale, these factors were calculated using the extent of the island as the analysis unit; at site scale, the analysis unit was the extent of a circle with the sampling site and 50 m as the center and radius, respectively.

(2) Single gradient effect.

The single gradient effect was analyzed to reveal the change of plant diversity along each single gradient factor. The scatter diagrams were generated using Excel, and regression analyses were conducted. At island scale, each gradient factor and the N value were used to analyze the single gradient effect; at site scale, each gradient factor and the H′/E value were used. Coefficient of determination (R^2) was obtained based on the scatter diagrams and regression analyses. The single gradient effects were evaluated based on the R^2, and considered as weak, intermediate, and strong effects when $R^2 \leq 0.3$, $0.3 < R^2 \leq 0.6$, and $R^2 > 0.6$, respectively.

(3) Comprehensive gradient effect.

The comprehensive gradient effect focuses on the spatial pattern of plant diversity under the multiple gradients. CCA ordination was adopted to reveal the comprehensive effects at the dual scales. At island scale, the matrices of "islands × species IVs" and "islands × gradient factors" were inputted as species and environmental data, respectively; at site scale, the matrices of "sampling sites × species IVs" and "sampling sites × gradient factors" were inputted. The CCA ordination diagrams were generated to reveal the spatial pattern of plant diversity under the multiple gradients. The effect degree of each gradient factor in the comprehensive effect was identified using the canonical eigenvalue (Chi et al., 2016).

3. Results

3.1. Spatial distribution of plant diversity

3.1.1. Species composition

A total of 130 plant species were recorded in the 62 sampling sites on the 15 uninhabited islands. The species belonged to 100 genera and 41 families. At the family level, Compositae possessed the highest species number (21), followed by Gramineae (14) and Liliaceae (12). At the genus level, *Artemisia* (7), *Cynanchum* (5), and *Lespedeza* (4) had the highest species numbers. The dominant species on all and each of the uninhabited islands are shown in Tables 1 and 2, respectively. *Artemisia lavandulaefolia* was the most important species in the study area. Great differences of dominant species exited among different islands, and a total of 27 dominant species were observed. *Cudrania tricuspidata* was the dominant species on five islands, i.e., Is 4, Is 7, Is 9, Is 12, and Is 13; *Phragmites australis* was the dominant species on four islands, i.e., Is 5, Is 6, Is 8, and Is 14; *Artemisia lavandulaefolia*, *Chenopodium album*, *Miscanthus sinensis*, and *Hemerocallis minor* were the dominant species on three islands. The others were the dominant species on one or two islands.

Species accumulation curves for species number versus numbers of sampling sites and uninhabited islands are shown in Fig. S1 in the Supplementary data. The species number increased with the increase

Table 2
Dominant species on different uninhabited islands.

Island	Rank 1	Rank 2	Rank 3
Is 1 (54)	*Artemisia lavandulaefolia*	*Chenopodium album*	*Grewia biloba*
Is 2 (50)	*Flueggea suffruticosa*	*Artemisia lavandulaefolia*	*Chenopodium album*
Is 3 (44)	*Flueggea suffruticosa*	*Cleistogenes hancei*	*Caragana leveillei*
Is 4 (36)	*Chenopodium album*	*Cudrania tricuspidata*	*Grewia biloba*
Is 5 (28)	*Phragmites australis*	*Imperata cylindrica*	*Leymus chinensis*
Is 6 (31)	*Vitis amurensis*	*Phragmites australis*	*Pueraria lobata*
Is 7 (19)	*Hemerocallis minor*	*Cudrania tricuspidata*	*Periploca sepium*
Is 8 (29)	*Phragmites australis*	*Artemisia lavandulaefolia*	*Oxalis corniculata*
Is 9 (22)	*Cudrania tricuspidata*	*Artemisia argyi*	*Clerodendrum trichotomum*
Is 10 (16)	*Hemerocallis minor*	*Lespedeza formosa*	*Miscanthus sinensis*
Is 11 (24)	*Allium ramosum*	*Polygonatum sibiricum*	*Artemisia capillaris*
Is 12 (18)	*Miscanthus sinensis*	*Cudrania tricuspidata*	*Hemerocallis minor*
Is 13 (16)	*Carex lanceolata*	*Vitis amurensis*	*Cudrania tricuspidata*
Is 14 (10)	*Phragmites australis*	*Ziziphus jujuba Mill. var. spinosa*	*Cynanchum chinense*
Is 15 (14)	*Dendranthema lavandulifolium*	*Miscanthus sinensis*	*Silene aprica*

The dominant species were determined by their IVs and ranked following a descending order of IVs. The abbreviations for the islands are the same as for Fig. 2. The number in the bracket after the island name indicates the species number on this island.

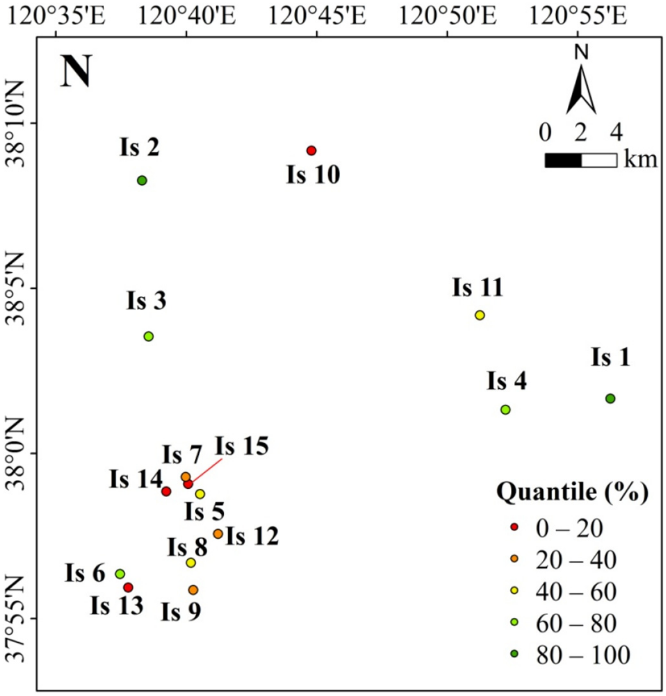


Fig. 3. Plant diversity map at island scale: N: species number. The legends were divided using a quantile method in ascending order of values.

in the numbers of sampling sites and islands. The slopes of the curves were decreasing, and the curves tended to be gentle, indicating that more sampling sites and islands yielded a fewer new species.

3.1.2. α diversity

The N map at island scale is shown in Fig. 3. The mean N value was 27.4. Is 1 and Is 2 possessed high N values of 54 and 50, respectively, followed by Is 3, Is 4, and Is 6 with N values of 44, 36, and 31, respectively. Is 8, Is 5, Is 11 had intermediate N values, and the other islands possessed low N values. The H′ and E maps at site scale are shown in Fig. 4. The mean H′ and E values were 2.155 and 0.911, respectively. The H′ and E exhibited considerable spatial heterogeneities among sampling sites on different islands and within one specific island.

3.1.3. β diversity

The W values ranged from 0 to 4.43 with the mean value of 1.45, and the highest and lowest values were achieved by Is 1 and Is 14, Is 15, respectively. The scatter diagrams for relationships of W with IA and PTI are shown in Fig. S2. The W distinctly increased with the increase in IA and PTI. The correlation coefficients of W with IA and PTI were 0.871 ($P < 0.01$) and 0.760 ($P < 0.01$), respectively; and the partial correlation coefficients of W with IA and PTI were 0.693 ($P < 0.01$) and 0.297 ($P = 0.302$), respectively (each of the IA and PTI were selected as the controlled variable for one another).

The J values between different uninhabited islands are shown in Table S2. All J values were <0.4, and the mean J value of all the combinations was 0.198, indicating the difference of species composition among different islands. All uninhabited islands showed the following descending order of the mean J values: Is 4, Is 1, Is 8, Is 12, Is 9, Is 3, Is 6, Is 5, Is 7, Is 13, Is 2, Is 11, Is 10, Is 14, and Is 15. The correlation coefficients of the J with area difference and mutual distance are shown in Table S3. For the area difference, Is 1–Is 4 showed significant negative correlations; for the mutual distance, Is 1, Is 2, Is 4, Is 10, and Is 11 exhibited significant negative correlations. The other islands had no significant correlations in the two aspects.

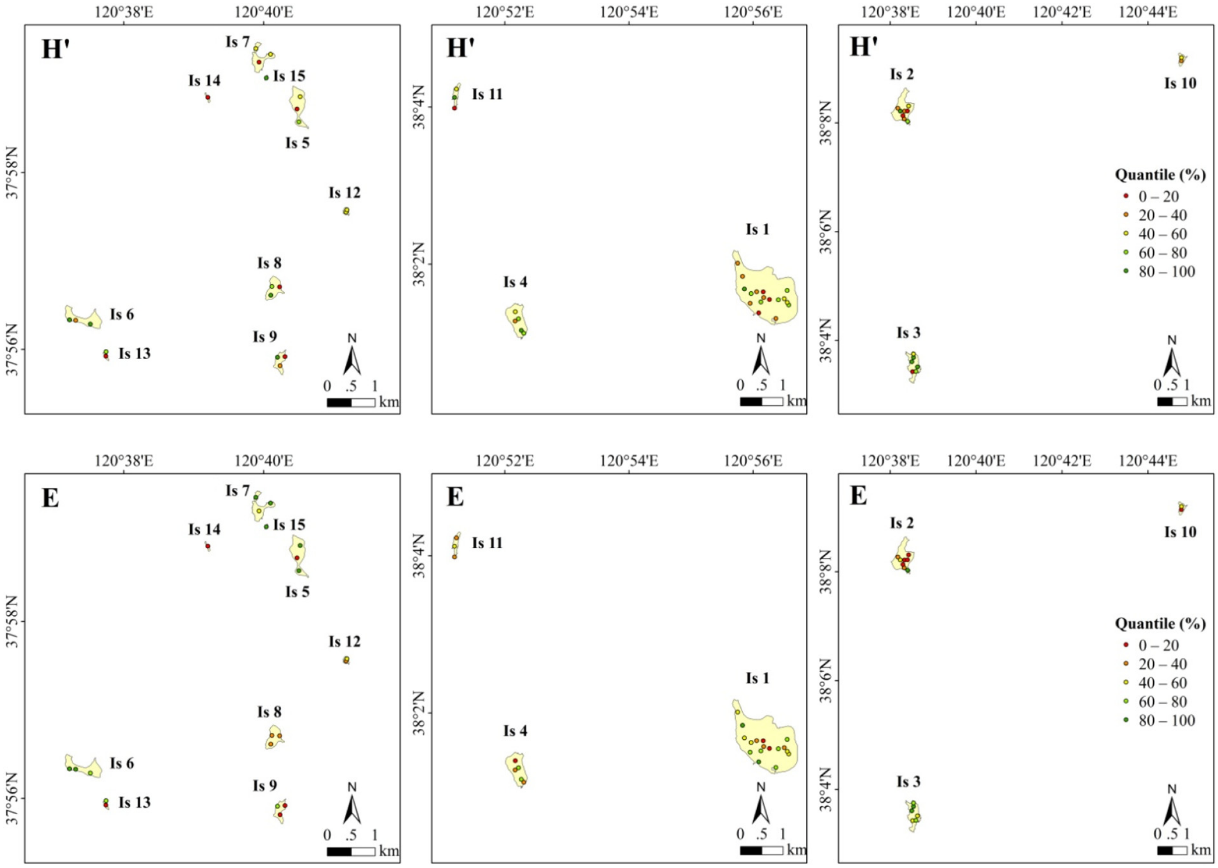


Fig. 4. Plant diversity maps at site scale: H′: Shannon-Wiener index; E: Pielou index. The legends were divided using a quantile method in ascending order of values.

3.2. Spatial pattern of plant diversity under the multiple gradient effects

3.2.1. Single gradient effect

The changes of N values along the gradient factors at island scale are shown in Fig. S3. The strong effects were observed in gradient factors of IA, PTS, NP, TE, and BT. The N values generally increased with the increase in these factors. The intermediate effects could be seen in gradient factors of PTI, VP, AWMSI, Al, NDVI, and NPP. The N values increased with the increase in PTI, VP, Al, NDVI, and NPP, and decreased with the increase in AWMSI. The other gradient factors showed weak effects.

The changes of H′ and E values along the gradient factors at site scale are shown in Figs. S4 and S5. All the gradient factors possessed weak effects on the H′ and E at site scale.

3.2.2. Comprehensive gradient effect

CCA ordination results showed that all the canonical axes were significant ($P < 0.01$). Based on axes 1 and 2, two-dimensional CCA ordination diagrams were generated. The projected position and length of the ray with an arrow on the axis referred to the nature and degree of the relationship between this axis and the gradient factor that the ray represented (Chi et al., 2016).

At island scale, the CCA ordination diagrams are shown in Fig. 5. From left to right along axis 1, ISI and BSI slightly increased, TC, FI, As, NP, NDVI, and VP slightly decreased, and TE, NPP, IA, Al, PTS, and PTI considerably decreased. From bottom to top along axis 2, BT, BSI, Al, and NP slightly decreased, and Sl greatly decreased. In Fig. 5a, species were in the 2nd and 3rd quadrants with concentrated distribution, and in the 1st and 4th quadrants with scattered distribution. In Fig. 5b, all dominant species except species 3 and 9 were distributed around the origin. Species 3 was mainly observed on islands with high NP, Al, Sl, BT, and BSI; species 9 was distributed mainly on islands with low IA, PTI, PTS, NP, TE, Al, Sl, BT, and BSI. In Fig. 5c, different colors of islands indicated different N value intervals as the legend. Most islands were distributed in the 1st and 2nd quadrants, of which the islands with low N values were mainly in the 1st quadrant. It indicated that the islands with high IA, PTI, PTS, VP, NP, TE, Al, Sl, As, FI, BT, and NDVI generally possessed high N values.

At site scale, the CCA ordination diagrams are shown in Fig. 6. From left to right along axis 1, PTI, IA, NPP, and PTS greatly increased, NDVI, Al, TC, and VP slightly increased, and BSI and ISI slightly decreased. From bottom to top along axis 2, PTI, BSI, Al, and BT slightly increased, and Sl considerably increased. In Fig. 6a, the species were distributed all over the diagram, and each species had its specific position. In Fig. 6b, the dominant species were relatively concentrated around the origin except for species 3, 5, and 9. Species 3 was mainly in sampling sites with high PTI, Al, Sl, BT, and BSI; and species 5 was on the contrary. Species 9 was always in sampling sites with low IA, PTI, PTS, VP, Al, Sl, BT, BSI, TC, NDVI, and NPP. In Fig. 6c and d, different colors of sampling sites indicated different H′ and E value intervals as the legend. Different colors of sampling sites were generally evenly distributed in the diagrams.

The effect degrees of gradient factors in the comprehensive effect were shown in Table 3. At island scale, 10 of the 20 gradient factors possessed significant effects, of which PTI, Al, and PTS had the highest effect degrees. At site scale, 15 of the 20 gradient factors showed significant effects, of which PTI, NPP, and BT had the highest effect degrees; compared to the results at island scale, ISI, As, MC, FI, TC, and NDVI changed to be significant, and TE changed to be insignificant.

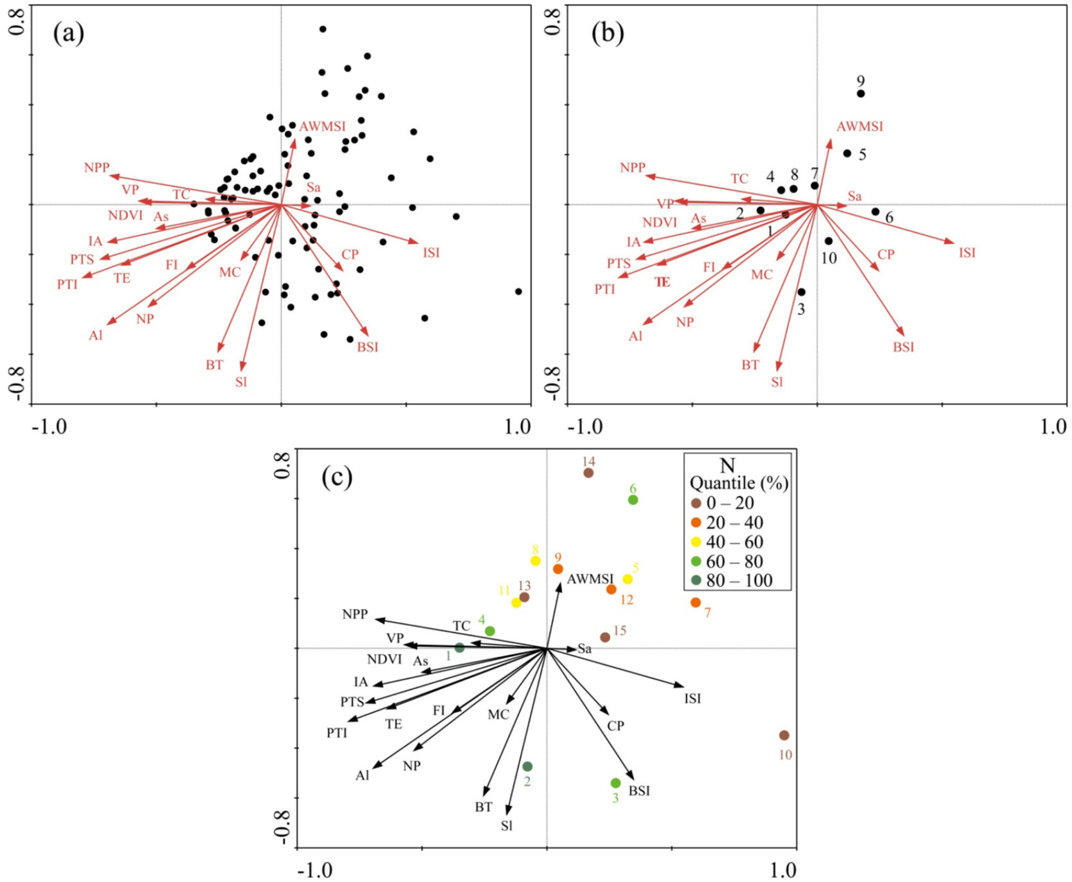


Fig. 5. CCA ordination diagrams of all species (a), dominant species (b), and all islands (c) at island scale: In (b), dominant species numbers of 1–10 indicate the corresponding dominant species in Table 1; in (c), different colors of islands indicate different values of N (species number) as for Fig. 3. Abbreviations for the gradient factors are the same as for Fig. 1.

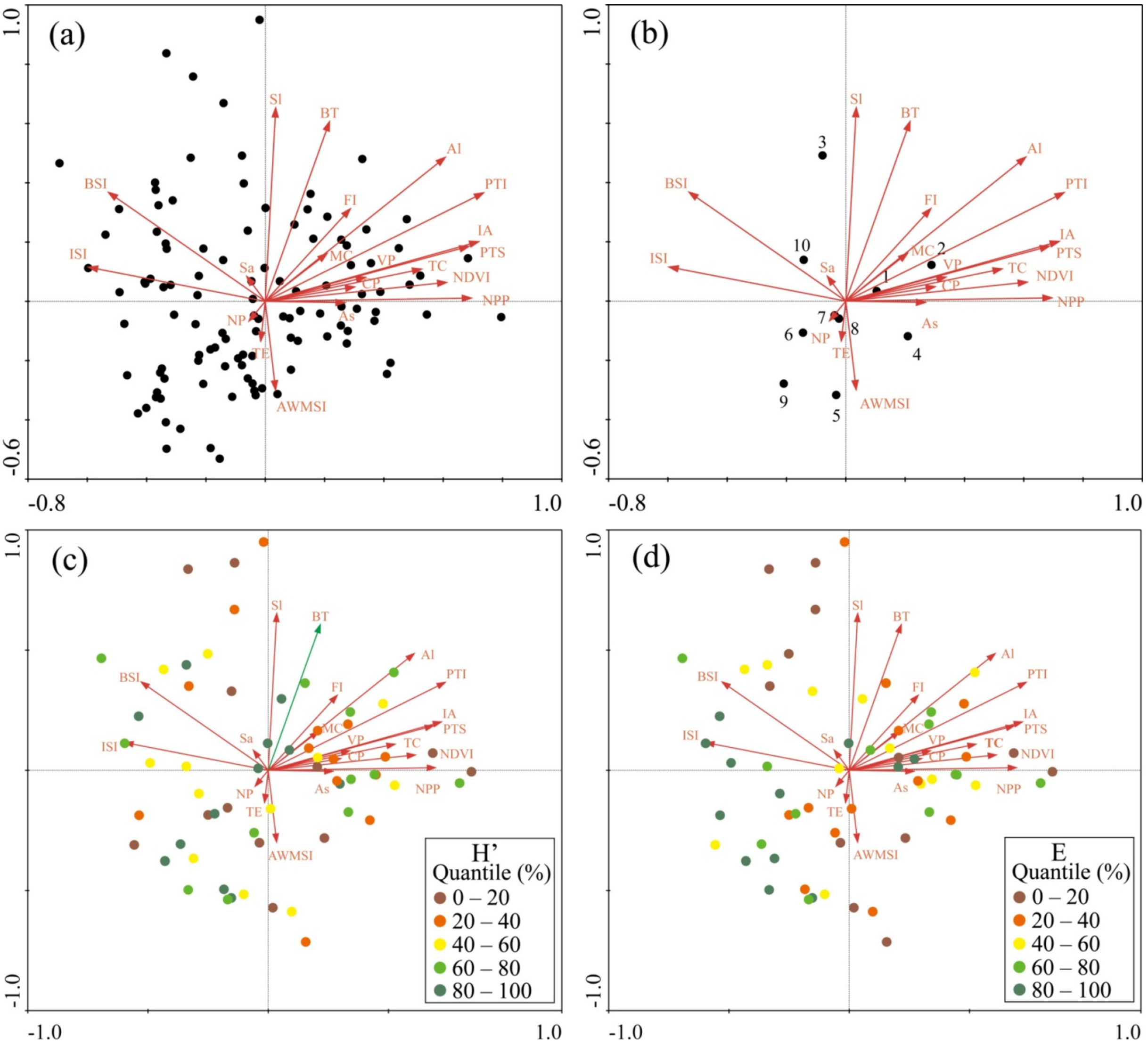


Fig. 6. CCA ordination diagrams of all species (a), dominant species (b), and all sampling sites (c and d) at site scale: in (b), dominant species numbers of 1–10 indicate the corresponding dominant species in Table 1; in (c) and (d), different colors of sampling sites indicate different values of H′ (Shannon-Wiener Index) and E (Pielou Index) as for Fig. 4. Abbreviations for the gradient factors are the same as for Fig. 1.

4. Discussion

4.1. Species composition

The total species number on the uninhabited islands in Miaodao Archipelago summed to 130 in 62 sampling sites. The species accumulation curve is an effective tool to clarify the species composition and to estimate the species richness (Ugland et al., 2003; Colwell et al., 2004; Bevilacqua et al., 2018). It could be used to verify the sufficiency of the islands and sampling sites to represent the overall characteristics of plant species composition in the study area. Generally, the curve initially drastically ascended because a large number of species were observed when the number of samples increased; then, the curve tended to be gentle when the samples reached a certain number (Ugland et al., 2003; Mao et al., 2005). The sufficiency of the islands and sampling sites was judged based on the aforementioned features. The islands and sampling sites were insufficient when the curve drastically ascended, and became sufficient when the curve was gentle. The species accumulation curve in this study indicated the sufficiency of the islands and sampling sites to represent the plant species diversity. Considering the difficulty of the field investigation due to the bad traffic condition and the complex terrain condition, our study has made a little but important contribution to the island plant species database in China. The species number in our study area was similar to other islands in China, such as the inhabited islands in Miaodao Archipelago which were in the same region to our study area and possessed 114 species (Chi et al., 2016), the Zhoushan Archipelago which was also a bedrock archipelago and possessed 125 species (Wang and Ye, 2017), and the Chongming Island which was the world's largest estuarine alluvial island and 129 species were recorded (Huang et al., 2008).

The species composition was compared with those in the neighboring mainland and inhabited islands. The Kunyu Mountain, which is located in the central Shandong Peninsular and a location of the National Forest Park, was selected to represent the species composition in the neighboring mainland (Zhang et al., 2003; Du et al., 2007; Sun et al., 2011); and the five southern islands in Miaodao Archipelago were used as the neighboring inhabited islands (Chi et al., 2016). Most of the recorded species in our study area could be frequently observed in the neighboring mainland and inhabited islands. In a large spatial scale, the uninhabited islands are offshore islands with positions close to the inhabited islands and mainland, and the highest PTI of all the uninhabited islands was 19.12 km, which was achieved by Is 1. The

Table 3
Effect degrees of each gradient factor in the comprehensive effects at island and site scales.

Gradient factor	Island scale		Site scale	
	Effect degree	P value	Effect degree	P value
IA	0.34*	0.014	0.34**	0.002
ISI	0.293	0.118	0.293**	0.002
PTI	0.379**	0.002	0.379**	0.002
PTS	0.357**	0.004	0.326**	0.002
VP	0.318*	0.028	0.275*	0.018
CP	0.261	0.48	0.205	0.274
NP	0.31	0.05	0.181	0.548
TE	0.326*	0.032	0.214	0.144
AWMSI	0.222	0.792	0.213	0.158
Al	0.379**	0.002	0.332**	0.002
Sl	0.331*	0.02	0.307**	0.002
As	0.291	0.092	0.276**	0.004
BT	0.343*	0.01	0.346**	0.002
BSI	0.327*	0.024	0.33**	0.002
MC	0.219	0.752	0.253*	0.02
Sa	0.231	0.696	0.227	0.172
FI	0.273	0.278	0.277**	0.008
TC	0.295	0.11	0.332**	0.002
NDVI	0.289	0.112	0.298**	0.002
NPP	0.341*	0.028	0.358**	0.002

Abbreviations for gradient factors are the same as for Fig. 1.
** $P < 0.01$.
* $P < 0.05$.

isolation was not as high as that on oceanic islands, resulting in the high rate of migration (Whittaker et al., 2017). Thus, the plant species list was generally identical to those in the neighboring mainland and inhabited islands. At the family level, the common families were similar in the mainland and the islands with the Compositae and Gramineae as the most two common families. At the genus level, *Artemisia* was the most common genus on the islands and possessed much higher species number than the other genera; however, it was just one of the common genera in the mainland. It indicated that the plant species composition between the islands and mainland were similar at the family level and began to show difference at the genus level. At the species level, the dominant species on the uninhabited islands were remarkably different from those on the inhabited islands. This could be explained by the difference in human activity intensity. For the inhabited islands, frequent transportation activities connecting the islands with the mainland increased the opportunity for species migration (Wu et al., 2004); extensive plantation considerably changed the understory habitat conditions and thereby influenced the specie composition (Michelsen et al., 2014); and intensive urban construction influenced the plant community through occupying the natural habitat and generating pollutants (Moffatt et al., 2004; Chi et al., 2015). All these activities resulted in the difference in the dominant species between the inhabited and uninhabited islands. The dominant species also greatly differed among different uninhabited islands, which was mainly driven by the natural conditions. *Cudrania tricuspidata* was the dominant species on five uninhabited islands with different natural conditions, indicating its wide distribution in these islands because of its high drought tolerance. *Phragmites australis* was the dominant species on four uninhabited islands, and it was always distributed near the shoreline due to its inclination to wet environment. *Chenopodium album* and *Artemisia lavandulaefolia* were mainly distributed on the uninhabited islands with large areas, whereas *Miscanthus sinensis* and *Hemerocallis minor* were always observed on small islands. Furthermore, no invasive alien species were observed in the 130 species based on the *Invasive Alien Species List in China*, which indicated the less influence from the anthropogenic introduction of alien species. As a contrast, five invasive alien species, namely, *Amaranthus retroflexus*, *Bidens pilosa*, *Conyza canadensis*, *Erigeron annuus*, and *Pharbitis purpurea*, were found on the inhabited islands (Chi et al., 2016). Therefore, the species composition on the studied uninhabited islands had the regional common characteristics, meanwhile, showed the unique features, which validated the first hypothesis of this study.

4.2. α and β diversities

The α diversity indicates the species richness and evenness in a specific area or site (Cingolani et al., 2010). The α diversity was measured using N at island scale and using H′ and E at site scale, and these indices showed distinct spatial heterogeneities at different scales. At island scale, the N values generally decreased with the increase in the island serial number, i.e., the decrease in the IA and the number of sampling sites, and the highest (54) and lowest (10) N values were achieved by Is 1 and Is 14, respectively. It can be easily understood that more sampling sites contributed a higher species number (Sun et al., 2011). However, even the Is 1 had N value lower than the half of the total N value in the study area, and each of the islands, except for Is 12 and Is 13, possessed species that only existed on this island, which indicated that almost all of the islands contributed to the plant diversity of the study area. At site scale, the mean H′ value was higher than that in the neighboring mainland and inhabited islands, and the mean E value was higher than that in the mainland but lower than that on the inhabited islands (Du et al., 2007; Chi et al., 2016). The results indicated the higher plant diversity on the islands than in the mainland, as well as the higher species complexity on the uninhabited islands than the inhabited islands, at site scale. The spatial heterogeneities of H′ and E can be observed among different sampling sites, across different islands and within the same island.

The β diversity is a metrics involving the changes of species diversity between sites or dates (Carvalho et al., 2012; Borges et al., 2018). In our study, the β diversity indicated the spatial difference of the species composition, and the W and J were adopted to reveal the species composition difference within an island and among different islands, respectively. For the β diversity within an island, the IA provides space and resource availability for different plant communities; the PTI refers to the possibilities for species migration from the inhabited islands and mainland (Whittaker et al., 2017). The significant correlation and partial correlation between W and IA revealed the decisive role of IA in generating the difference of species composition within an island, which validated the study of Ibanez et al. (2018). The significant correlation and insignificant partial correlation between W and DTI indicated the less effect of PTI on the W. For the β diversity among islands, the area difference and mutual distance of different islands represented the ecological niche and species diffusion, respectively, which were considered the main driving factors for the β diversity (Harrison et al., 1992; Soininen et al., 2007; Chi et al., 2016). Is 1–Is 4 had larger areas than the other islands, and Is 1, Is 2, Is 4, Is 10, and Is 11 were located in border positions with far mutual distances to the other islands, which resulted in the significant negative correlations of these islands in Table S3. The results indicated that both ecological niche and species diffusion processes influenced the species composition in the study area, and the larger area difference and farer mutual distance contributed to greater difference of species composition among different uninhabited islands. The studies on the β diversity have been constantly conducted and improved by different scholars (Condit et al., 2002; Anderson et al., 2010; Carvalho et al., 2012). Among the studies, Carvalho et al. (2012) proposed a new method to measure the β diversity using species replacement and species richness differences, and the method has been widely recognized. In our study, the W and J indices were clear to reveal the aspect of species replacement. In addition, the changes of α diversity along the multiple gradients were also belonging to the categories of β diversity in a broad sense (Borges et al., 2018). They corresponded to the aspect of species richness differences and were specifically elaborated in the following subsection. Furthermore, the spatial heterogeneities of the biodiversity indices corresponded to the second hypothesis of the study.

4.3. Multiple gradient effects at the dual scales

The multiple gradients on the uninhabited islands were unique and distinct, and seven "from macro to micro" aspects constituted the multiple gradients, which covered all aspects of factors influencing the plant diversity from the perspectives of island and site scales. We conducted single and comprehensive gradient effect analyses using the multiple gradient factors. The single effect analysis could reveal the changes of diversity indices, namely, N, H′, and E, along each of the gradient factors. The comprehensive effect analysis aimed to clarify not only the biodiversity index changes, but also the variations of species composition and distribution, under the multiple gradients.

At island scale, IA, PTI, PTS, VP, NP, TE, AWMSI, Al, BT, NDVI, and NPP exerted strong or intermediate effects on the plant diversity in the single gradient effect analysis, and the N values generally increased with the increase in all aforementioned factors except for AWMSI. The results were consistent with the results in the comprehensive gradient analysis, which indicated that high N values were always on the islands with high IA, PTI, PTS, VP, NP, TE, Al, Sl, As, BT, FI, and NDVI. As the aforementioned discussions, the N value increased with the increase in the IA, which is one of the basic regularities in ecology studies (Storch and Chiarucci, 2016; Whittaker et al., 2017). However, exceptions always existed. That is, some islands had the similar areas yet showed the distinct difference of N values. Among the aforementioned factors, IA, PTI, PTS, VP, TE, Al, Sl, BT, and NPP possessed significant effects in the comprehensive effect analysis (Table 3). They influenced the N values, as well as the species composition and distribution, at island scale. The IA is the fundamental factor for the plant diversity (MacArchur and Wilson, 1963, 1967; Patiño et al., 2017). The rate of the increase in the N value with the increase in the IA was closely relevant to the isolation (Whittaker et al., 2017). The island species-area relationship was further studied using the log transformed power model, which has been proven to be the best model for the relationship (Triantis et al., 2012; Matthews et al., 2016). The slope of the trend line was shallow and lower than the studies of Panitsa et al. (2006) and Sfenthourakis and Panitsa (2012), indicating the low rate of the increase (Fig. 7). It reconfirmed that the studied uninhabited islands were generally close to the continental region with frequent species migration. Some other gradient factors, including PTI, PTS, TE, Al, and BT, were closely related to the IA (Fig. S6). They influenced the N values through the IA. Many other factors influenced the island plant diversity (Helmus et al., 2014; Graham et al., 2017). In this study, The VP, Sl, and NPP had weak correlations with the IA (Fig. S6). Their influences on the N values were independent of the IA and explained the aforementioned exceptions. VP and NPP represent the vegetation area and growth condition, and higher VP and NPP contributed to higher N values regardless of the IA. It indicated the positive correlation between biodiversity and productivity on the uninhabited islands at island scale. The habitat conditions for plant growth are generally worse on the uninhabited islands compared to those in the mainland (Chi et al., 2016). Thus, the increase in vegetation area and productivity indicated the improvement of the carrier for the plant diversity. The Sl always denotes the terrain complexity (Wang et al., 2015). High Sl values resulted in complicated terrain conditions and then the high N values at island scale.

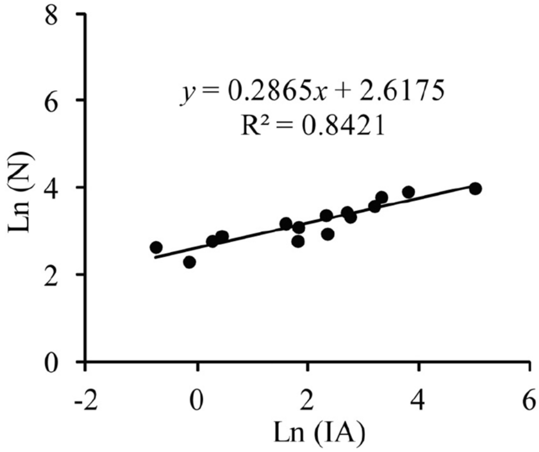


Fig. 7. Island species-area relationship: Ln (IA) and Ln (N) indicate the natural logarithmic values of IA and N, respectively. The scale units of vertical and horizontal axes are the same to exhibit the rate of the increase.

At site scale, the correlations of H′ and E values with each gradient factor were weak in the single effect analysis, which was in accordance with the results in the comprehensive gradient analysis, that is, the sampling sites with different H′ and E values were generally evenly located in the CCA ordination diagrams. The results revealed that the H′ and E values in different sampling sites changed irregularly along the multiple gradient factors, and the sampling sites with different H′ and E value intervals were scattered in the multiple gradients. The multiple gradient effects on the H′ and E values at site scale were not as distinct as those on the N value at island scale. For the morphology and proximity, which generated gradient effects at island scale, the plant diversity at site scale was not sensitive to them. This finding was in accordance with the study of Sfenthourakis and Panitsa (2012), who analyzed the plant diversity on 19 Aegean islands, however, somehow different from the study of Ibanez et al. (2018), who studied 41 tropical islands of the Indo-Pacific region and argued that the IA influenced the plant diversity at all scales, including archipelago, island, and site. The differences of the results may be determined by the spatial scales studied. For the other gradients, which was measured at site scale and represented the local habitat condition, the biodiversity indices did not show significant differences among different habitat conditions. However, the multiple gradients still influenced the species composition and distribution at site scale. For instance, the sites with low and high NPP, which was in vegetation gradient, always referred to shrub/herb and tree communities, respectively. They differed greatly in species composition, yet may have similar values of biodiversity index (Zhao et al., 2010). More gradient factors possessed significance than those at island scale for the effect degrees in the comprehensive effect analysis (Table 3). In the seven aspects of the gradients, all gradients exhibited significant effects. Only CP, NP, TE, and AWMSI in landscape gradient and Sa in soil gradient had insignificant effects, revealing that the landscape configuration and soil salinity content did not play a major role in the changes of plant species composition and distribution. The landscape configuration denoted the spatial distributions and interrelations of landscape patches and was characterized by the fragmentation in recent decades, which was caused mainly by human activities and resulted in decline in species number and hindered species migration (Ramalho et al., 2014; Lam et al., 2018). However, the landscape fragmentation was in a low level, which verified the little anthropogenic influences on the local plant community in our study area. For the Sa, seawater intrusion may result in the soil salinization in coastal areas, which threatened the plant community (Yu et al., 2014; Chi et al., 2019). Though the seawater intrusion was observed in Miaodao Archipelago (Cui et al., 2015), the Sa was less influenced and showed low values in our study area, and thus contributed little to the species composition and distribution. The mean H′ and E values at site scale was insignificantly correlated with the N value at island scale, reconfirming that the plant diversity could not be replaced or predicted across scales in the study area (Sfenthourakis and Panitsa, 2012). The differences of the multiple gradient effects across different scales verified the third hypothesis of the study.

The uninhabited islands in this study are generally in a small spatial scale with consistent climate, and the findings could reveal the spatial distribution of the plant diversity within the uninhabited islands and their neighboring areas. In the future work, more archipelagos across different climate zones will be focused on to reveal the spatial characteristics of island plant diversity in a large regional scale. Besides the spatial variance, the temporal dynamics is also an important issue in the studies of island biogeography (Whittaker et al., 2017; Borges et al., 2018). The temporal variations of plant diversity under the background of global changes should also be paid attention.

5. Conclusions

The multiple gradients of the uninhabited islands were identified and quantified at island and site scales based on field investigation and remote sensing methods. The multiple gradients included seven "from macro to micro" aspects of morphology, proximity, landscape, terrain, atmosphere, soil, and vegetation, and a total of 20 gradient factors were selected to cover all aspects of factors influencing the spatial pattern of plant diversity on the uninhabited islands. The single and comprehensive effects of the multiple gradients were analyzed, and the spatial patterns of plant diversity under the multiple gradients were revealed at island and site scales in the study area. The multiple gradients could be applied in analyzing the island plant diversity in different areas.

The results on the uninhabited islands of Miaodao Archipelago indicated that a total of 130 plant species were recorded. The 62 sampling sites on the 15 islands were adequate to represent the overall characteristics of plant diversity, which was proved by the species accumulation curves. The species composition on the uninhabited islands possessed common characteristics with the neighboring inhabited islands and mainland, meanwhile, showed unique features on the dominant species. The α diversity, represented by the N, H′ and E, showed distinct spatial heterogeneities at the dual scales. The β diversity, represented by the W and J, indicated the great difference of species composition within an island and among different islands. At island scale, the IA, vegetation condition, and Sl contributed the most to the spatial pattern of plant diversity, and the N values increased with the increase in these factors. At site scale, the H′ and E values in different sampling sites changed irregularly along the multiple gradient factors. However, most of the factors showed significant effects on the species composition and distribution, yet CP, NP, TE, and AWMSI in landscape gradient and Sa in soil gradient had insignificant effects. The IA played a fundamental role in determining the α diversity at island scale and generating the β diversity within an island, however, was not significantly correlated with the diversity at site scale.

Acknowledgments

This research was funded by the Basic Scientific Fund for National Public Research Institutes of China (2018Q07) and the National Natural Science Foundation of China (Nos. 41701214; 41871089). We thank the editor and anonymous reviewers for their valuable comments. We also thank USGS for the open source LANDSAT data (https://landsat.usgs.gov/).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2019.01.352.

References

Anderson, M.J., Ellingsen, K.E., Mcardle, B.H., 2010. Multivariate dispersion as a measure of beta diversity. Ecol. Lett. 9 (6), 683–693.

Ávila, S.P., Melo, C., Berning, B., Sá, N., Quartau, R., Rijsdijk, K.F., Ramalho, R.S., Cordeiro, R., De Sá, N.C., Pimentel, A., Baptista, L., Medeiros, A., Gil, A., Johnson, M.E., 2019. Towards a 'Sea-Level Sensitive' Dynamic Model: Impact of Island Ontogeny and Glacio-eustasy on Global Patterns of Marine Island Biogeography. https://doi.org/10.1111/brv.12492.

Bevilacqua, S., Ugland, K.I., Plicanti, A., Scuderi, D., Terlizzi, A., 2018. An approach based on the total-species accumulation curve and higher taxon richness to estimate realistic upper limits in regional species richness. Ecol. Evol. 8 (1), 405–415.

Borges, P.A.V., Cardoso, P., Kreft, H., Whittaker, R.J., Fattorini, S., Emerson, B.C., Gil, A., Gillespie, R.G., Matthews, T.J., Santos, A.M.C., Steinbauer, M.J., Thébaud, C., Ah-Peng, C., Amorim, I.R., Aranda, S.C., Arroz, A.M., Azevedo, J.M.N., Boieiro, M., Borda-de-Água, L., Carvalho, J.C., Elias, R.B., Fernández-Palacios, J.M., Florencio, M., González-Mancebo, J.M., Heaney, L.R., Hortal, J., Kueffer, C., Lequette, B., Martín-Esquivel, J.L., López, H., Lamelas-López, L., Marcelino, J., Nunes, R., Oromí, P., Patiño, J., Pérez, A.J., Rego, C., Ribeiro, S.P., Rigal, F., Rodrigues, P., Rominger, A.J., Santos-Reis, M., Schaefer, H., Sérgio, C., Serrano, A.R.M., Sim-Sim, M., Stephenson, P.J., Soares, A.O., Strasberg, D., Vanderporten, A., Vieira, V., Gabriel, R., 2018. Global Island Monitoring Scheme (GIMS): a proposal for the long-term coordinated survey and monitoring of native island forest biota. Biodivers. Conserv. 27, 2567–2586.

Boscutti, F., Casolo, V., Beraldo, P., Braidot, E., Zancani, M., Rixen, C., 2018. Shrub growth and plant diversity along an elevation gradient: evidence of indirect effects of climate on alpine ecosystems. PLoS One 13 (4), e0196653.

Carvalho, J.C., Cardoso, P., Gomes, P., 2012. Determining the relative roles of species replacement and species richness differences in generating beta-diversity patterns. Glob. Ecol. Biogeogr. 21, 760–771.

Chen, S., Wang, W., Xu, W., Wang, Y., Wan, H., Chen, D., Tang, Z., Tang, X., Zhou, G., Xie, Z., Zhou, D., Shangguan, Z., Huang, J., He, J., Wang, Y., Sheng, J., Tang, L., Li, X., Dong, M., Wu, Y., Wang, Q., Wang, Z., Wu, J., Chapin III, F.S., Bai, Y., 2018. Plant diversity enhances productivity and soil carbon storage. Proc. Natl. Acad. Sci. U. S. A. 115, 4027–4032.

Chi, Y., Shi, H., Guo, Z., Ding, D., 2015. Connotation, features and causes of island ecological vulnerability. Acta Oceanol. Sin. 37 (12), 93–105.

Chi, Y., Shi, H., Wang, X., Qin, X., Zheng, W., Peng, S., 2016. Impact factors identification of spatial heterogeneity of herbaceous plant diversity on five southern islands of Miaodao Archipelago in North China. Chin. J. Oceanol. Limnol. 34 (5), 937–951.

Chi, Y., Shi, H., Wang, Y., Guo, Z., Wang, E., 2017a. Evaluation on island ecological vulnerability and its spatial heterogeneity. Mar. Pollut. Bull. 125, 216–241.

Chi, Y., Shi, H., Zheng, W., Sun, J., 2017b. Multiple gradient effects on spatial distribution of island soil microbial biomass. Eur. J. Soil Biol. 83, 65–75.

Chi, Y., Shi, H., Zheng, W., Wang, E., 2018. Archipelagic landscape patterns and their ecological effects in multiple scales. Ocean Coast. Manag. 152, 120–134.

Chi, Y., Zhang, Z., Gao, J., Xie, Z., Zhao, M., Wang, E., 2019. Evaluating landscape ecological sensitivity of an estuarine island based on landscape pattern across temporal and spatial scales. Ecol. Indic. 101, 221–237.

China Islands Compiling Committee, 2013. Encyclopedia of China Islands. China Ocean Press, Beijing.

Chown, S.L., Gremmen, N.J.M., Gaston, K.J., 1998. Ecological biogeography of southern ocean islands: species-area relationships, human impacts, and conservation. Am. Nat. 152, 562–575.

Cingolani, A.M., Vaieretti, M.V., Gurvich, D.E., Giorgis, M.A., Cabido, M., 2010. Predicting alpha, beta and gamma plant diversity from physiognomic and physical indicators as a tool for ecosystem monitoring. Biol. Conserv. 143 (11), 2570–2577.

Colwell, R.K., 1997. Estimate S: Statistical Estimation of Species Richness and Shared Species From Samples. Version 5. (User's Guide and application published at: http://viceroy.eeb.uconn.edu/estimates).

Colwell, R.K., Mao, C., Chang, J., 2004. Interpolating, extrapolating, and comparing incidence-based species accumulation curves. Ecology 85, 2717–2727.

Condit, R., Pitman, N., Leigh Jr., E.G., Chave, J., Terborgh, J., Foster, R.B., Núñez, P., Aguilar, S., Valencia, R., Villa, G., Muller-Landau, H.C., Losos, E., Hubbell, S.P., 2002. Beta-diversity in tropical forest trees. Science 295 (5555), 666–669.

Cui, Z., Chen, G., Xu, X., Wang, D., Yu, L., 2015. Mechanism and assessment of seawater intrusion in the Northern Changshan Island. Mar. Environ. Sci. 34, 930–936.

Du, N., Wang, Q., Guo, W., Wang, R., 2007. Ecological characteristics of typical plant communities in Kunyu Mountain. Chin. J. Eco-Agric. 26, 151–158.

Eldridge, M.D.B., Meek, P.D., Johnson, R.N., 2014. Taxonomic uncertainty and the loss of biodiversity on Christmas Island, Indian Ocean. Conserv. Biol. 28 (2), 572–579.

Fan, X., Pedroli, B., Liu, G., Liu, Q., Liu, H., Shu, L., 2012. Soil salinity development in the Yellow River Delta in relation to groundwater dynamics. Land Degrad. Dev. 23, 175–189.

Fang, J., Wang, X., Shen, Z., Tang, Z., He, J., Yu, D., Jiang, Y., Wang, Z., Zheng, C., Zhu, J., Guo, Z., 2009. Methods and protocols for plant community inventory. Biodivers. Sci. 17 (6), 533–548.

Fu, B., Liang, D., Lu, N., 2011. Landscape ecology: coupling of pattern, process, and scale. Chin. Geogr. Sci. 21 (4), 385–391.

Gil, A., Fonseca, C., Benedicto-Royuela, José, 2018. Land cover trade-offs in small oceanic islands: a temporal analysis of Pico Island, Azores. Land Degrad. Dev. 29, 349–360.

Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecol. Lett. 4 (4), 379–391.

Graham, N.R., Gruner, D.S., Lim, J.Y., Gillespie, R.G., 2017. Island ecology and evolution: challenges in the Anthropocene. Environ. Conserv. 44, 323–335.

Harrison, S., Ross, S.J., Lawton, J.H., 1992. Beta diversity on geographic gradients in Britain. J. Anim. Ecol. 61, 151–158.

He, Y., Li, X., Craft, C., Ma, Z., Sun, Y., 2011. Relationships between vegetation zonation and environmental factors in newly formed tidal marshes of the Yangtze River estuary. Wetl. Ecol. Manag. 19 (4), 341–349.

Helmus, M.R., Mahler, D.L., Losos, J.B., 2014. Island biogeography of the Anthropocene. Nature 513, 543–546.

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol. Monogr. 75, 3–35.

Hu, X., Xu, H., 2018. A new remote sensing index for assessing the spatial heterogeneity in urban ecological quality: a case from Fuzhou City,China. Ecol. Indic. 89, 11–21.

Huang, B., Ouyang, Z., Zheng, H., Zhang, H., Wang, X., 2008. Construction of an eco-island: a case study of Chongming Island, China. Ocean Coast. Manag. 51 (8–9), 575–588.

Ibanez, T., Keppel, G., Baider, C., Birkinshaw, C., Culmsee, H., Cordell, S., Vincent Florens, F.B., Franklin, J., Giardina, C.P., Gillespie, T.W., Laidlaw, M., Litton, C.M., Martin, T.G., Ostertag, R., Parthasarathy, N., Randrianaivo, R., Randrianjanahary, M., Rajkumar, M., Rasingam, L., Ratovoson, F., Reza, L., Sack, L., Aiba, S., Webb, E., Whitfeld, T.J.S., Zang, R., Birnbaum, P., 2018. Regional forcing explains local species diversity and turnover on tropical islands. Glob. Ecol. Biogeogr. 27, 474–486.

Jactel, H., Gritti, E.S., Drössler, L., Forrester, D.I., Mason, W.L., Morin, X., Pretzsch, H., Castagneyrol, B., 2018. Positive biodiversity-productivity relationships in forests: climate matters. Biol. Lett. 14 (4), 20170747.

Janišová, M., Michalcová, D., Bacaro, G., Ghisla, A., 2014. Landscape effects on diversity of semi-natural grasslands. Agric. Ecosyst. Environ. 182, 47–58.

Lam, S.N., Cheng, W., Zou, L., Cai, H., 2018. Effects of landscape fragmentation on land loss. Remote Sens. Environ. 209, 253–262.

Li, S., Su, P., Zhang, H., Zhou, Z., Xie, T., Shi, R., Gou, W., 2018. Distribution patterns of desert plant diversity and relationship to soil properties in the Heihe River Basin, China. Ecosphere 9 (7), e02355.

Mac Nally, R., Fleishman, E., Bulluck, L.P., Betrus, C.J., 2004. Comparative influence of spatial scale on beta diversity within regional assemblages of birds and butterflies. J. Biogeogr. 31 (6), 917–929.

MacArchur, R.H., Wilson, E.O., 1963. An equilibrium theory of insular zoogeography. Evolution 37, 373–387.

MacArchur, R.H., Wilson, E.O., 1967. The Theory of Island Biogeography. Princeton University Press, Princeton.

Magurran, A.E., 2004. Measuring Biological Diversity. Blackwell Publishing, Oxford.

Mao, C., Colwell, R.K., Chang, J., 2005. Estimating the species accumulation curve using mixtures. Biometrics 61, 433–441.

Matthews, T.J., Guilhaumon, F., Triantis, K.A., Borregaard, M.K., Whittaker, R.J., 2016. On the form of species–area relationships in habitat islands and true islands. Glob. Ecol. Biogeogr. 25 (7), 847–858.

Maunder, M., Leiva, A., Santiago-Valentín, E., Stevenson, D.W., Acevedo-Rodríguez, P., Meerow, A.W., Mejía, M., Clubbe, C., Francisco-Ortega, J., 2008. Plant conservation in the Caribbean Island biodiversity hotspot. Bot. Rev. 74 (1), 197–207.

Michelsen, O., Mcdevitt, J.E., Coelho, C.R.V., 2014. A comparison of three methods to assess land use impacts on biodiversity in a case study of forestry plantations in New Zealand. Int. J. Life Cycle Assess. 19 (6), 1214–1225.

Moffatt, S.F., Mclachlan, S.M., Kenkel, N.C., 2004. Impacts of land use on riparian forest along an urban–rural gradient in southern Manitoba. Plant Ecol. 174 (1), 119–135.

Morgan, L.K., Werner, A.D., 2014. Seawater intrusion vulnerability indicators for freshwater lenses in strip islands. J. Hydrol. 508, 322–327.

Moujabber, M.E., Samra, B.B., Darwish, T., Atallah, T., 2006. Comparison of different indicators for groundwater contamination by seawater intrusion on the Lebanese coast. Water Resour. Manag. 20 (2), 161–180.

Nam, J., Chang, W., Kang, D., 2010. Carrying capacity of an uninhabited island off the southwestern coast of Korea. Ecol. Model. 221 (17), 2102–2107.

Ndubisi, F., 2014. The Ecological Design and Planning Reader. Island Press, Washington, DC.

Niu, C., Lou, A., Sun, R., Li, Q., 2015. Foundations in Ecology. Third edition. Higher Education Press, Beijing.

Nogué, S., de Nascimento, L., Froyd, C.A., Wilmshurst, J.M., de Boer, E.J., Coffey, E.E.D., Whittaker, R.J., Fernández-Palacios, J.M., Willis, K.J., 2017. Island biodiversity conservation needs palaeoecology. Nat. Ecol. Evol. 1, 181.

Panitsa, M., Tzanoudakis, D., Triantis, K., Sfenthourakis, S., 2006. Patterns of species richness on very small islands: the plants of the Aegean archipelago. J. Biogeogr. 33 (7), 1223–1234.

Patiño, J., Whittaker, R.J., Borges, P.A.V., Fernández-Palacios, J.M., Ah-Peng, C., Araújo, M.B., Ávila, S.P., Cardoso, P., Cornuault, J., de Boer, E.J., de Nascimento, L., Gil, A., Gonzáalez-Castro, A., Gruner, D.S., Heleno, R., Hortal, J., Carlos Illera, J., Kaiser-Bunbury, C.N., Matthews, T.J., Papadopoulou, A., Pettorelli, N., Price, J.P., Santos, A.M.C., Steinbauer, M.J., Triantis, K.A., Valente, L., Vargas, P., Weigelt, P., Emerson, B.C., 2017. A roadmap for island biology: 50 fundamental questions after 50 years of the theory of island biogeography. J. Biogeogr. 44, 963–983.

Peng, S., Hu, G., Yu, M., 2014. Beta diversity of vascular plants and its influencing factors on islands in the Thousand Island Lake. Acta Ecol. Sin. 34 (2014), 3866–3872.

Potter, C.S., Randerson, J.T., Field, C.B., Matson, P.A., Vitousek, P.M., Mooney, H.A., Klooster, S.A., 1993. Terrestrial ecosystem production: a process model based on global satellite and surface data. Glob. Biogeochem. Cycles 7, 811–841.

Ramalho, C.E., Laliberté, E., Poot, P., Hobbs, R.J., 2014. Complex effects of fragmentation on remnant woodland plant communities of a rapidly urbanizing biodiversity hotspot. Ecology 95 (9), 2466–2478.

Reaser, J.K., Meyerson, L.A., Cronk, Q., De Poorter, M., Eldrege, L.G., Green, E., Kairo, M., Latasi, P., Mack, R.N., Mauremootoo, J., O'Down, D., Orapa, W., Sastroutomo, S., Saunders, A., Shine, C., Thrainsson, S., Vaiutu, L., 2007. Ecological and socioeconomic impacts of invasive alien species in island ecosystems. Environ. Conserv. 34 (2), 98–111.

Schulze, E.D., Bouriaud, O., Weber, U., Roscher, C., Hessenmoeller, D., Kroiher, F., Schall, P., 2018. Management breaks the natural productivity-biodiversity relationship in forests and grassland: an opinion. For. Ecosyst. 5, 3.

Sfenthourakis, S., Panitsa, M., 2012. From plots to islands: species diversity at different scales. J. Biogeogr. 39 (4), 750–759.

Soininen, J., McDonald, R., Hillebrand, H., 2007. The distance decay of similarity in ecological communities. Ecography 30, 3–12.

Storch, D., Chiarucci, A., 2016. The theory of the nested species-area relationship: geometric foundations of biodiversity scaling. J. Veg. Sci. 27, 880–891.

Sun, Z., Zhang, X., Zhu, Y., Liang, J., Yu, S., Zhang, Y., Yang, X., 2011. Applications of species indicator for analyzing plant community types and their biodiversity at Kunyushan National Forest Reserve. Acta Ecol. Sin. 31, 3120–3132.

Taramelli, A., Valentini, E., Sterlacchini, S., 2015. A GIS-based approach for hurricane hazard and vulnerability assessment in the Cayman Islands. Ocean Coast. Manag. 108, 116–130.

Tilman, D., Reich, P.B., Knops, J.M.H., 2006. Biodiversity and ecosystem stability in a decade–long grassland experiment. Nature 441, 629–632.

Triantis, K.A., Guilhaumon, F., Whittaker, R.J., 2012. The island species–area relationship: biology and statistics. J. Biogeogr. 39 (2), 215–231.

Ugland, K.I., Gray, J.S., Ellingsen, K.E., 2003. The species-accumulation curve and estimation of species richness. J. Anim. Ecol. 72, 888–897.

USGS, 2018. Landsat Missions: Landsat 8. https://landsat.usgs.gov/landsat-8 (04/25/2018).

Wang, G., Ye, B., 2017. Floristic composition and diversity of typical plant community in Zhoushan Archipelago, East China. Chin. J. Eco-Agric. 36, 349–358.

Wang, X., Wang, C., Li, Q., 2015. Wind regimes above and below a temperate deciduous forest canopy in complex terrain: interactions between slope and valley winds. Atmosphere 6, 60–87.

Weigelt, P., Jetz, W., Kreft, H., 2013. Bioclimatic and physical characterization of the world's islands. Proc. Natl. Acad. Sci. U. S. A. 110 (38), 15307–15312.

Weigelt, P., Steinbauer, M.J., Cabral, J.S., Kreft, H., 2016. Late Quaternary climate change shapes island biodiversity. Nature 532, 99–102.

Whittaker, R.J., Fernández-Palacios, J.M., 2007. Island Biogeography: Ecology, Evolution, and Conservation. 2nd edn. Oxford University Press, Oxford.

Whittaker, R.J., Fernández-Palacios, J.M., Matthews, T.J., Borregaard, M.K., Triantis, K.A., 2017. Island biogeography: taking the long view of nature's laboratories. Science 357, eaam8326.

Wu, S., Hsieh, C., Chaw, S., Rejmánek, M., 2004. Plant invasions in Taiwan: Insights from the flora of casual and naturalized alien species. Divers. Distrib. 10, 349–362.

Xie, Z., Li, X., Zhang, Y., Chen, S., 2018. Accelerated expansion of built-up area after bridge connection with mainland: a case study of Zhujiajian Island. Ocean Coast. Manag. 152, 62–69.

Yang, T., Ying, R., 1997. The study on the typhoon surge in the regions of Zhejiang Islands. Mark. Forecast. 14 (2), 28–43.

Yu, J., Li, Y., Han, G., Zhou, D., Fu, Y., Guan, B., Wang, G.M., Ning, K., Wu, H.F., Wang, J.H., 2014. The spatial distribution characteristics of soil salinity in coastal zone of the Yellow River Delta. Environ. Earth Sci. 72 (2), 589–599.

Zhang, J., 2004. Quantitative Ecology. Science Press, Beijing.

Zhang, X., Zhang, Z., Zhang, S., Wang, R., 2003. Preliminary studies on the flora of Kunyu Mountain in Shandong Province. Bull. Bot. Res. 23, 492–499.

Zhang, Z., Feng, A., Li, P., Liu, D., 2012. Carrying capacity of uninhabited islands based on energy evaluation: a case of Da Island. Mar. Environ. Sci. 31 (572–575), 585.

Zhao, N., Wang, Z., Lv, J., Wang, K., 2010. Relationship between plant diversity and spatial stability of aboveground net primary productivity (ANPP) across different grassland ecosystems. Afr. J. Biotechnol. 9 (40), 6708–6715.

Zhou, X., 2014. Management of uninhabited islands based on the construction of strong marine country. Econ. Geogr. 34, 28–34.