7-9-2020

Relationships between vegetation and soil seed banks along a center-to-edge gradient on a tropical coral island

Yao Huang
Chinese Academy of Sciences

Hai Ren
Chinese Academy of Sciences

Jun Wang
Chinese Academy of Sciences

Nan Liu
Chinese Academy of Sciences

Shuguang Jian
Chinese Academy of Sciences

See next page for additional authors

Recommended Citation

Yao Huang, Hai Ren, Jun Wang, Nan Liu, Shuguang Jian, Hongyue Cai, Dafeng Hui, Qinfeng Guo, "Relationships between vegetation and soil seed banks along a center-to-edge gradient on a tropical coral island", Ecological Indicators, Volume 117, 2020, 106689, ISSN 1470-160X, https://doi.org/10.1016/j.ecolind.2020.106689.

Ecological Indicators 117 (2020) 106689

Contents lists available at ScienceDirect

Ecological Indicators

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

Relationships between vegetation and soil seed banks along a center-to-edge gradient on a tropical coral island

Yao Huang[a,b], Hai Ren[a,b,*], Jun Wang[a], Nan Liu[a], Shuguang Jian[a], Hongyue Cai[a,b], Dafeng Hui[c], Qinfeng Guo[d]

[a] CAS Engineering Laboratory for Vegetation Ecosystem Restoration on Islands and Coastal Zones, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou 510650, China

[b] University of Chinese Academy of Sciences, Beijing 100049, China

[c] Department of Biological Sciences, Tennessee State University, Nashville, TN 37209, USA

[d] Southern Research Station, USDA Forest Service, RTP, NC 27709, USA

ARTICLE INFO

Keywords:
Paracel Islands
Micro-habitats
Restoration
Species richness
Conservation practice

ABSTRACT

Few studies have focused on the relationships between vegetation and soil seed banks on small islands. To better understand the pattern and regeneration potential of seed banks on tropical coral islands, we measured environmental factors and the species composition, and species richness of soil seed banks and vegetation along a gradient from the center to the edges on East Island in the South China Sea. The results showed that the similarity between the species composition of vegetation and seed banks increased from the center to the edge. In the center, species richness in both vegetation and seed banks was positively correlated with soil organic matter, total nitrogen, and total phosphorus. At the edge, species richness in both vegetation and seed banks was positively correlated with soil pH. Our results indicate that plant communities contributed little to the seed banks in the center of the island and evidently played a minor role in vegetation regeneration at that location. Plant communities near the edge, in comparison, showed a greater potential for regeneration from seed banks. Conservation and management practices along the center-to-edge gradient should be designed in accordance with the differences in plant communities and soil seed banks at different locations on the gradient.

1. Introduction

The plant communities on small coral islands differ from those on main lands in several significant ways. As a relatively closed ecological system, an island has some barriers for exchange of materials with the outside world (Martinez-Escobar and Mallela, 2019) and usually has high habitat heterogeneity (Looney and Gibson, 1995). The plant communities on island undergo succession and regeneration, seed dispersal and germination, and biotic and abiotic interactions (Hayasaka et al., 2009; Philipp et al., 2018). Plant species on islands inhabit different niches according to the differences in the plants' biological characteristics (Prabakaran and Paramasivam, 2014).

The Paracel Islands in the South China Sea are the largest group of coral islands and have abundant natural resources but vulnerable ecosystems (Tong et al., 2013). The Parcel Islands support 310 species of vascular plants, which form four types of vegetation, including coral island tropical evergreen forest, tropical evergreen shrub forest, tropical herb-vine community, and artificially cultivated vegetation (Zhang, 1974; Zhang et al. 2011). All of the plant species on the islands originally immigrated from the neighboring continent and islands via sea currents, birds, wind, and humans. Over the past half century, the species and area of cultivated plants on the islands have increased (Zhang et al. 2011; Xing, 2018). Because of natural and human disturbance, the Paracel Islands face loss of vegetation coverage, vegetation degradation, and species invasion (Exploration Group of Paracel Islands of Institute of Soil Science of Chinese Academy of Sciences (CAS), 1977; Tong et al., 2013).

Vegetation and seed banks are important biotic components on coral islands because they have direct and indirect effects on the stability and resilience of the island ecosystem (Looney and Gibson, 1995). Species distributions are the result of long-term interactions of aboveground vegetation and soil seed banks as well as their relationships with the environments (Todo et al., 2019). Our knowledge of the characteristics of aboveground vegetation and soil seed banks and their

* Corresponding author at: CAS Engineering Laboratory for Vegetation Ecosystem Restoration on Islands and Coastal Zones, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou 510650, China.

E-mail address: renhai@scib.ac.cn (H. Ren).

https://doi.org/10.1016/j.ecolind.2020.106689
Received 5 February 2020; Received in revised form 21 June 2020; Accepted 30 June 2020
Available online 09 July 2020

correlations with environmental factors on coral islands in the South China Sea is limited (Zuo et al., 2014), but such knowledge is needed to support management decisions with respect to conservation or restoration.

In this study, we examined the characteristics of both vegetation and soil seed banks and their relationships with environmental factors on a center-to-edge gradient on East Island, a tropical coral island in the South China Sea. The primary objectives were to explore how environmental conditions influence vegetation and soil seed banks and to determine the potential of soil seed banks to support ongoing regeneration of vegetation on the island.

2. Methods

2.1. Study sites

The study was conducted on East Island (16°39′–16°41′N, 112°43′–112°45′E), which is a coral island and one of the Paracel Islands in the South China Sea; East Island is about 2.4 km long and 0.5 km wide (Liu et al., 2017). The island has been rarely disturbed by humans and has a typical tropical marine climate with year-round high temperatures ranging from 15.3 to 34.9 °C, a mean annual precipitation of 1500 mm, and a mean annual evaporation capacity of 2500 mm. The island has about 50 plant species. The mature soils on the island are mainly guano-phosphatic coral-sand soils, and the immature soils are predominantly coral sand (Exploration Group of Paracel Islands of Institute of Soil Science of Chinese Academy of Sciences (CAS), 1977).

2.2. Plot establishment, seed bank sampling, and vegetation survey

In October 2017 and April 2018, we divided the whole island into three areas (edge, middle, and center; Supplementary Fig. 1) based on a previous investigation of the vegetation and soil (Tong et al., 2013). The edge area included the zone between the shoreline and about 83 m inland from the shoreline; the middle area included a zone between about 83 m and about 167 m inland from the shoreline; and the center area included a zone between about 167 m to about 250 m inland from the shoreline (the location of the center point of the center area). The boundaries of the three areas would form concentric circles if the island were circular but, as noted earlier, the island is oblong.

The dominant plant species differed in the three areas. In the center area, a tree, *Pisonia grandis,* was dominant, but *Stenotaphrum subulatum*, *Guettarda speciose*, and *Morinda citrifolia* had scattered distributions in the understory. In the middle area, the shrubs *Cordia subcordata*, *G. speciose*, and *Scaevola sericea* were dominant, and *Lepturus repens* and *Portulaca oleracea* were common herbs. In the edge area, herbs and vines including *Suriana maritima*, *Messerschmidia argentea*, *S. sericea*, *Pemphis acidula*, and *Ipomoea pescaprae* were dominant. In addition, we found calcareous humus soils under trees and shrubs and alluval coral sand soils under herbs and vines. Sand dunes without vegetation were present in parts of the edge area.

In each area, we identified five sites. At each site, we randomly designated five plots (20 m × 20 m) (Supplementary Fig. 1). Each plot was divided into four quadrats (5 m × 5 m) and a subplot (1 m × 1 m) was established in the center of each quadrat. Using a soil auger (4 cm diameter), we collected four soil subsamples to a depth of 10 cm in every subplot. The four subsamples were combined and mixed to yield one sample per subplot, which was used to assess the soil seed bank (Daïnou et al., 2011). To assess the soil seed bank, stones and plant fragments were removed from the soil samples, which were then placed in germination trays (22 × 17 × 8 cm^3 each). The trays were kept in a greenhouse and were watered regularly. Six control trays with sterilized soils were interspersed among the germination trays to detect potential contamination. Emerging seedlings were removed after they could be identified. The experiment was terminated when additional seedlings failed to appear for several consecutive weeks, which occurred after about 8 months.

The aboveground vegetation was assessed immediately after the soil was sampled in each subplot. The number of individuals of each species was determined (Wang et al., 2009). The Moosehom method was used to evaluate the coverage of trees in the forest (Garrison, 1949). The sample point method was used to evaluate the coverage of shrubs and herbs (Vales and Bunnell, 1990). In addition, six soil samples were collected using a soil auger (diameter 4.0 cm, depth 10 cm) with five replicates from the four corners of each quadrat (Luo et al., 2019). The following soil variables were measured as described by Liu (1996): pH, salinity, and contents of organic matter (SOM), total nitrogen (TN), total phosphorus (TP), and available phosphorus (AP).

2.3. Data analysis

We used detrended correspondence analysis (DCA; Hill and Gauch, 1980) to analyze species composition.

Sørenson's coefficient (S’) was used to evaluate the similarity between the species richness of the aboveground vegetation and seed banks (Liu et al., 1998). S’ was calculated as follows:

$S' = 2C/(A + B)$, where A is the aboveground vegetation species richness, B is the seed bank species richness, and C is the common species richness of A and B,

Soil TN, TP, AP, SOM, and salinity were included as environmental factors, and habitat was considered as a dummy variable. We compared the influence of soil physicochemical variables on species richness of seed banks and aboveground vegetation among sampling locations using redundancy analysis (RDA). All data analyses were conducted with the software R 3.5.3 (ter Braak and Šmilauer, 2012).

3. Results

In all plots across all three areas on the island, 43 species were detected in the seed bank and 46 species were detected in the aboveground vegetation. Four weed species and three cultivated species were detected in both the soil seed banks and aboveground vegetation (Supplementary Table 1). Mean (± SE) species richness per plot was significantly higher in the aboveground vegetation (9.89 ± 5.42 species) than in the seed banks (7.92 ± 2.87 species). Seed density in the soil seed bank (as indicated by the germination assay) was 144.6·m^{-2} in the center area, 170.6·m^{-2} in the middle area, and 171.5 m^{-2} in the edge area.

The similarity between the species composition of the aboveground vegetation and the soil seed banks was highest in the edge area for herbs (annual or perennial, Supplementary Table 1). In both November and April, the DCA results indicated that the species composition of the aboveground vegetation and the soil seedbank seldom overlapped in center area plots (Fig. 1a, d), frequently overlapped in middle area plots (Fig. 1b, e), and almost always overlapped in edge area plots (Fig. 1c, f).

In other words, the similarity between the species composition of the aboveground vegetation and soil seed bank in different seasons increased from the center to the edge. In the same area, the similarity was higher in November 2017 than in April 2018. In November 2017, the similarity was significantly higher in middle and edge areas than in the central area. In April 2018, the similarity in the species composition of the aboveground vegetation and the soil seed bank was significantly higher in the edge area than in the other two areas (Fig. 2).

Soil properties were highly consistent between November and April. The concentrations of AP, TN, and TP were significantly affected by area ($p < 0.05$, Table 1). TN and TP were highest in the center area. AP in the center and middle areas was significantly higher than in the edge area. SOM was significantly higher in the middle area than in the edge area. The difference in salinity between the middle and center or edge was substantial due to a small area of marshy saline soil in the middle area. Soil pH did not significantly differ among the three areas.

The RDA analysis revealed significant correlations in both

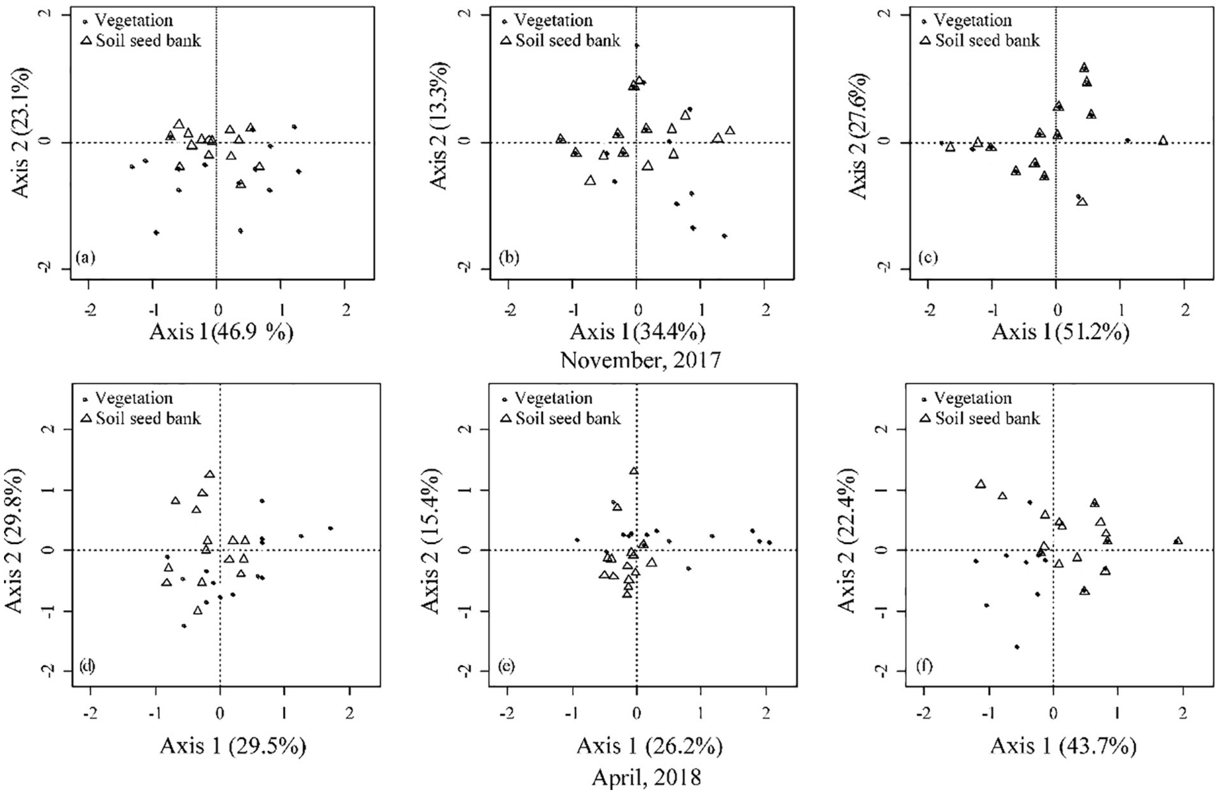

Fig. 1. Results from detrended correspondence analysis (DCA) of species composition between aboveground vegetation and the soil seed bank in three areas of the island: the center (a and d), the middle (b and e), and the edge (c and f).

November and April between soil physicochemical characteristics and species richness of the aboveground vegetation in the center and edge areas (Fig. 3a,c) and of species richness of the soil seed bank in center and edge areas (Fig. 3b,d). The species richness of the aboveground vegetation was positively correlated with soil pH in the edge area, and was positively correlated with SOM, AP, TN, and TP in the center area (Fig. 3a,c). The species richness of the soil seed bank was positively correlated with pH in the edge area, and with SOM, AP, TN, and TP in the center area (Fig. 3b,d). In the middle area, the species richness of the aboveground vegetation and of the soil seed bank were positively related with soil pH in some plots and with SOM, AP, TN, salinity, and TP in other plots (Fig. 3). The species richness of the aboveground vegetation and soil seed bank also varied seasonally (Supplementary Table 1 and Fig. 3).

4. Discussion

Our results showed that the vegetation on the coral island was mostly mono-dominant and that seed availability in the soil seed bank appeared to be an important limiting factor with respect to regeneration, especially in the center area of the island, where the vegetation was dominated by *P. grandis* but where the soil seed bank contain few *P. grandis* seeds. Our findings are consistent with previous reports, which indicated that seed availability was important to restoration and was

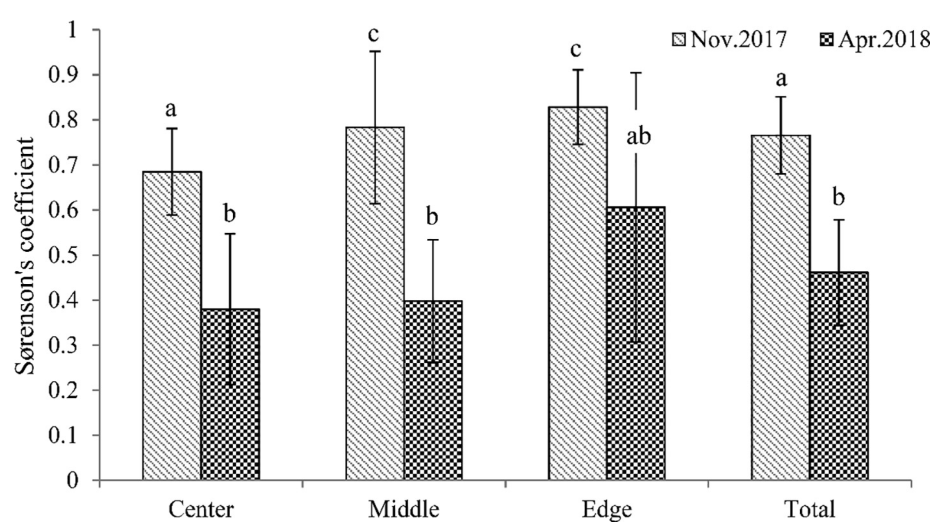

Fig. 2. Sørenson's similarity coefficient between the species composition of the aboveground vegetation and the soil seed bank in three areas and two seasons. Total = Entire island. Values are means ± SE; means with different letters are significantly different.

Table 1
One-way ANOVAs and multiple comparisons for soil physicochemical characteristics in two seasons and the three areas of the coral island. Values are mean ± SE; n = 75 for each combination of season and area. Nov. = November, Apr. = April.

Month	Area	pH	Salinity (%)	Organic matter ($g{\cdot}kg^{-1}$)	Total nitrogen ($g{\cdot}kg^{-1}$)	Total phosphorus ($g{\cdot}kg^{-1}$)	Available phosphorus ($g{\cdot}kg^{-1}$)
Nov.	center	8.09 ± 0.15	6.64 ± 1.56a	9.97 ± 1.99ab	19.33 ± 3.87a	99.24 ± 10.77a	4.51 ± 0.79a
	middle	8.22 ± 0.17	12.3 ± 0.09b	39.86 ± 33.59a	11.80 ± 7.89a	13.11 ± 11.96b	3.61 ± 2.32a
	edge	8.18 ± 0.22	7.3 ± 0.15a	3.01 ± 2.22b	0.08 ± 0.04b	1.56 ± 1.00c	1.38 ± 0.91b
Apr.	center	8.04 ± 0.14	6.16 ± 0.02a	11.59 ± 3.05ab	19.52 ± 4.39a	99.93 ± 12.16a	4.63 ± 0.74a
	middle	8.19 ± 0.14	14.2 ± 0.09b	32.89 ± 30.73a	13.60 ± 8.50a	14.61 ± 12.28b	3.57 ± 2.47a
	edge	8.24 ± 0.21	6.92 ± 0.14a	2.39 ± 1.81b	0.09 ± 0.04b	2.01 ± 1.22c	1.31 ± 0.84b

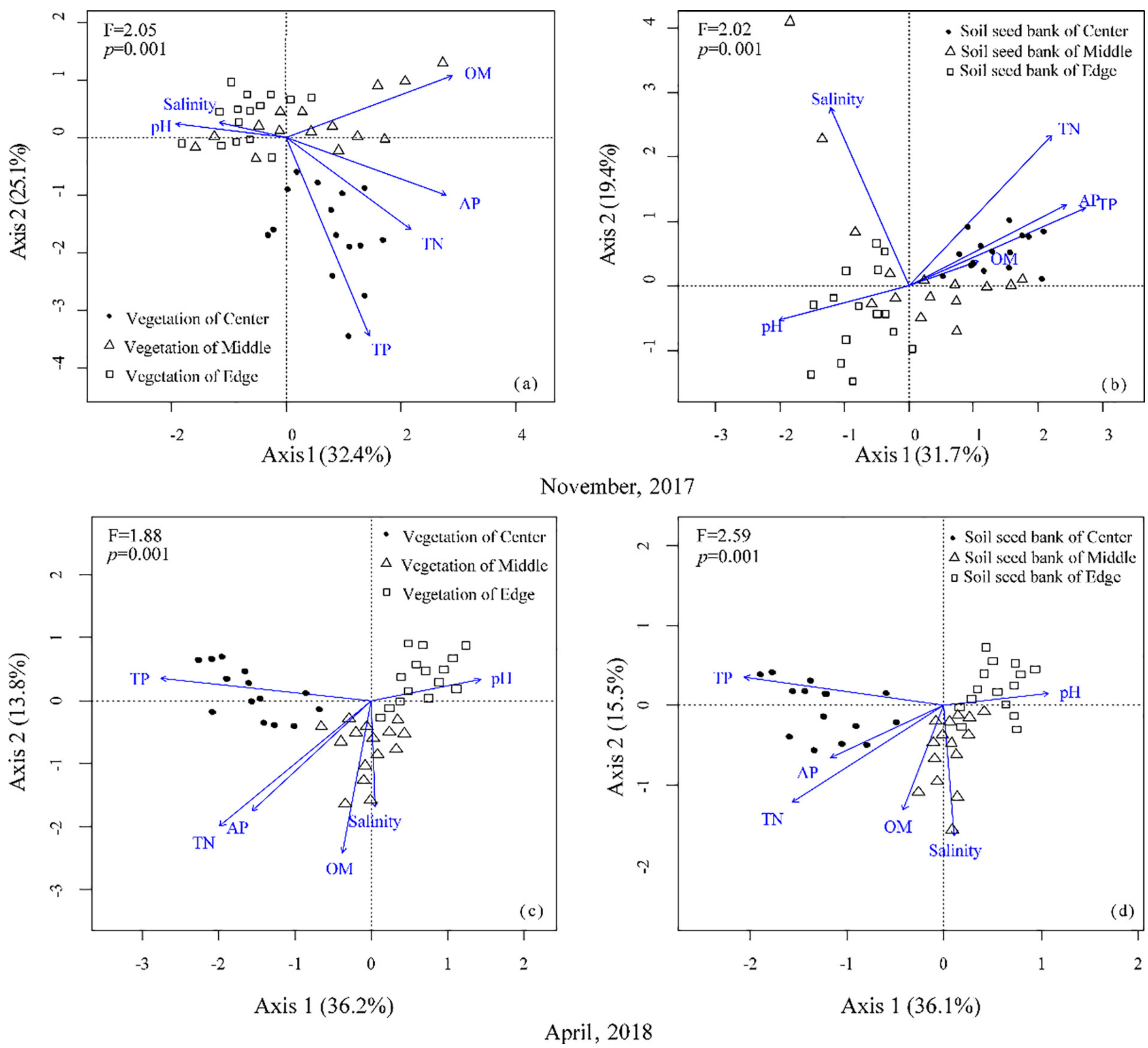

Fig. 3. Redundancy analysis (RDA) of the correlation between environmental factors and the species richness of the aboveground vegetation (a and c) and of the soil seed bank (b and d) in three areas of the coral island in April and November.

influenced by many environmental factors including soil properties (Fosberg, 1976; Rogers and Morrison, 1994). From the edge to the center area of the coral island, changes in the physical and chemical properties of soil documented in the current study were likely to facilitate soil/plant restoration. Although Li et al. (2017) found that guano deposition increased soil nutrients, especially phosphorus, the excessive input of phosphorus significantly reduced microbial decomposition of organic matter in the central area. Li et al. (2017) also found that the standing vegetation had a more complex community structure and produced more litterfall in the middle area than in the center or edge areas, such that organic matter input was highest in the middle area.

The similarity in the species composition of the aboveground vegetation and the soil seed bank increased from the center area to the edge area (Fig. 1). Perhaps seabird guano deposition and light-limited germination of seeds explain the low similarity between vegetation and seed banks in the center area (Irick et al., 2015). Whereas the standing vegetation in the central area was poorly represented in its soil seed bank, the standing vegetation and seed bank contained similar species in the middle and edge areas. Perennial herbaceous species were found in both aboveground vegetation and seed bank in the middle and edge areas, which contributed to strong correlations with above-ground vegetation and seed bank. The seed banks of the island's barren coastal dunes contained an abundant mix of pioneer and early successional plant propagules, which could potentially contribute to establishment of endemic and rare pioneer species in the early succession stage of coral island vegetation. In addition, the similarity between aboveground vegetation and soil seed banks in terms of species composition was significantly higher in November 2017 than in April 2018 in the same area. This seasonal difference suggests that the soil seed banks may be replenished in winter with new seeds from standing vegetation, and that the seeds of some species in the soil seed bank may be lost to germination or to herbivory in the summer (Yuan, 2011).

We found that the species richness of the aboveground vegetation and the soil seed bank on the coral island was closely related to soil properties and especially to soil nutrient levels. In the center area, the species richness of the aboveground vegetation and soil seed bank was positively correlated with the contents of SOM, TN, TP, and AP, but was negatively correlated with soil pH (Fig. 2). In the central area, the aboveground vegetation attracts seabirds, which deposit guano and thereby input abundant nutrients to the soil (unpublished observation). Plants in the center area also produced large amounts of litter that led to more accumulation of organic matter (unpublished data). Unlike the species richness of the aboveground vegetation and soil seed bank in the center area of the island, the species richness of the aboveground vegetation and soil seed bank in the edge area were negatively correlated with SOM, TN, TP, and AP, and positively correlated with soil pH (Fig. 2). These results indicate that the species in the edge area tolerate high soil pH and low soil nutrients. The plants in the middle area live in a mode moderate environment. We infer that the differences in the relationships between aboveground vegetation, soil seed banks, and soil environmental properties in the three areas on the island correspond with the differences in species in the aboveground vegetation and soil seed banks in the three areas.

The richness and abundance of plants in both the aboveground vegetation and seed banks suggest that the spatial pattern of vegetation may be maintained, at least in the near term, on the island. Climax species in the center area may not have been represented in the soil seed bank perhaps because their seeds do not undergo dormancy, while pioneer species in the other areas may have been represented in the soil seed banks because their seeds do undergo dormancy (Swaine and Hall 1988). We also infer that the restoration potential of the coral island vegetation varies from the center to edge. The island center could provide favorable habitats for some climax tree species, but regeneration of those species is unlikely to involve the soil seed bank. In contrast, many endemic species that are resistant to drought and low nutrient conditions seem adapted to the island edge, and their regeneration is likely to involve soil seed banks. It follows that management of the island's vegetation should differ among the areas. Vegetation conservation in the center of the island is important because the lack of seeds in the soil seed bank and the lack of vegetative propagation (unpublished observations) would restrict natural regeneration and succession. In addition, the sand dunes on the edge of the island could rely on seed banks to produce more plants that would protect the coastal zone.

CRediT authorship contribution statement

Yao Huang: Investigation, Writing - original draft. **Hai Ren:** Conceptualization, Writing - review & editing, Supervision. **Jun Wang:** Investigation, Writing - review & editing. **Nan Liu:** Investigation, Writing - review & editing. **Shuguang Jian:** Investigation. **Hongyue Cai:** Investigation. **Dafeng Hui:** Writing - review & editing. **Qinfeng Guo:** Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This study was supported by the Strategic Priority Research Program of the Chinese Academy of Sciences (XDA13020500), NSFC-Guangdong Province Union Funds (U1701246), the Guangdong Science and Technology Program (2019B21201005) and the Youth Innovation Promotion Association CAS (2019340). We thank Beibei Xu, Jing Huang, Chunqing Long and Prof Bangyu Chen for assistance with field work and plant species identification. We also thank Prof Bruce Jaffee for help with English, and two anonymous reviewers for their valuable comments.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2020.106689.

References

Daïnou, K., Bauduin, A., Bourland, N., Gillet, J.F., Fétéké, F., Doucet, J.L., 2011. Soil seed bank characteristics in Cameroonian rainforests and implications for post-logging forest recovery. Ecol. Eng. 37, 1499–1506. https://doi.org/10.1016/j.ecoleng.2011.05.004.

Exploration Group of Paracel Islands of Institute of Soil Science of Chinese Academy of Sciences (CAS), 1977. Soil and Guano Phosphorus Mine in Paracel. Science Press, Beijing (in Chinese with English abstract).

Fosberg, F.R., 1976. Coral Island Vegetation. Biol. Geol. Coral Reefs. 3, 255–277. https://doi.org/10.1016/B978-0-12-395527-2.50015-9.

Garrison, G.A., 1949. Uses and modifications for the 'Moosehorn' crown closure estimator. J. Forestry 47, 733–735.

Hayasaka, D., Fujiwara, K., Box, E.O., 2009. Recovery of sandy beach and maritime forest vegetation on Phuket Island (Thailand) after the major Indian Ocean Tsunami of 2004. Appl. Veg. Sci. 12, 211–224. https://doi.org/10.2307/27735061.

Hill, M.O., Gauch, H.G., 1980. Detrended correspondence analysis: an improved ordination technique. Vegetatio. 42, 47–58. https://doi.org/10.1007/BF00048870.

Irick, D.L., Gu, B.H., Li, Y.C., Inglett, P.W., Frederick, P.C., Ross, M.S., Wright, A.L., Ewe, S.M.L., 2015. Wading bird guano enrichment of soil nutrients in tree islands of the Florida Everglades. Sci. Total Environ. 532, 40–47. https://doi.org/10.1016/j.scitotenv.2015.05.097.

Li, L., Qu, Z., Jia, R., Wang, B.L., Wang, Y.Y., Qu, D., 2017. Excessive input of phosphorus significantly affects microbial Fe (III) reduction in flooded paddy soils by changing the abundances and community structures of *Clostridium* and *Geobacteraceae*. Sci. Total Environ. 607, 982–991. https://doi.org/10.1016/j.scitotenv.2017.07.078.

Liu, C.R., Ma, K.P., Lü, Y.H., Kang, Y.L., 1998. Measurement of biotic community diversity VI: the statistical aspects of diversity measures. Chinese Biodiversity 6 (3), 229–239.

Liu, G.S., 1996. Soil Physical and Chemical Analysis and Description of Soil Profiles. Chinese Standard Press, Beijing.

Liu, X.T., Ge, C.D., Zou, Q.X., Huang, M., Tang, M., Li, Y.L., 2017. Nitrogen geochemical characteristics and their implications on environmental change in the lagoon sediments of the Dongdao Island of Xisha Islands in South China Sea. Acta Oceanol. Sin. 39 (6), 43–54.

Looney, P.B., Gibson, D.J., 1995. The relationship between the soil seed bank and aboveground vegetation of a coastal barrier island. J. Veg. Sci. 6, 825–836. https://doi.org/10.2307/3236396.

Luo, X.Z., Hou, E.Q., Zang, X.W., Zhang, L.L., Yi, Y.F., Wen, D.Z., 2019. Effects of elevated atmospheric CO_2 and nitrogen deposition on leaf litter and soil carbon degrading enzyme activities in a Cd-contaminated environment: a mesocosm study. Sci. Total Environ. 671, 157–164. https://doi.org/10.1007/0-306-48051-4_30.

Martinez-Escobar, D.F., Mallela, J., 2019. Assessing the impacts of phosphate mining on coral reef communities and reef development. Sci. Total Environ. 692, 1257–1266. https://doi.org/10.1016/j.scitotenv.2019.07.139.

Philipp, M., Hansen, K., Monrad, D., Adsersen, H., Nordal, I., 2018. Hidden biodiversity in the Arctic-a study of soil seed banks at Disko Island, Qeqertarsuaq, West Greenland. Nord. J. Bot. 36, 1–12. https://doi.org/10.1111/njb.01721.

Prabakaran, N., Paramasivam, B., 2014. Recovery rate of vegetation in the tsunami impacted littoral forest of Nicobar Islands. India. For. Ecol. Manage. 313, 243–253. https://doi.org/10.1016/j.foreco.2013.11.023.

Rogers, R.W., Morrison, D., 1994. Floristic change on Heron Island, a coral cay in the Capricorn-Bunker Group, Great Barrier Reef. Aust. J. Bot. 42, 297–305. https://doi.org/10.1071/bt9940297.

Swaine, J.B., Hall, M.D., 1988. The Mosaic Theory of forest regeneration and the

determination of forest composition in Ghana. J. Tropical Ecol. 4, 253–269. https://doi.org/10.2307/2559389.
ter Braak, C.J.F., Šmilauer, P., 2012. Canoco reference manual and user's guide: software of ordination (version 5.0). Microcomputer Power (Ithaca, NY. USA).
Todo, C., Tokoro, C., Yamase, K., Tanikawa, T., Ohashi, M., Ikeno, H., Dannoura, M., Miyatani, K., Doi, R., Hirano, Y., 2019. Stability of *Pinus thunbergii* between two contrasting stands at differing distances from the coastline. For. Ecol. Manage. 413, 44–53. https://doi.org/10.1016/j.foreco.2018.05.040.
Tong, Y., Jiang, S.G., Chen, Q., Li, Y.L., Xing, F.W., 2013. Vascular plant diversity of the Paracel Islands, China. Biodiversity Sci. 21, 364–374. https://doi.org/10.3724/SP.J.1003.2013.11222.
Vales, D.J., Bunnell, F.L., 1990. Comparison of methods for estimating forest overstory cover: differences among techniques. Can. J. Forest Res. 20, 101–107. https://doi.org/10.1139/x90-014.
Wang, J., Ren, H., Yang, L., Li, D.Y., Guo, Q.F., 2009. Soil seed banks in four 22-year-old plantations in South China: implications for restoration. For. Ecol. Manage. 258, 2000–2006. https://doi.org/10.1016/j.foreco.2009.07.049.
Xing, F.W., 2018. Flora of the South China Sea islands. China Forestry Publishing House, Beijing (English Version).
Yuan, H., 2011. The soil seed bank and relationship with the above-ground vegetation in the degradation areas of the Napahaireserve of Plateau wetlands in Northwest Yunnan. Yunnan Unver.
Zhang, H.D., 1974. The vegetation of the HSI-SHA Islands. J. Integr. Plant Biol. 16 (3), 183–190.
Zhang, L., Liu, Z.W., Jiang, D.Q., 2011. Ecological Investigation of the Vegetation in the Paracel Islands. Chinese Agri. Sci. Bull. 27 (14), 181–186.
Zuo, X., Wang, S., Zhao, X., Lian, J., 2014. Scale dependence of plant species richness and vegetation-environment relationship along a gradient of dune stabilization in Horqin Sandy Land, Northern China. J. Arid Land 6 (3), 334–342. https://doi.org/10.1007/s40333-013-0221-8.