

EXPLORING THE SPECIES AND PHYLOGENETIC DIVERSITY, PHYLOGENETIC STRUCTURE OF MIXED COMMUNITIES ALONG THE COASTAL GRADIENT. A CASE STUDY IN A SUBTROPICAL ISLAND, CHINA

ZHENG, J. M.^{1,2,3*} – ZHENG, Y. S.²

¹College of Civil Engineering, Putian University, Putian 351100, PR China

²College of Landscape Architecture, Fujian Agriculture and Forestry University, Fuzhou 350002, PR China

³Fujian University Engineering Research Center for disaster prevention and mitigation of engineering structures along the southeast coast, Putian University, Putian 351100, PR China

*Corresponding author
e-mail: zjm1991@foxmail.com

(Received 28th Jan 2022; accepted 2nd May 2022)

Abstract. To better understand the effect of distance from seashore on the pattern of species diversity, phylogenetic diversity, and phylogenetic structure, four sample sites on Dongshan Island, China with varied distances to seashore were selected, the soil and species composition of *Casuarina equisetifolia* and *Dendrocalamus minor* var. *amoenus* mixed communities were investigated, and species diversity, phylogenetic diversity, and phylogenetic structure were analyzed. The result showed that there are existed 44 taxa in the communities, 18.8% of which were exotic species. Species diversity and phylogenetic diversity exhibited an increasing trend with shorter distance. The EC (Electrical conductivity) and SOC (Soil organic matter) determined the species diversity and phylogenetic diversity. The phylogenetic structure does not change with distance from the seashore, which may be caused by human disturbance and niche competition that has altered the environmental filtering effect.

Keywords: sandy coast, distance to seashore, species richness, phylogenetic structure, phylogenetic diversity, bamboo

Introduction

Almost all coasts in Fujian Province, China are sandy, except for a few bedrocks and muddy coasts (Kong, 1999). The windbreak constructed in sandy coasts serves to protect the manmade environment from sandy dust by wind blowing and alleviate the damage caused by salt spray to plants or crops. In the harsh environment of coastal sandy zones, there are few suitable species, such as *Casuarina equisetifolia* and *Pinus elliottii*. More than 20 years ago, many bamboo species were introduced to Dongshan Island, Fujian Province, China to build a mixed community of windbreak in the coast, which has contributed to better soil quality and higher community stability (Zheng et al., 2020; Zheng et al., 2021b). Bamboo-dominated patches facilitate species coexistence and promote species richness and phylogenetic diversity (Schweizer et al., 2017). Phylogenetic diversity and phylogenetic structure were selected to evaluate the priority of conservation of plant communities and animals (Liu et al., 2017a; Gumbs et al., 2020). Therefore, it is meaningful to study the species diversity, phylogenetic diversity, and phylogenetic structure of windbreak.

Plant diversity is the result of responses to environmental filtering (Faith, 1992; Japhet et al., 2009). Species richness was changed with soil pH and precipitation

(Palpurina et al., 2017). The soil texture and nutrients influenced the distribution of plant communities (Ahmed and Shawky, 2017). Huang et al. (2020) suggested that the species component and seed bank were highly correlated along a center-to-edge gradient. The phylogenetic structure might change with the distance to coast in an island. In the Kunlun Mountains, habit filtering has a higher impact on plant diversity and its ecological process (Du and Hesp, 2020). Anthropogenic changes in the environment have a subsequent impact on plant diversity and evolution (Tilman and Lehman, 2001). The phylogenetic structure of communities varies with spatial distance (Cavender-Bares et al., 2006), slope and aspect (Kitagawa et al., 2015), and elevation (Qian et al., 2014), and so on. Nevertheless, the pattern that the relationship between species diversity, phylogenetic structure with the distance to coast needs to be explored.

In this study, the typically mixed communities of *Casuarina equisetifolia* and *Dendrocalamus minor* var. *amoenus* were selected as objects in Dongshan Island, China. It is meaningful that *Casuarina equisetifolia* and *Dendrocalamus minor* var. *amoenus* mixed communities distributed widely with strong adaptability. Four sample plots with varying distances to the coast were sampling, the species diversity, phylogenetic diversity, and phylogenetic structure were analyzed to evaluate the health of ecosystem, find out the determining factors of environmental stress, and reveal the mechanism of species co-exist in sandy coast. This study would provide proposal for the windbreak forest management, and conversation of coastal vegetation.

Materials and Methods

Study site

The study site is located at Dongshan Island (23°40'N, 118°18'E) in Zhangzhou City, Fujian Province, China (Fig. 1). The study area has a subtropical maritime monsoon climate. The mean annual precipitation is 1113.9 mm and the mean annual evaporation is 2013.2 mm. The temperature ranged from 13.1~27.3 °C (Kong, 1999). Typhoons usually occurred from July to August. The windbreak is dominated by *Casuarina equisetifolia* on the sandy coast.

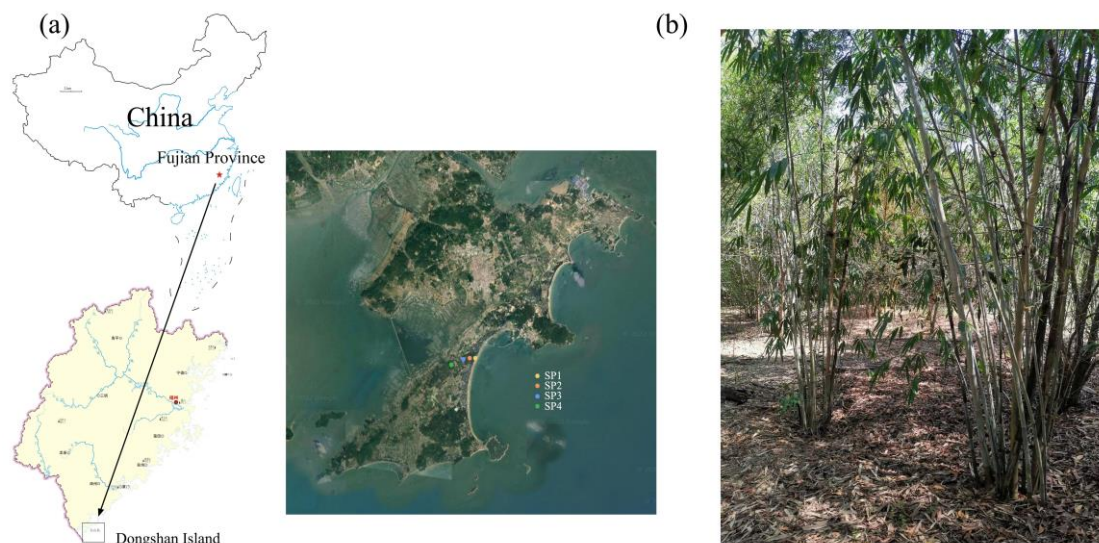


Figure 1. The location of study area (a), and the situation of sample plots (b)

Sampling and investigation

The sampling and investigation were conducted from August to October 2020. According to the distribution and size of mixed communities of *Casuarina equisetifolia* and *Dendrocalamus minor* var. *amoenus*, Four plots with different distances from coastline vertical to inland (SP1. 50~60 m, SP2. 60~200 m, SP3. 200~600 m, SP4. 600~1200 m) were selected. Four subplots of 20 m × 20 m were randomly selected at each sample plot. The species name and number of individual species were recorded. The latitude, longitude, elevation, slope, and canopy density of the sample plots were also recorded (Table 1).

Table 1. The situations of *Dendrocalamus minor* var. *amoenus*

Sample plot	Elevation/m	Slope/°	Canopy density/%	Distance to seashore/m
SP1	0~10	3~10	40~50	50~60
SP2	3~11	4~8	45~60	60~200
SP3	2~12	5~7	45~65	200~600
SP4	1~11	3~12	55~65	600~1200

The species diversity determined

Species richness (SR), Simpson's index, Shannon-Wiener's index, and Pielou's evenness index were selected to assess the species diversity of the *Casuarina equisetifolia* and *Dendrocalamus minor* var. *amoenus* mixed community. The formulae of these indicators were followed by Greig-Smith (1983), as follow:

Species richness, SR

$$SR=S \quad (\text{Eq.1})$$

Simpson index, D

$$D = 1 - \sum_{i=1}^S P_i^2 \quad (\text{Eq.2})$$

Shannon-Wiener's index, H'e

$$H'_e = -\sum_{i=1}^S P_i \ln P_i \quad P_i = \frac{n_i}{N} \quad (\text{Eq.3})$$

Pielou index, J_e

$$J_e = \frac{H'_e}{H'_{\max}} \quad H'_{\max} = \ln S \quad (\text{Eq.4})$$

where n_i – the number of individuals of i species; n – the total number of samples plots. S – the number of all species, N – the total number of individuals of all species, $i=1,2,3,\dots,n$.

The phylogenies of communities constructed

The information of all species and their phylogeny were entered into Phylomatic Version 3.0 (Webb et al., 2008), and selected the evolutionary tree skeleton followed by Zanne et al. (2014), then the phylogenetic tree with branch lengths was selected to construct.

The phylogenetic diversity and phylogenetic structure calculated

The Faith Phylogenetic diversity (PD) was selected to assess phylogenetic diversity (Faith, 1992), representing the sum of the shortest branch lengths connecting species within a sample plot to a phylogenetic tree. Net related index (NRI) and nearest taxon index (NTI) represent the phylogenetic structure of the community (Webb et al., 2008). NRI is based on mean phylogenetic distance (MPD), which estimates the mean relatedness between possible pairs of taxa. NTI is based on the mean nearest taxon distance (MNTD), which estimates the mean relatedness between each taxon and its nearest relative (Qian et al., 2014).

Species attribute query

The invasiveness of plants in the communities was referred to the Chinese Invasive Alien Species Database (<http://www.iplant.cn/ias/protlist>) (Ma, 2013; Yan et al., 2014), and classified into five classes, namely Class I, malignant invasive; Class II, severely invasive; Class III, locally invasive; Class IV, generally invasive; and Class V, yet to be observed.

The soil sampling and determined

Soil samples were collected from two soil layers, 0-20 cm and 20-40 cm, at five points in the sample plot for mixing and processing, and the soil samples were brought back to the laboratory for air-drying to determine the physicochemical properties of the soil. The soil sample were sieved through 2 mm sieve and 0.149 mm sieve to get sub-samples. Soil pH was measured using the potentiometric method (LYT 1239-1999). Soil organic matter was measured by the potassium dichromate - external heating method (LYT 1237-1999), soil total nitrogen was evaluated by the semi-micro Kjeldahl method (LYT 1228-1999) and total phosphorus was determined by the molybdenum antimony colorimetric method (LYT 1232-1999). Soil water content was measured by the ring knife method (LY/T 1215-1999) and hydrolysis nitrogen was estimated by the alkaline diffusion method (LY/T 1229-1999). Quick-acting potassium was determined by the ammonium acetate leaching - flame photometric method (LY/T 1236-1999). Effective phosphorus was evaluated by leaching with hydrochloric acid and sulphuric acid solution (LY/T 1233-1999). The EC value (Electrical conductivity) of the soil leachate at 25 °C was used as the soil water-soluble salt content (LY/T 1251-1999). The details of determination of soil physical and chemical parameters were described by Bao (2005) and Tu (2014).

Data analysis

Data were collected and analyzed using Excel 2013. The Plantlist package in R 3.6.0 was used to search for species scientific names, ICUN Red List, and Chinese endemics (Zhang, 2018). Phylogenetic trees were drawn using Figtree Version 1.4.4. The difference of species diversity, phylogenetic diversity, and phylogenetic structure at

different distances was analyzed for One-way ANOVA and Tukey multiple comparisons (Tukey HSD). The Redundant analysis (RDA) of species diversity, phylogenetic diversity and phylogenetic structure and environmental factors were performed by Canoco 5.0, *P*-value was corrected by Bonferroni method. Values presented in the tables are means \pm SD. The statistics were performed on the R 3.6.1 with Ape package, Vegan package, Spaa package.

Results

Species composition

There are a total of 44 taxa in mixed communities (Fig. 2), including eight invasive alien species, accounting for 18.18% of the total, *Bidens pilosa*, *Lantana camara*, *Mimosa bimucronata*, *Malvastrum coromandelianum*, *Panicum repens*, *Casuarina equisetifolia*, *Ageratum conyzoides*, *Acacia confusa*, respectively.

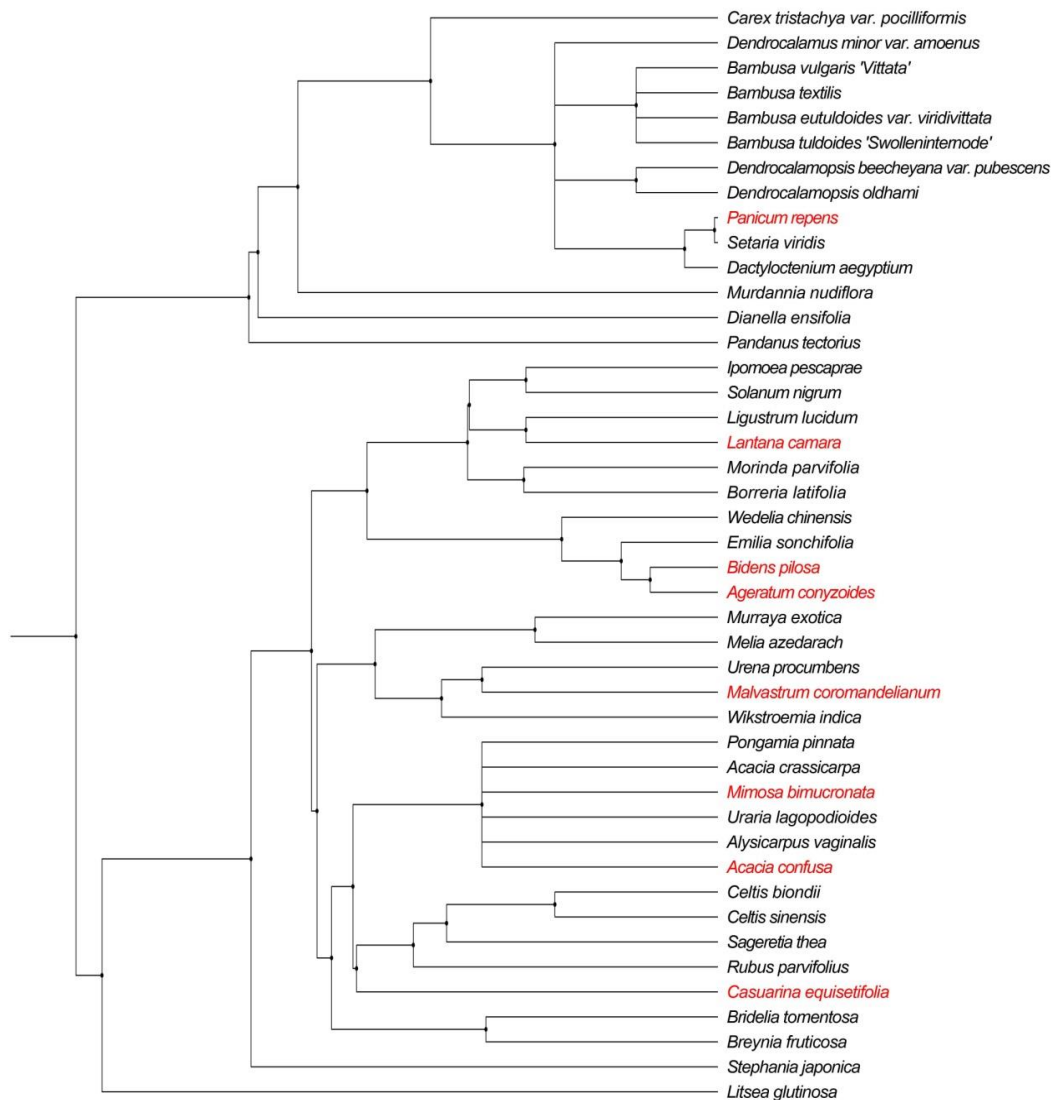


Figure 2. Phylogenetic tree of forty-four angiosperms species

Species diversity

The Shannon-Wiener diversity index and Pielou index were not significantly different among the four sample plots ($P > 0.05$, Fig. 3). The Simpson index in SP3 was significantly higher than that in SP1 ($P < 0.05$). The species richness in SP4 was significantly higher than that in SP1 ($P < 0.05$).

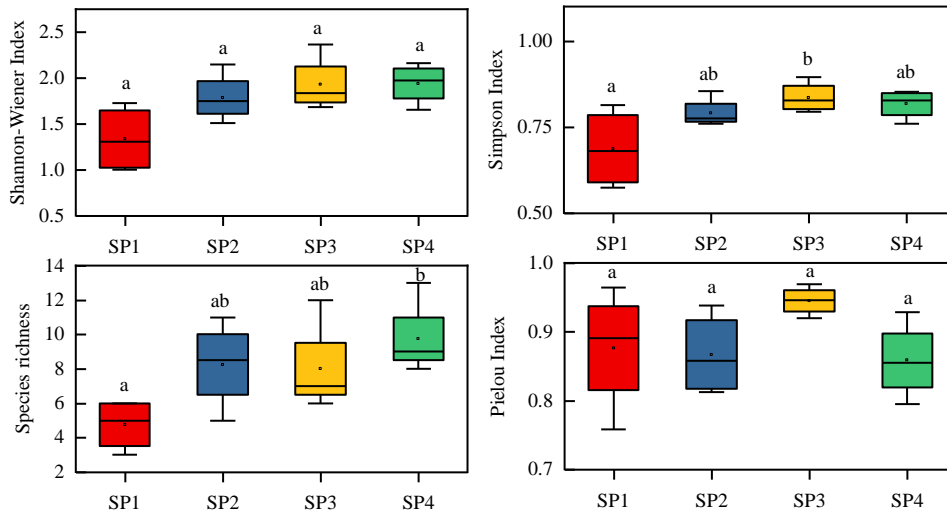


Figure 3. The species diversity plot showing the difference of species richness, species diversity and phylogenetic diversity in various distance to seashore. * Different lowercase letters indicate that the index is significantly different at $P < 0.05$

Phylogenetic diversity and phylogenetic structure

The phylogenetic diversity of SP4 was the highest at 1371.91 and the lowest at 871.01 for SP1 (Fig. 4). the NRI and NTI values for SP1 were both more than 0, indicating that the phylogenetic structure of SP1 tended to be clustering. The NRI and NTI values for SP2 and SP3 were less than 0, indicating that the phylogenetic structure tended to be over-dispersion.

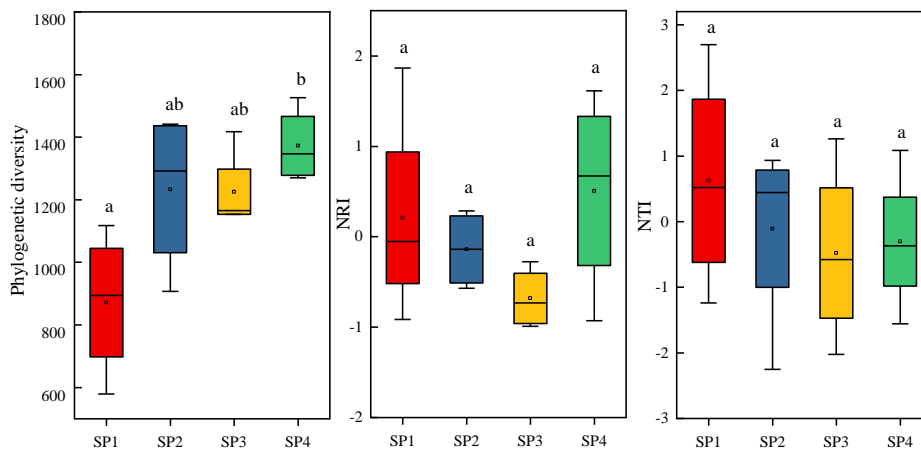


Figure 4. The phylogenetic diversity and phylogenetic structure plot showing the difference of phylogenetic diversity and phylogenetic structure in various distance to seashore. * Different lowercase letters indicate that the index is significantly different at $P < 0.05$

Soil environment

Water content in SP1 is higher than in other sample plots ($P < 0.05$, Table 2). The soil organic matter, total nitrogen, and pH were the highest in SP4 at $14.50 \text{ g}\cdot\text{kg}^{-1}$, $0.49 \text{ g}\cdot\text{kg}^{-1}$, and 6.59, respectively. SP1 had the highest EC value of $117.31 \mu\text{S}\cdot\text{cm}^{-1}$.

Table 2. Soil environmental factors

Sample plot	WC (%)	SOC (g/kg)	TN (g/kg)	TP (g/kg)	TK (g/kg)	AN (mg/kg)	AK (mg/kg)	AP (mg/kg)	pH	EC ($\mu\text{S}\cdot\text{cm}^{-1}$)
SP1	6.39±0.50b	5.62±0.33a	0.21±0.01a	0.15±0.05ab	51.75±3.59c	10.87±0.76b	29.51±1.79c	9.79±1.59b	5.40±0.03a	117.31±1.46d
SP2	4.50±0.25a	10.40±0.51c	0.25±0.02b	0.13±0.01a	50.63±0.84bc	5.71±0.82a	21.51±0.75a	7.62±0.53a	5.39±0.02a	24.92±0.30c
SP3	5.14±0.23a	8.03±0.21b	0.19±0.02a	0.20±0.01b	45.65±1.07ab	6.88±0.42a	24.51±2.23ab	6.43±0.89a	5.64±0.05b	19.15±0.47b
SP4	5.09±0.29a	14.50±2.15d	0.49±0.03c	0.18±0.01ab	40.78±3.94a	11.94±0.73b	26.80±2.01bc	11.86±0.72b	6.59±0.02c	15.96±0.53a

*Different letters in the same column indicate that the same index has significant differences between different plots at $P < 0.05$; WC. Soil water content; SOC. Soil organic matter; TN. Soil total nitrogen; TP. Soil total phosphorus; TK. Soil total potassium; AN. Soil available nitrogen; AP. Soil available phosphorus; AK. Soil available potassium; pH. Hydrogen ion concentration; EC. Soil electric conductivity

The relationship between environment and species diversity, phylogenetic diversity and phylogenetic structure

Environmental factors explained 61.7% of species diversity, phylogenetic diversity, and phylogenetic structure (Figure 5). EC was negatively correlated with SR and PD. EC was negatively correlated with SOC, TN, and pH.

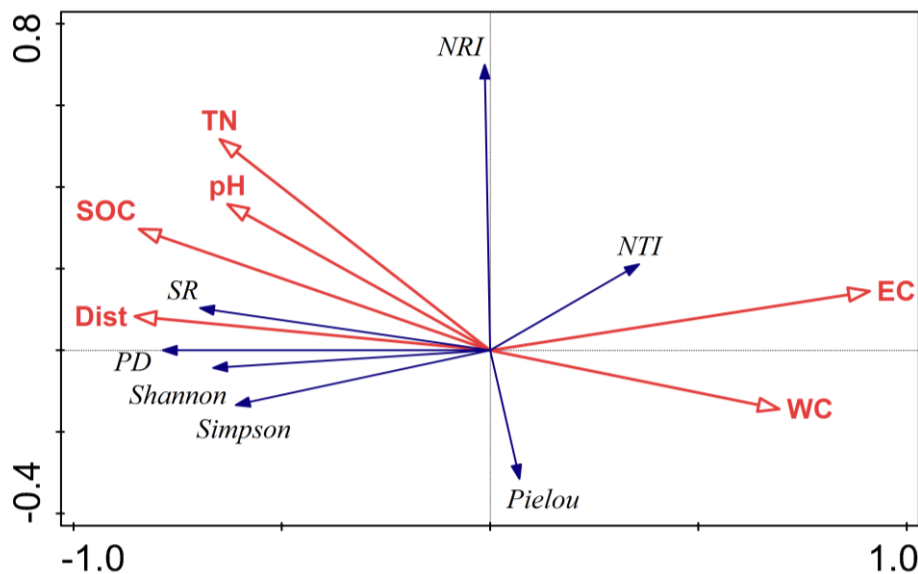


Figure 5. Redundancy analysis biplot showing the the relationship between species diversity, phylogenetic diversity and phylogenetic structure and environmental factors. Where EC. Soil electric conductivity; WC. Soil water content; SOC. Soil organic matter; TN. Soil total nitrogen, pH. Hydrogen ion concentration; Dist. distance

EC, Dist, and SOC have a significant impact on species diversity, phylogenetic diversity, and phylogenetic structure ($P < 0.05$, Table 3), the explain rate is 51.2%, 5.7%, 0.6%, respectively. The EC, Dist, and SOC were the determining factors influencing species diversity, phylogenetic diversity, and phylogenetic structure.

Table 3. Explanation rate of environmental factors on species diversity, phylogenetic diversity and phylogenetic structure under coastal gradients

Environmental Factors	Explains %	F-value	P	P _{adj}
EC	51.2	14.7	0.004	0.024
Dist	5.7	11.4	0.006	0.036
SOC	0.6	10.9	0.008	0.048
WC	2.3	5.9	0.020	0.120
TN	1.7	4.9	0.040	0.240
pH	0.2	4.6	0.050	0.300

Correlation analysis

The distance was significantly and positively correlated with the Shannon-Wiener index, Simpson diversity index, PD, and SR ($P < 0.05$, Table 4). The correlation between distance and NRI and NTI was not significant ($P > 0.05$). Species richness was significantly positively correlated with phylogenetic diversity ($r = 0.963$, $P < 0.01$).

Table 4. Spearman correlation analysis of species diversity, phylogenetic diversity, and phylogenetic structure

	Distance	Shannon-Wiener	Pielou	Simpson	PD	SR	NRI
Shannon-Wiener	0.620*						
Pielou	0.045	0.322					
Simpson	0.586*	0.955**	0.502*				
PD	0.670**	0.880**	-0.093	0.775**			
SR	0.614*	0.911**	-0.031	0.768**	0.924**		
NRI	0.045	-0.151	-0.104	-0.240	-0.170	0.015	
NTI	-0.273	-0.140	0.173	-0.174	-0.423	-0.056	0.421

SR:species richness, PD:phylogenetic diversity, NRI:net related index, NTI. nearest taxon index
*: $P < 0.05$, **: $P < 0.01$ (two-tails)

Discussion

Species composition

The species composition of *Casuarina equisetifolia* and *Dendrocalamus minor* var. *amoenus* mixed communities existed coastal native species, such as *Ipomoea pes-caprae*, *Pandanus tectorius* and *Pongamia pinnata*, which have a strong adaptive capacity to coastal stress. However, there are a high proportion of exotic species in the communities, accounting for 18.18% of the total number of species. It indicating that the invasive exotic species can adapt to the harsh coastal environment. The harsh habitat can accommodate a great number of invasive alien species (Hope et al., 2006; Liu et al.,

2017a). These species can colonize harsh habitats, such as roadsides and rock crevices. *Lantana camara* spreads rapidly and widely, posing a threat to the local ecosystem and can reduce agricultural productivity (Ranjan, 2019). This species is a potential ecological threat to native and endemic species in the sandy coast. It had been proved that *Lantana camara* has a highly positive interspecific association with *Dendrocalamus minor*, resulting in unstable communities of *Casuarina equisetifolia* and *Dendrocalamus minor* var. *amoenus* (Zheng et al., 2021a). *Casuarina equisetifolia* is an introduced exotic species for the protection of windbreak forests, and it is irreplaceable with strong colonization ability in the coastal zone (Lin et al., 2017). *Casuarina equisetifolia* is a potential threat to native tree species, but the severity is yet to be proven.

The effect of distance on the species diversity and phylogenetic diversity

Distance is an important factor influencing species composition (Abdelaal et al., 2019; Valli et al., 2019). The species diversity and habitat changed with the distance to seashore (Chen et al., 2015). The species diversity increased with the distance increased (Liu, 2009). The similarity of vegetation increased from the center to the edge of the island (Huang et al., 2020). These results consist with this study, the Simpson index in SP3 is significantly higher than in SP1 ($P>0.05$). The species diversity reflects the environment of communities. “Luxury effect” means the environment with a rich resource can live more species than the poor environment (Liu et al., 2017b). The species richness is highly correlated with phylogenetic diversity ($r=0.963$, $P<0.01$). The Simpson index, species richness, and phylogenetic diversity increased with distance increased (Fig. 4), which suggested that further the distance from shore, the sample plot was more stable and resource-rich. Distance to seashore showed a certain environmental gradient (Liu et al., 2017a), which is supported by the findings of this study. Soil organic matter and soil total nitrogen in SP4 were highest, while soil total phosphorus, effective phosphorus, and hydrolytic nitrogen were also relatively high than other sample plots (Table 2), This also demonstrating that soil quality in SP4 were better than other sample plots.

The effect of distance on the phylogenetic structure

The phylogenetic structure was correlated with environmental factors (Qian et al., 2014). In this study, the phylogenetic structure has not significantly relationship with distance from shore (Fig. 4), indicating that phylogenetic structure would not change along with the distance to the seashore. The environmental gradients related to distance to the seashore caused the species richness and diversity to change, but it has a low impact on the phylogenetic structure.

The NRI and NTI values in SP2 and SP3 were both less than 0, which indicated that the competition of communities caused the phylogenetic structure tended to be over-dispersion. The NRI and NTI values in SP1 are both more than 0, indicating that the phylogeny of the community tended to be clustering due to environmental filtering. The NRI and NTI were opposite in SP4, which suggested that the determining factors of phylogenetic structure are random or the combination of habitat filtering and species competition. Our result is consistent with previous studies (Kress et al., 2009; Liu et al., 2017a). The differences in phylogenetic structure are related to the environmental factors, local species pool, and the seed bank associated with land use (Stadler et al., 2017).

The determining factors of species diversity, phylogenetic diversity, and phylogenetic structure

In this study, EC, distance and SOC are the determining factors affecting species diversity, phylogenetic diversity, and the phylogenetic structure of communities under coastal gradients. Plant lived on the coast suffered salt damage mainly caused by salt spray (Li, 2017). Salt spray is blown from sea to inland, settles on the leave and soil surface, and salt spray decreased with increasing distance to seashore (Du and Hesp, 2020), resulting in an increase in species richness and phylogenetic diversity with decreasing distance from shore. Soil organic matter facilitates carbon uptake and tissue growth by plants and it is closely related to other nutrient contents. The communities in site further to seashore would attract large numbers of seabirds, and seabird feces are supplied to the soil nutrient pool, and large amounts of litter also lead to an increase in soil organic matter (Huang et al., 2020). As a result, differences in soil organic matter along the coastal gradient lead to changes in species diversity and phylogenetic diversity. Habitat environment, human disturbance and ecological niche competition combined to constrain community phylogenetic structure (Liu et al., 2017a). There are no differences of NRI and NTI among sample plots with varying distances to the seashore ($P>0.05$). The phylogenetic structure in SP1 is clustering, and the phylogenetic structure in SP2 and SP3 is over-dispersion. The phylogenetic structure in SP4 tends to be random. These results suggested that distance had some influence on the phylogenetic structure, but the differences were not significant among sample sites. The same with previous studies, the phylogenetic structure is not statistically significantly different across distinct topographic variation (Kitagawa et al., 2015). This result may be related to the short spatial distance to the seashore with small elevational variation, thus having a weaker effect on phylogenetic structure. It is probably that the greater influence of human disturbance and niche competition on phylogenetic structure covered the effect of habitat filtering.

Conclusions

The species composition *Casuarina equisetifolia* and *Dendrocalamus minor* var. *amoenus* mixed communities existed endemic species and exotic species under coastal gradients. The species richness, phylogenetic diversity, Simpson index, and Shannon-Wiener index showed a decreasing trend with decreasing distance from shore. The determining factors of species diversity, phylogenetic diversity are EC and SOC. The phylogenetic structure did not change with distance from shore. Future research can focus on revealing the patterns and determining factors (i.e. soil types, growth habits, and elevations) of phylogenetic structure in the coastal area.

Acknowledgements. This project was jointly supported by the Introduction of Talents Project of Putian University of Science & Technology Grant (No. 2021074); Fujian Province educational research project of young and middle-aged teachers (No. JAT210386); Special project of scientific research and innovation of Putian University (No. 2021ZP02); Fujian Province Regional Development Program (2015N3015). Foundation for scientific and technological innovation of Fujian agriculture and forestry university (CXZX2017089); Fujian University Engineering Research Center for disaster prevention and mitigation of engineering structures along the southeast coast (No. JDGC03).

Author contributions. ZJM conceived of the research idea, wrote the manuscript and conducted the fieldwork. ZYS supervised the experiment. Both authors discussed the results and comments on the manuscript.

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