Ecological Indicators 120 (2021) 106947

Contents lists available at ScienceDirect

Ecological Indicators

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

Bryophyte diversity is related to vascular plant diversity and microhabitat under disturbance in karst caves

Hai Ren[a,b,*,1], Faguo Wang[a,1], Wen Ye[a,1], Qianmei Zhang[a], Taotao Han[a], Yao Huang[a,b], Guowei Chu[a], 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, Asheville, NC 28804, USA

ARTICLE INFO

Keywords:
Plant diversity
Habitat heterogeneity
Light and water status
Soil nutrient
Restoration

ABSTRACT

Plant diversity, habitat properties, and their relationships in karst caves remain poorly understood. We surveyed vascular plant and bryophyte diversities and measured the habitat characteristics in six karst caves in south China with different disturbance histories (one had been disturbed by poultry feeding, three had been disturbed by tourism, and two were undisturbed). The plant diversity differences among the six caves were analyzed using cluster analysis, and the relationships of plant diversity and microhabitat were assessed using canonical correspondence analysis. We found a total of 43 angiosperm species from 27 families, 20 lycophyte and fern species from 9 families, and 20 species of bryophytes from 13 families in the six caves. Habitat characteristics including light intensity, air relative humidity, air temperature, and soil properties varied among the caves. The plant diversity in karst caves was not rich, but the species composition was unique. The caves with high disturbance had the lowest species richness, numbers of individuals, and Shannon-Wiener diversity indices but the highest Simpson's dominance indices. The caves with less disturbance had the highest numbers of species, numbers of individuals, and Shannon-Wiener diversity indices but the lowest Simpson's dominance indices. The disturbed caves were often dominated by drought-tolerant, tenacious mosses (bryophytes), while the relatively undisturbed caves contained abundant liverworts (bryophytes), which were better adapted to humid environments. Plant diversity in karst caves was closely related to habitat heterogeneity, light and water status, and nutrient availability. Tourism and poultry farming were associated with the degradation of vegetation in some karst caves. Protecting and restoring bryophytes might facilitate the settlement, growth, and succession of vascular plants in karst caves. Bryophytes can be used as indicators of overall plant diversity and restoration status in karst caves.

1. Introduction

Karst landscapes are widely distributed and account for nearly 15% of the world's land surface. The karst regions of China cover 1.9 million km^2 (about 0.54 million km^2 are underlain by carbonate rocks) and are among the largest karst regions in the world (Yuan, 1994). The average density of karst caves is 6.4/km^2 in China as a whole and is 41.8/km^2 in South China (Zhang, 1986). Topographic features of karst regions include caves, sinkholes, and mogotes. Because of these geological features, the ecosystems in karst regions are fragile and extremely vulnerable to human disturbance (Brandt et al., 2018). Increased human exploitation of natural resources and agricultural activities have resulted in vegetation loss and land degradation during the last half century in the karst regions of China (Tong et al., 2018). Karst soils are thin and have great spatial heterogeneity, and these properties affect the conservation and restoration of the plant communities that they support (Cong et al., 2017; Wang et al., 2020). The structure, function, and dynamics of karst vegetation in China have been recently

* 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 addresses: renhai@scib.ac.cn, renhai@scbg.ac.cn (H. Ren), wangfg@scbg.ac.cn (F. Wang), wenyescib@scbg.ac.cn (W. Ye), zqm@scbg.ac.cn (Q. Zhang), tthan@rcees.ac.cn (T. Han), huangyao.ok@scbg.ac.cn (Y. Huang), cgw@scbg.ac.cn (G. Chu), dhui@tnstate.edu (D. Hui), qinfeng.guo@usda.gov (Q. Guo).

[1] Contribute equally.

https://doi.org/10.1016/j.ecolind.2020.106947
Received 28 February 2020; Received in revised form 13 August 2020; Accepted 8 September 2020
1470-160X/

investigated (Wang et al., 2011, 2020; Voloscuk et al., 2016; Zhang et al., 2016; Cong et al., 2017; Cao et al., 2020; Tong et al., 2020).

Although caves are threatened biodiversity hotspots, they receive little governmental attention or appropriate management (Barr, 1964; Medellin et al., 2017). There is no governmental agency or non-governmental organization concerned with the conservation of cave ecosystems in China or in many other countries (Whitte, 2009). There are caving expeditions, but such expeditions concentrate on exploration rather than on the investigating cave organisms. Disturbances by farming, visitors, tourism infrastructure, and changes in water flow can have devastating effects on the highly adapted and range-restricted organisms that live in caves (Whitte, 2009). Cave conservation and restoration therefore require the attention of researchers and governmental agencies (Elliott, 2006). The use of mosses as nurse plants to restore endangered herbs in karst caves is one of the few studies of karst cave restoration (Ren et al., 2010a).

Although cave vegetation and soils are important in the study of autogenic/primary succession, cave ecology, evolutionary biology, and global change biology, they are poorly understood (Barr, 1964; Bai et al., 2020). Karst caves and their entrances have dim light with limited nutrient availability, high humidity, and relatively low temperature fluctuations (Northup and Lavoie, 2001). The karst cave plant community is a relic of the surrounding karst forest community and is strongly dominated by understory life forms and taxa. The vegetation at cave entrances usually has low species richness and a small number of individuals (Supplementary Fig. 1 and Supplementary Fig. 2). In contrast, the plant communities in karst caves are often diverse (Monro et al., 2018). Bryophytes are the most common plants in karst caves (Mulec and Kubešová, 2010; Cong et al., 2017; Puglisi et al, 2019). Bryophytes may be used as indicators of plant diversity and ecosystem health in karst caves. The plant diversity in karst caves is closely related to micro-habitat properties. As noted earlier, human disturbance such as tourism and agriculture can lead to habitat and vegetation degradation in karst caves (Belnap and Lange, 2013; Liu et al., 2019; Pakeman et al., 2019). Leaf nutrient concentrations of cave-dwelling plants often reveal convergent adaptations to cave environments (Bai et al., 2020).

This study focused on the relationships between vegetation and soil in karst caves that differ in their level of disturbance. We hypothesized that plant diversity and especially bryophyte diversity and species composition in karst caves would differ depending on disturbance level, and that the differences in plant diversity would be related to the habitat conditions in the caves. We attempted to answer the following questions: (1) How does plant diversity, and especially bryophyte diversity, differ between highly disturbed and relatively undisturbed karst caves? (2) How do habitat characteristics differ between highly disturbed and relatively undisturbed karst caves? (3) How does plant diversity relate to habitat characteristics? The findings from this study should be useful for the protection and restoration of plant communities in karst caves.

2. Materials and methods

2.1. Study area

The study site is located in Dixiahe and Shangbaichang, Lianzhou City (24°59′-25°58′ N, 111°98′-113°11′ E), Guangdong Province, south China. About 70% of the area consists of karst underlain by carbonate rocks. There are more than 100 caves in the area, but only 31 caves are more than 500 m long. The region is dominated by a central subtropical monsoon climate, and the elevation ranges from 130 to 450 m asl. The zonal original soil is lateritic with a low pH. The mean annual temperature is 19.5°C, and the mean annual rainfall is 1,571 mm (Data sources: http://cdc.cma.gov.cn/home.do). The vegetation is dominated by the evergreen broad-leaved forests that are typical of the subtropics (Ren et al., 2010a).

2.2. Plant survey, soil sampling, and analysis

The study involved six caves of similar size and altitude: Caves A, B, C, and D are located in Dixiahe (the distance between them is $<$ 2 km), and Caves E and F are located in Shangbaichang (the distance between them is about 1 km). Shangbaichang is about 21 km away from Dixiahe. Caves A, B, and C were developed into tourist spots in 1988. At present, there are 800,000 visitors every year at Cave A. Cave B was closed to tourism and subjected to natural restoration after 2000. Cave C was protected after 2010. Caves D and E were relatively undisturbed. Cave F has long been used to feed poultry and is highly disturbed. The major disturbances to caves A, B, and C included atmospheric, water, and noise pollution, the damage and interference on animals and plants, and the damages caused by the construction of scenic spots. The major disturbances at cave F included atmosphere pollution and the consumption of plants by poultry. We could not find three replicate caves with similar size and altitude for each disturbance type in Lianzhou City. Therefore, we did not conduct any univariate statistical comparisons of richness and diversity values among disturbance types or location types within the caves.

At each cave, we established three plots, each with an area of 5 m × 5 m, along a transect from the entrance of the cave to deep into the cave; the intervals between plots (from the entrance inward) were 10, 30, and 60 m. Hereafter, the plots at the entrance, at the deepest location, and at the intermediate location are referred to as entrance plots, deep plots, and intermediate plots. A light gradient existed among the plots at each cave because the light exposure declined with distance from the cave entrance. Field sampling was conducted at the beginning of November 2018.

All plant species were identified in each plot, and the height, density, and crown of all plant species were measured (Ren et al., 2010b). Three subplots with an area of 1 m × 1 m each were established in each plot; the bryophyte, lichen, and algal species and their coverage area were recorded in each subplot (Li et al., 2015; Cong et al., 2017; Wu et al., 2019). We also collected soil samples during vegetation surveys. Because the soils around the cave entrances are very thin and highly heterogeneous in space, soil samples were randomly collected from nine points in each plot using a 5-cm-diameter soil corer to a depth of 0.1 to 3.3 cm (according to the depth of soil layer). The soil samples collected at each plot were mixed to form one composite soil sample per plot, i.e., three composite soil samples (entrance, intermediate, and deep plot) at each cave.

The soil samples were transported to the laboratory where they were air-dried and passed through a 2-mm sieve for analysis of soil chemical characteristics, including soil water content, pH, and the contents of nitrogen (N), and phosphorus (P), and soil organic matter (SOM) (Pan et al., 2019).

2.3. Microclimate measurement

For microclimate data for the six caves, we used the data from 2007 and 2008 reported by Ren et al. (2010b). Photosynthetically active radiation (PAR), air temperature, and relative humidity were measured using a Li-6400 Photosynthesis System and its accessories (Li-COR, Lincoln, NB, USA) at each plot on 1 day in July 2007, October 2007, January 2008, and April 2008. Measurements were made hourly between 08:00 and 18:00. The average values of PAR, air temperature, relative humidity, and transmittance were calculated for each plot on each day (Ren et al., 2010b).

2.4. Data analysis

The Shannon-Wiener diversity index, Simpson's dominance index, and Pielou's evenness index (Pielou, 1975; Krebs, 1985) for vascular plants were calculated. R Language 3.5.2 (Vegan package) was also used to conduct a cluster analysis. Our calculations took into account the number of individuals of each species in each of the 18 plots (six caves × three plots per cave), and the Bray Curtis index was used to calculate the similarity of species composition among the plots. The distance of the plots' species composition was calculated by Vegan package and then the cluster analysis was carried out (Borcard et al., 2014). Canonical correspondence analysis (CCA) was used to analyze the relationship between habitat characteristics and plant species composition by grouping locations together. The vegetation and habitat data matrices were subject to CCA using R Language 3.5.2 and the Vegan package (ter Braak and Šmilauer, 2012), which is an eigenvalue ordination method developed to directly relate multivariate ecological data matrices. For each scale, two matrices were created (ter Braak and Šmilauer, 2012): one for 'vegetation properties' × 'sampling plots' (response variables), and another for 'habitat variables' × 'sampling plots' (explanatory variables).

3. Results

3.1. Plant diversity

A total of 63 vascular plant species (from 37 families) were found in the 18 plots. These included 43 species of spermatophytes (from 27 families) and 20 species of lycophytes and ferns (from 10 families). Twenty species of bryophytes (from 13 families) were also found. Among the vascular plants, Gesneriaceae, Poaceae, Gramineae, and Moraceae were the most common families, and most of these were represented by herbaceous species. No single plant was found in all six caves in November 2018, but *Primulina tabacum* Hance, *Polystichum deltodon*, *Ctenitis rhodolepis*, and *Pellionia scabra* were found in four or five caves. The most abundant species was *Primulina tabacum*, followed by *Polystichum deltodon*, *Pellionia scabra*, *Adiantum lianxianense*, and *Neolepisorus fortunei* (Supplementary Table 1).

Most of the ferns in karst caves were calcium-preferring species (Yan, 2013), such as *Hypodematium crenatum*, *Adiantum lianxianense*, *Pteris deltodon*, *Ctenitis rhodolepis*, *Tectaria devexa*, and *Polystichum deltodon*. The lycophytes and ferns formed multi-species communities at the cave entrances but single-species communities in the deep cave. Lycophyte and fern species in the entrance plots were mainly represented by higher families in evolutionarily older, such as Tectariaceae, Dryopteridaceae, Polypodiaceae; lycophyte and fern species in intermediate and deep plots were mainly represented by lower Lycopsida plants. Fern spores, young fern prothalli, and lichens were also found in intermediate and deep plots in some caves. Both entrance plots and intermediate plots contained species of Pteridaceae, Dryopteridaceae, Adiantaceae, and Tectariaceae (Supplementary Table 1). Ferns were restricted to the calcareous areas, and these included *Pteris cretica, Pteris deltodon*, *Hypodematium crenatum*, *Ctenitis rhodolepis*, and *Tectaria devexa*. Plant and species abundance were greater in less-disturbed caves, except that *Pteris vittata*, which is heliophilic, was abundant in both disturbed and less-disturbed caves. Some ferns endemic to China, such as *Adiantum lianxianense* and *Polystichum deltodon*, were restricted to limestone habitats and were more abundant in less-disturbed caves than in disturbed caves.

The distribution of bryophytes in the karst caves also followed patterns. From the entrance plots with light intensity close to that of the outside cave to intermediate and deep plots with weak light, the number of bryophyte species tended to decrease (Fig. 1). Bryophytes included mosses and liverworts. Among the 20 bryophyte species in the six caves, three mosses including *Eurhynchium hians*, *Fissidens teysmannianus*, and *Taxiphyllum taxirameum* were found in entrance plots, intermediate plots, and deep plots. Four mosses including *Ectropothecium zollingeri*, *Hypopterygium tamarisci*, *Plagiomnium vesicatum*, and *Racopilum cuspidigerum* and one liverwort, *Lejeunea sordida*, were found only in entrance plots. *Fissidens taxifolius* and *Hyophila javanica* were found only in intermediate plots, and *Radula kojana* was found only in deep plots (Supplementary Table 2). The results showed that the liverworts were adapted to low-light conditions, while the mosses were more drought tolerant and strong-light tolerant.

The proportion of bryophytes and vascular plants changed with distance from the cave entrance. The deep plots contained almost no seed plants, only a few ferns, but many bryophytes, lichens, and algae. In cave F, only the drought-tolerant bryophyte *Chionoloma tenuirostre* (Pottiaceae) was found. There were bryophytes associated with human presence in Cave B, which were not found in other caves (Supplementary Table 2). The caves that had experienced only limited disturbance were more suitable for liverworts. The disturbed caves were often dominated by drought-tolerant, tenacious moss species, while the relatively undisturbed caves were often dominated by liverworts, which are adapted to humid environments.

In terms of diversity, cave F had the lowest species richness, number of individuals, and Shannon-Wiener diversity index, but the highest Simpson's dominance index. Caves D and E had the highest species richness, number of individuals, and Shannon-Wiener diversity index, but the lowest Simpson's dominance index. The Pielou's evenness index was relatively similar among the caves (Table 1). The coverage of bryophytes in five of the caves ranged from 20.5 to 34.5%, except for the highly disturbed cave F. The species number and coverage of bryophytes in cave F were the lowest, and the coverage of bryophytes in cave B was relatively low. The coverage of bryophytes was highest in caves D and E. The number of bryophytes species was highest in cave E (Table 1, Supplementary Table 2).

Based on the results of a cluster analysis of vascular plants and bryophytes (Fig. 2), the species in caves B and F, which had experienced high human disturbance, were similar; the species in caves A, C, and D in Dixiahe were similar, and the species in cave E (in Shangbaichang) differed from those in the other caves. Bryophyte species and coverage in those caves showed similar patterns (Fig. 3, Supplementary Table 2). Cave F had long been used to raise poultry, and its plant diversity was the lowest. Cave B was used for tourists and had intermediate disturbance, and its plant diversity was relatively rich. Caves D and E suffered relatively less disturbance and thus maintained more natural or intact plant communities. Vascular plants in those caves showed slightly different patterns from both vascular plants + bryophytes and bryophytes (Fig. 4).

3.2. Habitat characteristics

Habitat characteristics including light intensity, air humidity, air temperature, and soil properties varied among the six caves. In all six caves, the soil was alkaline and the soil layer was thin, but soil fertility was moderate to high. The light intensity in six caves was low, and the transmittance was $< 61.1\%$. The temperature and humidity were similar in the caves (Table 2). In cave F, the soil layer was very thin, the content of SOM and total N were very high, and the soil water content was lower than in the other caves. The soil water contents in caves D and E were high (Table 2).

3.3. Relationships between vegetation and habitat characteristics

According to the CCA ordination diagram (Fig. 5), the eigenvalues of the first and second axis were 0.67 and 0.43, respectively, accounting for 54% of the total variation. The cumulative variance of the species–habitat relationships was 87% (Supplementary Table 3). The first axis was significantly related to light intensity, relative humidity, SOM, and total N content, and was correlated with temperature and light transmittance. Most of the bryophyte species were located on the right side of the ordination axis, indicating that these bryophyte species were adapted to habitats with relatively weak light intensity, high soil nutrient content, and relatively high moisture. The second order axis was significantly related to soil thickness, soil water content, total P content, and pH. There were also some bryophyte species in the upper left region of the diagram, indicating that these species preferred habitats with a

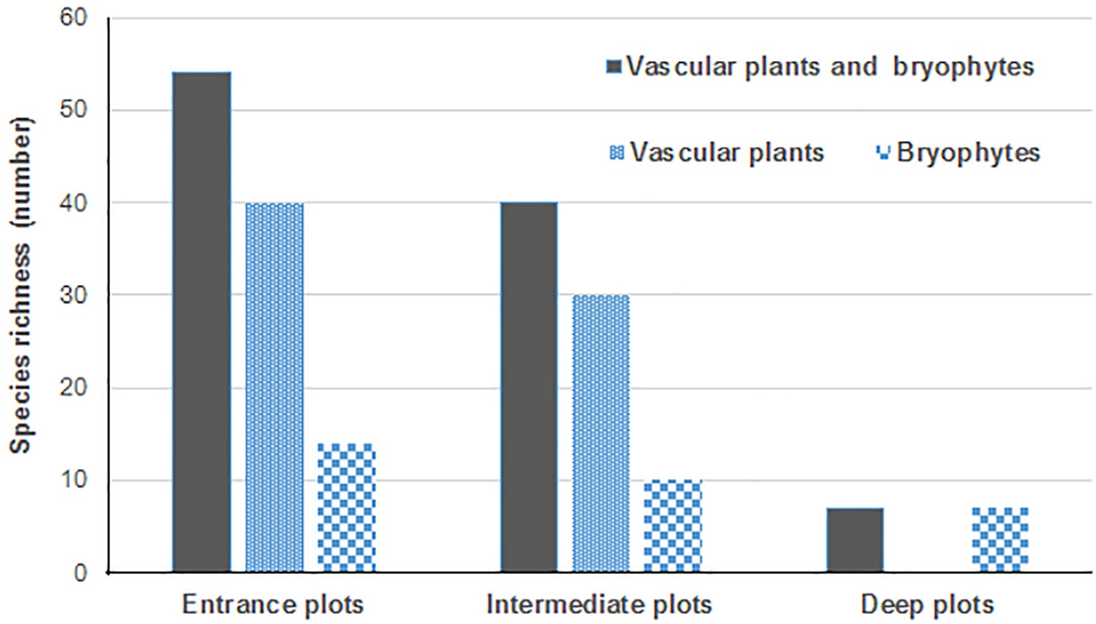

Fig. 1. Species richness per plot of vascular plants and bryophytes together, of vascular plants alone, and of bryophytes alone in the cave entrance, intermediate, and deep plots.

Table 1
Plant diversity in each of six karst caves (values are totals of three 25-m^2 plots per cave).

Index	Cave A	Cave B	Cave C	Cave D	Cave E	Cave F
Vascular plant						
Number of vascular plant species	12	17	10	27	21	12
Total number of individuals	41	21	27	50	47	16
Shannon-Wiener index	1.28	1.36	1.78	2.13	1.83	1.03
Dominance index	0.45	0.47	0.22	0.19	0.28	0.61
Evenness index	0.52	0.48	0.77	0.65	0.60	0.42
Bryophytes						
No of bryophyte species	7	7	4	7	9	1
Coverage of bryophytes (%)	23.9	20.5	28.2	34.3	34.5	3.3

thick soil layer, more alkaline soil, and higher soil water content. The species in caves F, B, D, and E were grouped in two areas of the diagram (top right and bottom right circles), while the species in caves A and C were grouped in two other areas (more central circles). In addition, there were significant correlations between plant diversity indices and habitat characteristics (Fig. 5, Table 1 and Table 2).

4. Discussion

The plant diversity in karst caves was not rich but was unique relative to the vegetation out of the caves, which was previously documented (Ren et al., 2010b). The number of species per cave never exceeded 27, and the number of individuals of a particular species in a cave was often found to be only one. Calciphilic herbaceous species accounted for a large proportion of all individuals. The number of plant species in the areas surrounding the caves exceeded 130 (Ren et al., 2010b). Therefore, the karst caves had limited species richness and small population sizes. Some higher plants from Gesneriaceae and Poaceae, and some calciphilic ferns and bryophytes were endemic in karst caves. With the weakening of light intensity from the entrance plots to the intermediate plots and then to the deep plots, plant diversity decreased, i.e., the spatial changes of plant diversity in karst caves seems to be closely related to light intensity.

The level of human disturbance apparently affected the composition of plant communities and soil physiochemical properties, and was negatively related to plant diversity in the karst caves. With the increase of disturbance intensity, the species richness and soil fertility decreased.

Bryophytes can be used as indicators of the spatial distribution of plant diversity and the degree of ecological restoration/health in karst caves (Belnap and Lange, 2013; Pakeman et al., 2019). In the current study, the species of bryophytes and habitat changed depending on location in the cave (entrance, intermediate, or deep plots), which was consistent with previous reports for cave-dwelling plants in the Mediterranean region (González-Mancebo et al., 1992; Pilaš, 2016; Puglisi et al., 2018). The cluster analysis of vascular plants and bryophytes (Fig. 2) showed that only bryophytes were similar to each other and clustered together (Fig. 3), indicating that bryophyte diversity can indicate the plant diversity of karst caves, as well as the degree of degradation or protogenesis. Bryophytes are primitive and pioneer plants, which can grow well in harsh environments and have an irreplaceable function in soil formation, soil and water conservation, plant succession, and environmental improvement in karst caves (Cao et al., 2020). Some bryophytes, especially mosses, are drought-tolerant and have unique physical structures and strong adaptive mechanisms that enable them to thrive on calcareous rocks (Belnap and Lange 2013). The desiccation tolerance of mosses results from their ability to protect cellular integrity but also to repair desiccation- and rehydration-induced cellular damage (Li et al., 2015; Cao et al., 2020). Bryophytes usually coexist with algae, bacteria, fungi, and rhizosphere fine particles on exposed rocks to form bryophyte crusts. In addition to having high biomasses, bryophyte crusts facilitate colonization by other plants and thereby enhance the restoration of degraded ecosystems (Humphrey et al., 2002; Belnap and Lange, 2013; Cao et al., 2020).

Plant diversity in karst caves is closely related to habitat heterogeneity, energy and water status, and nutrient availability. Differences in soil properties, light intensity, and air humidity contribute to the differences in bryophyte composition and coverage in different karst caves. As the habitat becomes more suitable, the number of bryophyte species and their coverage increase. Some endemic bryophyte species can adapt to arid, very humid, or weak-light environments. Previous studies have also shown that species diversity in ecosystems is closely related to habitat heterogeneity (Cramer and Willig, 2002), energy and water balances (Hawkins et al., 2003), and nutrient balance (Firn et al.,

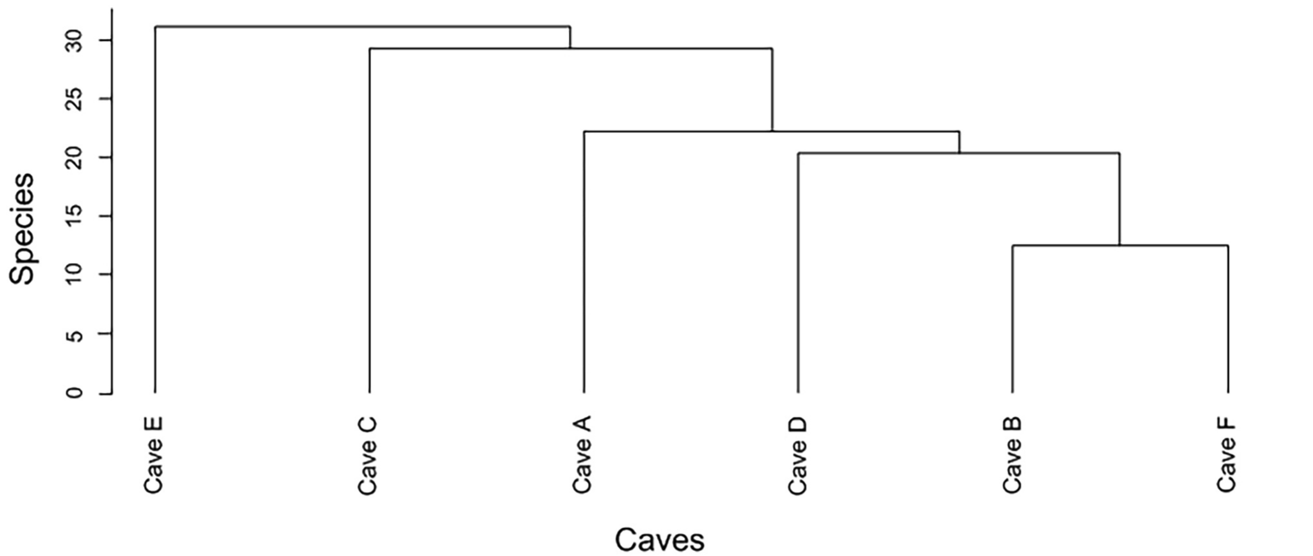

Fig. 2. Cluster analysis of vascular plants and bryophytes in six karst caves. Caves A, B, C, and D are located in Dixiahe, and caves E and F are located in Shangbaichang. Caves A, B, and C were developed for tourism in 1988. Cave B was closed for tourists and kept natural after 2000. Cave C was protected from disturbance after 2010. Cave F had a long history of high disturbance associated with the feeding of poultry on plants. Caves D and E were relatively undisturbed.

2007).

In addition to light, humidity, and soil properties, phylogeny was found to be important in determining plant diversity in karst caves. The species and coverage of higher plants, ferns, and bryophytes, even lichens and algae, differed in different areas of the caves and differed with the degree of cave degradation. Plant diversity revealed convergent adaptations by different species to cave environments. Species diversity also reflects contrasting degrees of phylogenetic conservatism for the co-existing plants, ferns, and bryophytes in the caves (Bai et al., 2020).

Tourism and poultry farming may led to the degradation of vegetation in some karst caves; the degradation has involved a reduction in habitat heterogeneity and changes in the water–energy balance (Liu et al., 2019) and the nutrient balance and therefore reductions in biodiversity. The maintaining and protecting of karst cave habitats is needed to protect or restore bryophytes, which in turn facilitate the settlement, growth, and succession of vascular plants. Conservation of bryophytes might be beneficial to karst biodiversity and resilience by promoting biological interactions among several species and by

Fig. 4. The cluster analysis of vascular plants in six karst caves. See the Fig. 2 legend for descriptions of the six caves.

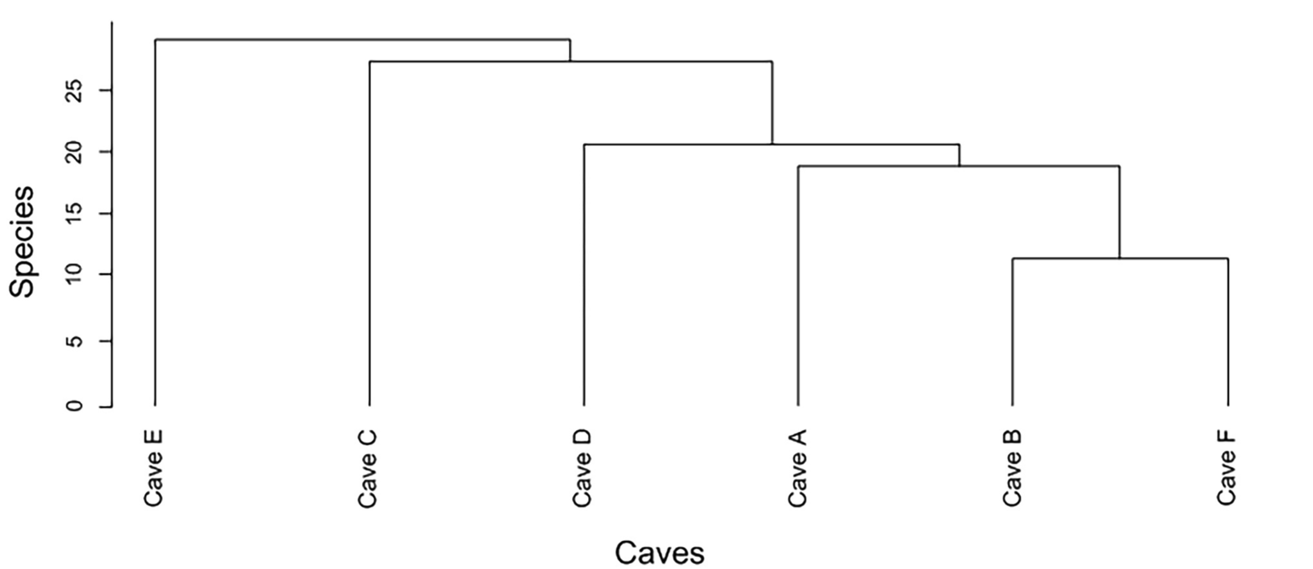

Fig. 3. The cluster analysis of bryophytes in six karst caves. See the Fig. 2 legend for descriptions of the six caves.

Table 2
The habitat characteristics in six karst caves. Values are means + SE of three plots (entrance, intermediate, and deep) per cave.

Characteristic	Cave A	Cave B	Cave C	Cave D	Cave E	Cave F
Soil thickness (cm)	3.3 ± 0.3	0.2 ± 0.1	2.8 ± 0.5	1.5 ± 0.3	1.9 ± 0.2	0.3 ± 0.1
Soil water content (%)	14.1 ± 2.45	18.30 ± 3.33	16.03 ± 8.2	19.53 ± 8.96	24.5 ± 1.21	11.85 ± 8.84
pH	7.41 ± 0.23	7.39 ± 0.21	8.04 ± 0.30	7.82 ± 0.27	8.16 ± 0.40	7.85 ± 0.11
Total N (g/kg)	4.57 ± 0.53	4.28 ± 1.11	2.49 ± 1.43	4.92 ± 1.12	2.71 ± 1.34	7.45 ± 2.34
Total P (g/kg)	5.73 ± 2.01	1.19 ± 0.21	2.10 ± 0.32	2.91 ± 1.15	1.91 ± 0.79	1.72 ± 0.91
Organic matter (%)	4.76 ± 1.67	8.39 ± 1.37	3.36 ± 1.44	5.6 ± 1.12	3.93 ± 1.86	10.91 ± 1.54
Transmittance (%)	47.0 ± 15.4	61.1 ± 12.1	42.3 ± 5.6	38.9 ± 3.4	35.5 ± 17.8	54.7 ± 12.2
Photosynthetic active radiation (μmol/(m^2s))	65.0 ± 40.1	60.3 ± 40.1	86.3 ± 12.7	63.0 ± 45.1	59.7 ± 9.0	85.3 ± 7.7
Temperature (°C)	20.3 ± 0.1	20.2 ± 0.1	20.2 ± 0.2	20.4 ± 0.3	19.9 ± 0.4	20.4 ± 0.1
Relative humidity (%)	96.0 ± 2.0	85.3 ± 1.0	97.0 ± 2.0	94.3 ± 1.3	95.0 ± 1.0	90.2 ± 1.7

improving ecological functions.

5. Conclusions

Karst caves are unusual habitats with low light intensity, moist air, thin soil, and rocky environments that make it difficult for vascular plants to colonize and survive; non-vascular plants, such as bryophytes, in contrast, can grow on the rocks in karst caves. The current study found that plant diversity in karst caves was low but soil fertility was high. Bryophytes were found to be important components of plant diversity in the karst caves. Differences in the species richness of bryophytes in these caves were associated with habitat differences including plant community structure, humidity, soil nutrient content, and light intensity. The diversity, coverage, and endemism of bryophytes could serve as indicators of the health of plant communities and probably of entire ecosystems in karst caves. Human disturbance, including tourism and poultry farming, may have changed the micro-habitats, species composition, and species richness of vegetation in karst caves that were associated with ecosystem degradation. With an increase in disturbance intensity, plant species richness and soil fertility decreased. Further studies on the interaction of plants and soil and on mechanisms underlying changes in plant diversity in karst caves are needed to guide vegetation restoration in karst areas.

CRediT authorship contribution statement

Hai Ren: Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Writing - original draft, Writing - review & editing. **Faguo Wang:** Investigation, Writing - original draft. **Wen Ye:** Investigation, Writing - original draft. **Qianmei Zhang:** Data curation, Investigation, Project administration. **Taotao Han:** Software, Data curation. **Yao Huang:** Software, Validation, Visualization. **Guowei Chu:** Investigation. **Dafeng Hui:** Funding acquisition, 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.

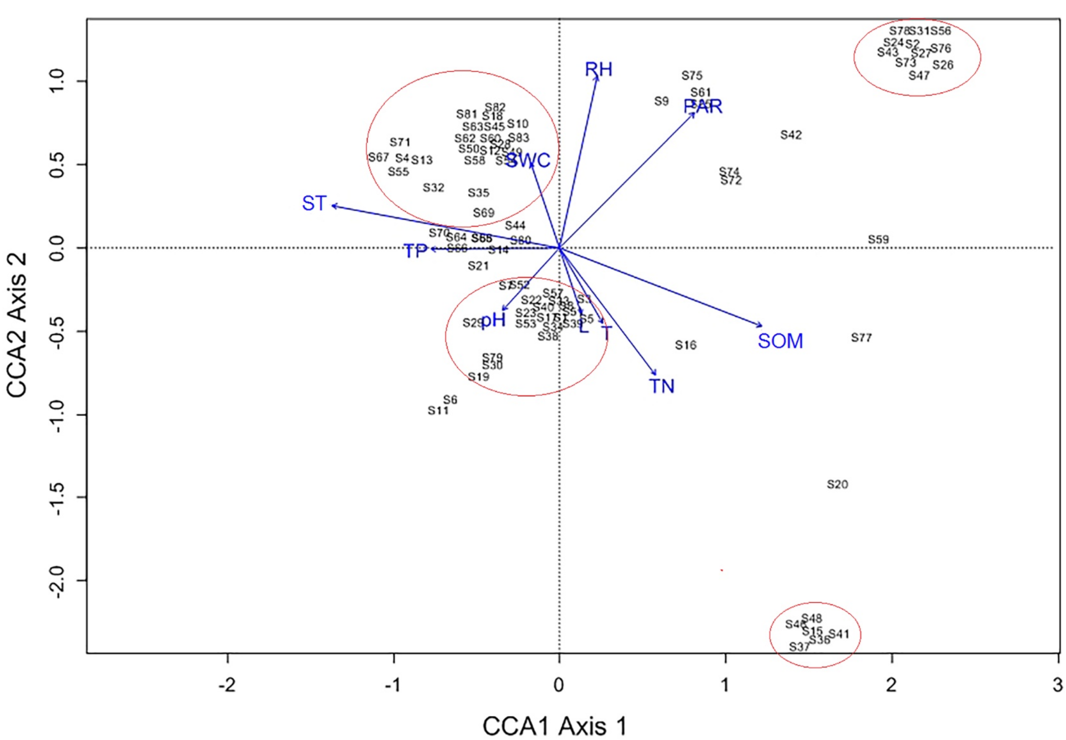

Fig. 5. Canonical correspondence analysis of the vegetation and 10 environmental factors in 18 plots in six karst caves. TN, total nitrogen content; TP, total phosphorus content; SOM, soil organic matter; pH, pH value; SWC, soil water content; ST, soil thickness; PAR, photosynthetically active radiation; RH, relative humidity; T, air temperature; L, light transmittance. The species codes are explained in Supplementary Table 1 (S1–S63) and Supplementary Table 2 (S64–S83).

Acknowledgements

This work was supported by the Strategic Priority Research Program of the Chinese Academy of Sciences (grant numbers XDA13020500). DH was supported by the US National Science Foundation projects (DEB-2000058). We also thank Prof. Bruce Jaffee for proof-reading the manuscript, and three 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.2020.106947.

References

Bai, K.D., Wei, Y.G., Zhang, D.N., Fu, L.F., Lv, S.H., Deng, L.L., 2020. Contrasting effects of light, soil chemistry and phylogeny on leaf nutrient concentrations in cave-dwelling plants. Plant Soil. https://doi.org/10.1007/s11104-020-04422-6.

Barr, T.C., 1964. Cave ecology. Science 144, 321–322. http://www.jstor.com/stable/1713361.

Belnap, J., Lange, O.L., 2013. In: Biological soil crusts: structure, function, and management. Springer Science & Business Media, Berlin. https://doi.org/10.1007/978-3-642-56475-8_1.

Borcard, D., Gillet, F., Legendre, P., et al., 2014. Quantitative Ecology: the application of R language (Chinese Version, Lai JS translated). Higher Education Press, Beijing.

Brandt, M., Yue, Y.M., Wigneron, J.P., Tong, X.W., et al., 2018. Satellite-Observed Major Greening and Biomass Increase in South China Karst During Recent Decade. Earth's Future 6, 1017–1028. https://doi.org/10.1029/2018EF000890.

Cao, W., Xiong, Y.X., Zhao, D.G., Tan, H.Y., Qu, J.J., 2020. Bryophytes and the symbiotic microorganisms, the pioneers of vegetation restoration in karst rocky desertification areas in southwestern China. Appl. Microbiol. Biotechnol. 104, 873–891. https://doi.org/10.1007/s00253-019-10235-0.

Cong, C.L., Liu, T.L., Kong, X.Y., Zhang, X.Q., 2017. Flora and species diversity of epilithic mosses on rock desertification in the Puding karst area. Carsologica Sinica 36, 179–186.

Cramer, M.J., Willig, M.R., 2002. Habitat heterogeneity, habitat associations, and rodent species diversity in a sandshinnery-oak landscape. J. Mammal. 83, 743–753. https://doi.org/10.1644/1545-1542(2002)083<0743:HHHAAR>2.0.CO;2.

Elliott, W.R., 2006. Biological dos and don'ts of cave restoration and conservation. In: Hildreth-Werker, J., Werker, J. (Eds.), Cave Conservation and Restoration. National Speleological Society, Huntsville, AL, pp. 33–44.

Firn, J., Erskine, P.D., Lamb, D., 2007. Woody species diversity influences productivity and soil nutrient availability in tropical plantations. Oecologia 154, 521–533. https://doi.org/10.1007/s00442-007-0850-8.

González-Mancebo, J., Losada-Lima, A., Hernández, C., et al., 1992. Bryophyte flora of volcanic caves in the Azores and the Canary Islands. Lindbergia 17, 37–46 www.jstor.org/stable/20149800.

Hawkins, B.A., Field, R., Cornell, H.V., et al., 2003. Energy, water, and broad-scale geographic patterns of species richness. Ecology 84, 3105–3117. https://doi.org/10.1890/03-8006.

Humphrey, J.W., Daveyb, S., Peacec, A.J., Harding, K., 2002. Lichens and bryophyte communities of planted and semi-natural forests in Britain: the influence of site type, stand structure and dead wood. Biol. Conserv. 107, 165–180. https://doi.org/10.1016/s0006-3207(02)00057-5.

Krebs, C.J., 1985. Ecology: The Experimental Analysis of Distribution and Abundance, Third edition. Harper & Row, New York.

Li, J.F., Jia, S.H., Wang, Z.H., 2015. The diversity of bryophytes and their distribution associated with environmental factors during the process of karst rocky desertification. Ecol. Sci. 34, 68–73. https://doi.org/10.14108/j.cnki.1008-8873.2015.01.010.

Liu, R., Zhang, Z., Shen, J., 2019. Bryophyte diversity in karst sinkholes affected by different degrees of human disturbance. Acta Societatis Botanicorum Poloniae 88, 1–7.

Medellin, R.A., Wiederholt, R., Lopez-Hoffman, L., 2017. Conservation relevance of bat caves for biodiversity and ecosystem services. Biol. Conserv. 211, 45–50. https://doi.org/10.1016/j.biocon.2017.01.012.

Monro, A.K., Bystriakova, N., Fu, L., Wen, F., Wei, Y., 2018. Discovery of a diverse cave flora in China. PLoS One 13, e0190801. https://doi.org/10.1371/journal.pone.0190801.

Mulec, J., Kubešová, S., 2010. Diversity of bryophytes in show caves in Slovenia and relation to light intensities. Acta Carsol. 39, 587–596. https://doi.org/10.3986/ac.v39i3.86.

Northup, D.E., Lavoie, K.H., 2001. Geomicrobiology of caves: a review. Geomicrobiol J. 18, 199–222. https://doi.org/10.1080/01490450152467750.

Pakeman, R., Brooker, R., O'Brien, D., Genney, D., 2019. Using species records and ecological attributes of bryophytes to develop an ecosystem health indicator. Ecol. Ind. 104, 127–136. https://doi.org/10.1016/j.ecolind.2019.04.084.

Pan, X.Z., Guo, Z.Y., Pan, K., 2019. Protocols for standard soil observation and measurement in terrestrial ecosystems. China Environmental Press, Beijing.

Pielou, E.C., 1975. Ecology Diversity. John Wiley and Sons, New York.

Pilaš, I., 2016. Climate variability, soil, and forest ecosystem diversity of the Dinaric Mountains. In: Zhelezov, G. (Ed.), Sustainable Development in Mountain Regions. Springer, Cham, pp. 281–304.

Puglisi, M., Kürschner, H., Privitera, M., 2018. Phytosociology and life syndromes of bryophyte communities from Sicilian caves, a clear example of relationship between bryophytes and environment. Plant Sociol. 55, 3–20. https://doi.org/10.7338/pls2018551/01.

Puglisi, M., Privitera, M., Minissale, P., Costa, R., 2019. Diversity and ecology of the bryophytes in the cave environment: a study on the volcanic and karstic caves of Sicily. Plant Biosyst. 153, 134–146. https://doi.org/10.1080/11263504.2018.1478903.

Ren, H., Ma, G.H., Zhang, Q.M., Wang, J., 2010a. Moss is a key nurse plant for reintroduction of the endangered herb, *Primulina tabacum* Hance. Plant Ecol. 209, 313–320. https://doi.org/10.1007/s11258-010-9754-5.

Ren, H., Zhang, Q.M., Wang, Z.F., Guo, Q.F., Wang, J., Liu, N., Liang, K.M., 2010b. Conservation and possible reintroduction of an endangered plant based on an analysis of community ecology: a case study of *Primulina tabacum* Hance in China. Plant Species Biol. 25, 43–50. https://doi.org/10.1111/j.1442-1984.2009.00261.x.

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).

Tong, X., Brandt, M., Yue, Y., et al., 2018. Increased vegetation growth and carbon stock in China karst via ecological engineering. Nat Sustain. 1, 44–50. https://doi.org/10.1038/s41893-017-0004-x.

Tong, X., Brandt, M., Yue, Y., et al., 2020. Forest management in southern China generates short term extensive carbon sequestration. Nat. Commun. 11, 129. https://doi.org/10.1038/s41467-019-13798-8.

Voloscuk, I., Uhliarova, E., Sabo, P., et al., 2016. Succession dynamics of vegetation in the Slovak Karst biosphere reserve landscape (Western Carpathisans). Ekologia 35, 13–31.

Wang, J.L., Zhang, Z.H., Hu, G., 2020. Bibliometric analysis of research trends on karst vegetation ecology. Acta Ecologica Sinica 40, 1–13.

Wang, Z., Zhang, J.C., Yu, S.Q., Wang, X., Wang, R.Y., Cui, X.X., 2011. The vanguard role of bryophytes in the course of vegetation restoration of Karst degradation area. J. Nanjing For. Univ. (Nat. Sci. Ed.) 35, 137–140.

Whitte, T., 2009. Applying ecology for cave management in China and neighbouring countries. J. Appl. Ecol. 46, 520–523. https://doi.org/10.1111/j.1365-2664.2009.01630.x.

Wu, D.X., Zhang, L., Song, C.Y., Zhang, S.M., 2019. Protocols for standard biological observation and measurement in terrestrial ecosystems. China Environmental Press, Beijing.

Yan, Y.H., 2013. Diversity and geographical distribution of Pteridophytes in China. Science Press, Beijing.

Yuan, D.X., 1994. Karstology of China. Geological Publishing House, Beijing.

Zhang, Y.G., 1986. The regional difference of karst cave development in China. Geogr. Res. 5, 36–46 In Chinese.

Zhang, X., Wang, L.L., Liu, Y.H., Wen, T., Cui, Y.C., Jiang, X., Zhang, Z.Y., Huo, D., Li, D., 2016. Correlation on plant diversity indices and soil physical and chemical indicators of karst natural forest, Southern Guizhou Province, China. Acta Ecol. Sinica 36, 3609–3620. https://doi.org/10.5846/stxb201403220514.