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Plant secondary succession and soil degradation in humid red beds areas, South China

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ABSTRACT

In South China, large amounts of strongly eroded badlands that are difficult for natural recovery formed in red beds soft rock, posing serious environmental hazards. This process is thought to be related to a unique nutrient cycle and plant-soil feedback in alkaline soil. In this study, we investigated 44 plant communities and some soil samples to explore the reasons for this erosion from the perspective of secondary succession and its driving factors. The results showed that the natural secondary succession (NSS) in red beds soft rock is the sequence of primary forest to scrub grass, xerophytes, and badlands. *Masson pine* and *Masson pine/Schima superba* communities have formed under the efforts of artificial intervention restoration. The community ecological gradient (CEG) and deciduosity rate substantially increased along the NSS, whereas the biomass, and diversity index rapidly decreased. The plantation community showed the opposite trend with increasing recovery years. Limitations in terms of soil water content, pH value, and available nitrogen (AN) for the community markedly increased, and we confirmed these were the largest contributors to redundancy analysis at the community scale. Compared with acidic soil, alkaline soil with a rough texture and high pH could not maintain enough water for plants during dry seasons, which inhibited the absorption of AN by plants. Therefore, in primary forests, the CEG and deciduosity rates need to be increased so that the plant community can adapt to harsh environments. plantation forests achieved soil acidification through litter accumulation. In the scrub grass and xerophyte, continuous reduction in litter and the intensification of soil erosion destroyed the balance between red argillaceous rock bed erosion and species invasion, leading to community degradation. Therefore, much attention should be given to primary forest protection and limiting factors mitigation in degraded communities.

1. Introduction

Secondary succession has irreplaceable value in protecting biodiversity and restoring essential ecosystem services of vegetation communities (Gibson et al. 2011, Farneda et al. 2018). This process is widely affected by climate change, species invasion, soil erosion, and other anthropogenic interferences (Yelenik and Levine 2011, Diwediga et al. 2015, Turner et al. 2016, Gunn et al. 2019). This is especially crucial in fragile ecological environment areas with unique climates or geological backgrounds, such as the Mediterranean zone, desert edge, and karst in South China (Hüttl and Schneider, 1998; Montanarella 2007, Bai et al. 2008, Robinson, 2016). Much attention has been given to the species composition and dynamics of secondary succession in special environments, where biodiversity values are often hidden and vulnerable to degradation (Newbold et al. 2015, Crouzeilles et al. 2016). Understanding the species' composition and its succession in special climates and geological environments is critical for selecting conservation approaches and the feasibility of reconstruction.

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The limitation of plant water use caused by the dry season profoundly affects the vegetation community structures and succession process. The seasonal drought existing in the Mediterranean region leads to species changes to sclerophylls and shrubs or summer deciduous and strong root systems to utilize deep soil water (Rigling et al. 2013, Barbeta et al. 2015, Bussotti and Pollastrini 2020). Moreover, water limitation will affect the nutrient utilization of plants since soil water content affects nutrient concentration, availability, migration, and the uptake ability by plant roots through soil microbial activity, aeration, and temperature (Lima et al. 2010, Miki et al. 2017). Multidimensional analyses have shown that poor soil, high temperature, and water deficit are the reasons for *pirzus pinea* community degradation (Piraino et al. 2013). In addition to climatic drought, low water use efficiency and soil nutrient limits also exist in special geological environments in South China, such as karst regions and red beds. In secondary succession, low water content and nutrient absorption become critical factors for karst vegetation recovery (Tang et al. 2019).

Nutrient utilization limitations may be further exacerbated under an alkaline soil environment. In alkaline soil, phosphorus forms precipitate with metal complexes (such as Ca-P and Mg-P), so only a small amount of phosphorus, iron, manganese, copper, and other trace elements are available for plants (Kerley et al. 2001, Ström et al., 2005; Hou et al. 2020). At the same time, more evaporation and less precipitation in a seasonally dry climate will lead to calcium, magnesium, and potassium ions accumulated on the surface (Brady and Weil 2002, Slessarev et al. 2016). Redundancy analysis with soil nitrogen, phosphate, and extractable ions in the central Italian coastal ecosystem found that higher NaCl and $CaCO_3$ are the key factors limiting nutrient utilization in alkaline soil (Baribault et al. 2010, Angiolini et al. 2013). This finding is further supported by the increased $CaCO_3$ content identified as a key factor contributing to rocky desertification in the Chinese karst region, based on the analysis of 11 soil samples and vegetation quadrats (Tang et al. 2019). Additionally, the application of two-way indicator species analysis (TWINSPAN) demonstrated the formation of distinct plant communities in alkaline soil, which differ from those observed in silicate soils. This discrepancy arises due to the limited bioavailability of soil nutrients and high pH value, rendering alkaline soils inhospitable to many vascular plants (Frouz et al. 2008; El-Sherbeny et al., 2021). The relationship between the above plant community and soil conditions will differ in an alkaline environment (Ström et al., 2005; Moss et al. 2020). However, until now, there is no systematic research on the mechanism of vegetation secondary succession and soil degradation in alkaline soil environments.

Exploring vegetation succession and its driving factors is crucial for protecting species diversity in fragile habitats and preventing ecosystem degradation. In South China, a large number of strongly eroded badlands exist that are difficult to naturally recover in red beds soft rock, posing serious environmental hazards. Therefore, TWINSPAN and redundancy analysis were conducted based on the previous quadrat survey and soil laboratory analysis, to reveal the ecological mechanism of this degradation. We hypothesize that the formed badland is the result of the retrograde succession of vegetation communities in red beds soft rock, and this process is determined by the rock weathering and alkaline enrichment. The objective of this research is: (1) build the secondary succession process of vegetation communities in red beds soft rock; (2) identify key determinants of land degradation due to secondary succession.

2. Materials and method

2.1. Study area

A typical red beds soft rock basin named Nanxiong located in South China was selected to explore the adaptation of species composition and community sequence to alkaline soil. The coordinates range from 114°04′ E, 24°59′N to 114°36′E, 25°18′N (Fig. 1). As a type of continental sedimentary rock, the red beds mainly contain siltstone and argillaceous rock, which exhibit weak resistance to weathering and erosion (Peng et al. 2015). The soil formed on the red beds soft rock represents an alkaline reaction for the abundant $CaCO_3$ derived from the parent material, belonging to Alfisols, Inceptisols or Entisols according to weathering degree (Zhang et al. 2016, Li 2021). The climax community is subtropical evergreen broad-leaved forest, with annual precipitation of 1535 mm that rain season is from March to August except 30 days of dry weather during July and August. The annual temperature is 19.6 °C, with an average temperature of 8 °C in January and 34 °C in July. The dominant arbor species are *Celtis sinensis., Pistacia chinensis., Photinia glabra.,* and artificially planted *Pinus massoniana.* forest mixed with *Schima superba.*, while shrub and herbaceous species are mainly *Xylosma racemosum., Vitex negundo.,* and *Heteropogon contortus* (Liao et al. 2021).

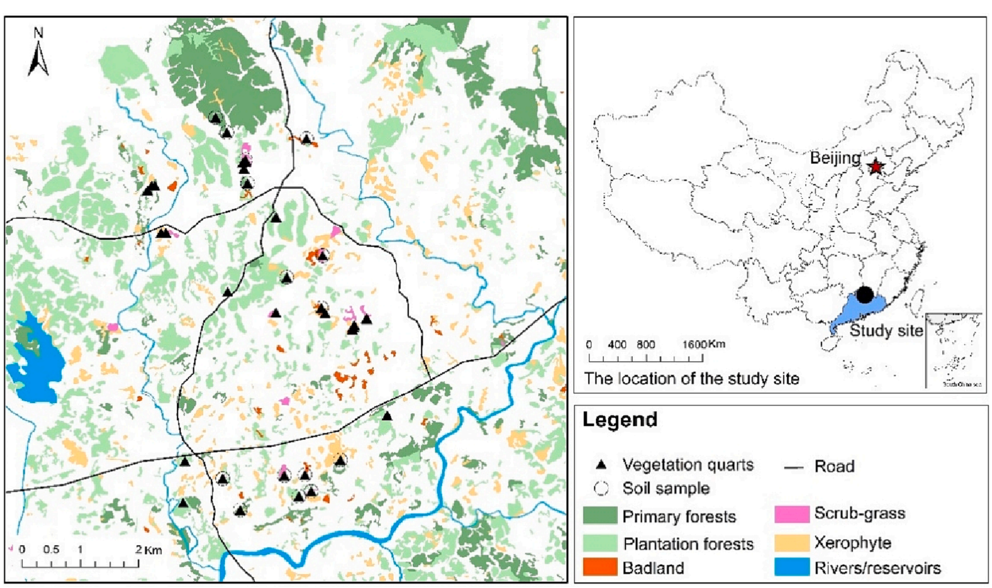

Fig. 1. The community sample location map in the red beds soft rock area, South China. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.2. Vegetation investigation

The main vegetation communities were selected to carry out the quadrat investigation, including primary forests, plantation forests, scrub-grassland, and xerophytes (Fig. 2). The investigated quadrat area followed the principle that the minimum area can represent the general community structures (Chao et al. 2009). Therefore, the quadrat area is 600 m^2 for primary forests, 200–400 m^2 for plantation forests, and 100 m^2 for scrub-grassland and xerophytes, referring to similar surveys of evergreen broad-leaved forests (Lin et al. 2013). Forty-four typical community quadrats, including 3 default samples located in acidic backgrounds, were collected. The purpose of choosing 3 default samples was to analyze the influence of alkaline conditions on plant community succession and soil degradation under the similar climatic conditions.

Quadrat survey method: (a) Every forest quadrat was divided into 10 m × 10 m subquadrats before investigation, and the species of trees, shrubs, and vines higher than 2 m were recorded. The height and bust circumference of each tree were also measured. (b) In each subquadrat, a 2 m × 2 m measurement square was made to record the species, height, crown diameter, cover degree, and number of shrubs and vines. (c) The crown density of the forest and coverage of the shrub and grass layers were estimated manually, and the litter was weighed and sampled in a 1 m × 1 m quadrat. (d) The scrub-grassland and xerophyte community survey set a 10 m × 10 m quadrat, using the same survey method, while biomass and litter were collected in sizes of 1 × 1 m by harvesting (Casper et al. 2008). Quadrat site conditions, including locations, altitude, slope and aspect, were recorded. Detailed information is shown in Table S1.

Based on the vegetation data, the community ecological gradient (CEG), deciduosity rate, biomass, vegetation coverage, diversity, and richness index were further calculated among the natural succession and plantation restoration sequences (Poorter and Markesteijn 2008, Silva et al. 2017). Among them, the deciduosity rate is the ratio of deciduous species to the total. Vegetation coverage determined by field observations ranged from 0 ~ 100%. The diversity and richness index is calculated by Shannon-Wiener's diversity and the Margalef richness index method (Van Loon et al. 2018). Previous studies have shown that therophyte and deciduous plant species usually indicate arid growth environments (Tomlinson et al. 2013). So the CEG index (1 to 5) which is used to indicate the arid environment of the community, is calculated by:

$$CEG = \left(\sum_{i=1}^{s} n_i W_i\right)/N \tag{1}$$

where S is the number of species in the quadrat, N is the number of species, n_i is the number of individuals of the i_{th} species, and W_i is the weight value of the species ecotype, divided into 5 levels: hygrophyte set 1, mesophyte set 2, weak xerophyte set 3, xerophyte set 4, and strong xerophyte set 5. If tree species are deciduous, weight + 0.2, thorny or vine species + 0.5 (Whittaker 1978).

The biomass was calculated by the empirical formula (Xin et al. 1990):

Fig. 2. The landscape of different vegetation community types. (a. Primary forests, b. Plantation forests, c. Scrub-grassland, d. Xerophytes, e. Badland).

$$Bm\left(10^3 kg.dryweight\right) = 0.00003982895\left(D^2 h\right) \quad (2)$$

where D (cm) is the diameter at breast height (DBH) and h (m) is the tree height.

2.3. Soil sampling and laboratory analysis

The soil texture, water content, pH value, and N/P/K content were investigated because they influence plant community dynamics and nutrient cycling (Kardol et al. 2006). Soil sampling was carried out simultaneously with the quadrat survey, including 5 primary forest, 3 plantation forest, 8 scrub-grassland, 2 xerophyte grass, and 2 badland samples (Table 1). Three default samples were collected from acid-purple soil. Karst and red soil from other regional soil parameters were used to understand the influence of alkaline soil conditions. The sampling depth ranged from 0 to 40 cm in primary and plantation forests, while 0 ~ 20 cm was collected in scrub grassland and xerophytes. Only 0 ~ 5 cm of soil for badland can be collected on steep slopes. Therefore, soil vertical profiles were established for sampling according to different vegetation types. Before sampling, bulk density was measured using a bulk density ring at 0–10 cm, 10–20 cm, and 20–40 cm (Table S2) (Timm et al. 2005). Soil mixture samples were then collected by layered sampling at 10 cm intervals from 20 cm to the parent material. Samples were collected using cloth bags on-site and transported to the laboratory to dry naturally.

With a 2 mm mesh sieve, the fine earth fraction was obtained for further detection. The following soil indicators were determined in the laboratory: (a) soil water content (SWC) was measured using an aluminum box after baking in a 105 °C oven for 24 h in the laboratory after weighing wet soil on site; (b) soil texture (clay, slit, sand, and coarse sand proportions) was analyzed using laser-diffraction analysis (Taubner et al. 2009); (c) soil pH was determined by the glass electrode method in distilled H_2O (1:2.5 soil/extract ratio); (d) soil organic matter (SOM), and organic carbon (SOC) were measured by the Walkley-Black acid digestion method (de Souza et al. 2016);(e) total nitrogen (TN) was measured by the Kjeldahl-method (Kirk 1950); and (g) available nitrogen(AN), available phosphorous(APH), and available potassium (APO) were measured by the Kjeldahl method, Olsen method, and atomic absorption spectroscopy method after distillation and titration using sulfuric acid and hydrogen peroxide solution digestion (Mulvaney and Khan 2001, Hosseinpur and Samavati 2008). The plants litter parameter test follows the same method as that used for soil after completing air-drying, crushing, and sieving. Laboratory analyses are strictly implemented by international or Chinese national standards with CMA certification (China Inspection Body and Laboratory Mandatory Approval).

Table 1
The sample data of vegetation communities and soil.

Vegetation type group	Constructive species	Community quadrat	Soil profile/ sample	Litter sample
I. Primary forests (Pri)	*Up, Xr, Pc, Pg, Ceb, Ces*	4	2/5	2
II. Plantation forests (Pla)	*Pim, Lf, Scs, Rt, Lc*	10	2/3	3
III. Scrub-grassland (SG)	*Up, Li, Rc, Aa, Vn, Ll, Ni*	15	8/8	3
IV. Xerophyte grass (Xer)	*Aa, Ci, Hc, Tj, Bb*	8	2/2	2
V. Badlands (BL)	a few xerophytic	4	2/2	
Ib*. Primary forests(Pri*)	*Scs, Scr, Cas, Cac, Cc*	1	1/3	1
IIb*. Plantation forests(Pla*)	*Pim, Pie, Scs*	1	1/3	1
IIIb*. Scrub-grassland (SG*)	*Pyc, Lc, Bb, Ep*	1	1/2	
Total		44	19/28	12

Latin name of plants and their abbreviations: ***Aa***: *Arundinella anomala*; ***Bb***: *Bothriochloa bladhii*; ***Cac***: *Castanopsis carlesii*; ***Cas***: *Castanopsis sclerophylla*; ***Cc***: *Camellia caudata*; ***Ceb***: *Celtis biondii*; ***Ces***: *Celtis sinensis*; ***Ep***: *Eriachne pallescens*; ***Hc***: *Heteropogon contortus*; ***Lc***: *Loropetalum chinense*; ***Lf***: *Liquidambar formosana*; ***Li***: *Lagerstroemia indica*; ***Ll***: *Leucaena leucocephala*; ***Ni***: *Nerium indicum*; ***Pie***: *Pinus elliottii*; ***Pim***: *Pinus massoniana*; ***Pg***: *Photinia glabra*; ***Pc***: *Pistacia chinensis*; ***Pyc***: *Pyrus calleryana*; ***Rc***: *Rosa cymosa*; ***Rt***: *Rhodomyrtus tomentosa*; ***Scr***: *Schima remotiserrata*; ***Scs***: *Schima superba*; ***Tj***: *Themeda japonica*; ***Up***: *Ulmus parvifolia*; ***Vn***: *Vitex negundo*; ***Xr***: *Xylosma racemosum*. *: Acidic purple soil background as comparison samples.

2.4. Statistical analysis

Many quantitative ecology methods have been used to explore plant-soil interactions in alkaline environments, such as detrended correspondence analysis (DCA), two-way indicator species analysis (TWINSPAN), and redundancy analysis (RDA). First, the DCA was used for the quadrat data to find the community and species environmental gradients (Diwediga et al. 2015), and then TWINSPAN was applied to classify the plant communities based on the occurrence probability of species in each quadrat (Roleček et al., 2009). Redundancy analysis (RDA) was performed to analyze the relative contribution of the environmental variables to the plant community structure to understand the variable environmental limitations to community succession (McArdle and Anderson 2001).

Before RDA, the soil pH, water content, soil density, and particle composition ratio were compared in different plant communities. Among them, soil particle composition is expressed as the percentage of clay, silt, sand, and coarse sand. Soil nutrient content levels mainly focus on the available soil that plants can use directly, including AN, APH, and APO. The total nutrient content, such as SOC and TN, is also considered (LeBauer and Treseder 2008). The nutrient content of litter, including TN, TPH, and TPO, was also analyzed because it acts as the main source of soil nutrients. The above soil parameters were set as environmental factors in the RDA, and quadrats, and plant species data (importance value > 10) are set as explanatory variables. In addition, we used the Pearson correlation coefficient to verify the strength of the environmental variables in the plant communities. Linear models were adopted as the ranking method for community and species to facilitate comparison. DCA and RDA sorting were conducted in Canoco 5.0, and TWINSPAN classification was performed using PC_Ord_v5.0 software.

3. Results

3.1. DCA ordination and classification

Fig. 3 shows the community sequence of 131 species and 44 plant quadrats and the quantitative classification results by TWINSPAN. Among them exacerbated water stress from left to right along Axis 1 was found in 131 species and 44 quadrats because therophytes and deciduous plants had a higher proportion on the right by DCA analysis. In Part A of Fig. 3-a, therophytes and deciduous plants account for 55% and 26%, respectively, while evergreen species account for only 16%. This percentage changed to 25% and 0 in Part D. Large phanerophytes accounted for 31% of Part C. A similar distribution was also identified in the DCA ordination of 44 quadrats (Fig. 3-b). Scrub-grassland quadrats were on the right side of Axis 1, and most xerophyte species were concentrated on the further right side. Axis 2 showed a gradient of human interference degree from weak to strong because primary forests were focused on the upper side of Axis 1, while plantation forests were on the lower side.

The above community sequence can be divided into 13 community types and belongs to 4 major groups by TWINSPAN (Fig. 3-c). Using the traditional soil-community ecological method, 44 quadrats can be divided into 10 community types, which also belong to 4 vegetation types (Table S3). In TWINSPAN, 3 types of vegetation communities

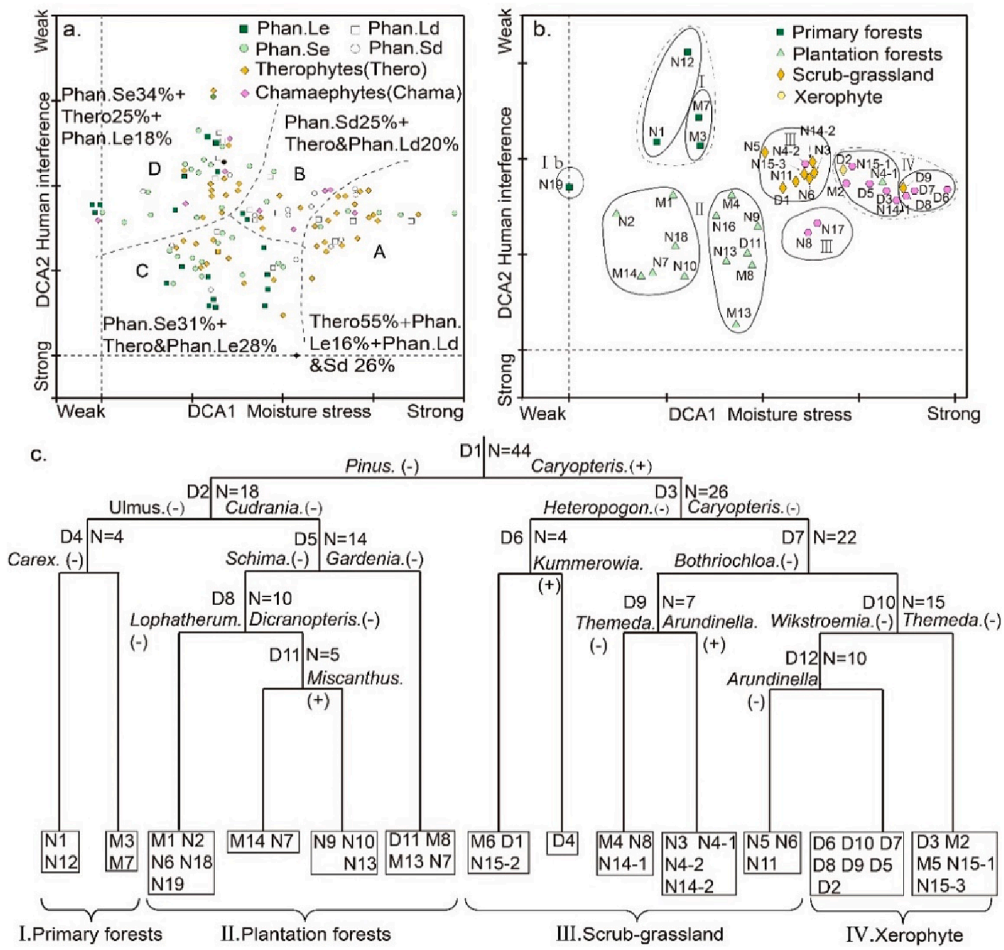

Fig. 3. DCA ordination of the 131 investigated species (a) and 44 quadrats (b) and TWINSPAN classification (c). (a. Therophytes and deciduous species are concentrated on the right axis of DCA1. Le & Ld indicate large evergreen or deciduous species, Se & Sd indicate evergreen or deciduous shrub species; b. The primary forests are concentrated on the upper side of DCA2, while plantation forests are in the lower; c. These differences can be classified by the TWINSPAN. Latin name of plant (genus): ***Arundinella***: *A.anomala* ; ***Bothriochloa***: *B.bladhii*; ***Carex***: *C.brunnea;* ***Caryopteris***: *C.incana*; ***Cudrania***: *C.cochinchinensis*; ***Dicranopteris***: *D.dichotoma*; ***Gardenia***: *G. jasminoides;* ***Heteropogon***: *H. contortus*; ***Kummerowia***: *K.striata*; ***Lophatherum***: *L.gracile*; ***Miscanthus***: *M. floridulus*; ***Pinus***: *P. massoniana*; ***Schima***: *S.superba;* ***Themeda***: *T.japonica*; ***Ulmus***: *U. parvifolia*; ***Wikstroemia***: *W.monnula.*

formed a natural secondary succession (NSS): primary forests, scrub-grassland, and xerophyte, according to the species *Pinus massoniana Lamb.* and *Caryopteris incana (Thunb.) Miq*. The primary forests developed in alkaline soil have special species compositions. *Ulmus parvifolia*, *Xylosma racemosum*, *Pistacia chinensis*, *Photinia glabra*, and *Leucaena leucocephala* are the dominant forest species, while in acidic soils, *Schima superba*, *Castanopsis sclerophylla*, *Castanopsis carlesii*, and *Camellia caudate* are dominant (Table S1). For plantation forests, artificial intervention restoration (AIR) sequence was detected by the *Cudrania., Schima., and Lophatherum*. The average recovery time of plantation forests was estimated to range from 19 years to 43 years (Table S1).

3.2. Species composition and community sequence

The vegetation sequence in NSS (from I to III and IV), showed species ecotype aridification and plant community productivity degradation (Fig. 4). The average CEG in the NSS and AIR increased from 2.07 to 3.56 and 2.4 respectively with secondary succession. The CEG in primary forest Ia was higher than 7.5% of default sample Ib (Table S3). Biotope aridification is also reflected in the deciduous components. Deciduous species in primary forests were approximately 35%, while in scrub and xerophyte communities, they increased to over 80% (Fig. 4-b). Another trend was a significant reduction in the biomass and diversity of communities from primary forests to scrubs and xerophytes. The biomass of scrubs and xerophytes was only 1%-5% of that of primary forests due to the removal of the arbor layer (Fig. 4c). The vegetation coverage, Shannon-Wiener's diversity, and Margalef richness index of communities all represented a decreasing trend (Fig. 4-d, e, f). At the same time, the relationship between the CEG, deciduous plants, biomass, and the diversity index showed that the diversity index was positively correlated with biomass (R^2 = 0.64, Fig. 4-g) and negatively associated with the CEG (R^2 = 0.5, Fig. 4-h). The CEG positively correlates with the deciduous percentage (R^2 = 0.3, Fig. 4-i). In addition, species diversity and biomass were linearly correlated in communities with primary and plantation forests but showed a unimodal pattern in scrub-grassland and xerophyte communities (Fig. S1).

In the AIR sequence, the CEG and deciduosity rate decreased significantly with increasing of recovery years, from 2.95 to 1.99, and 0.37 to 0.08 respectively (Fig. 5). In contrast, the biomass, vegetation coverage, diversity, and richness index will increase gradually. The study also found that the highest biomass and diversity index were at the IIc stage which recovered after approximately 30 years, rather than the oldest IId community.

The decline in community productivity in NSS also led to a rapid reduction in shrub and xerophyte litter accumulation, and the source tended to be single (Table 2). Primary forest had the highest litter amount, approximately 630 g/m^2, while the litter amount was approximately 452 g/m^2 in plantation forests. The litter amount of shrubs-grasses and xerophytes was significantly lower than that in primary forests, which were only 23% and 14% of the primary forests, respectively. The litter mass of primary and plantation forests is mainly from dead branches and deciduous tree leaves, accounting for 30%~50% of the total mass. The evergreen trees occupied an average of 20%. In addition, dead branches and xerophytes occupied 40% of the shrub litter. Xerophyte litter comes from the accumulation of perennial herbs. In general, vegetation litter gradually shifted from dead deciduous tree leaves to deciduous shrubs and perennial herbs when the communities changed from primary forests to shrubs and xerophytes.

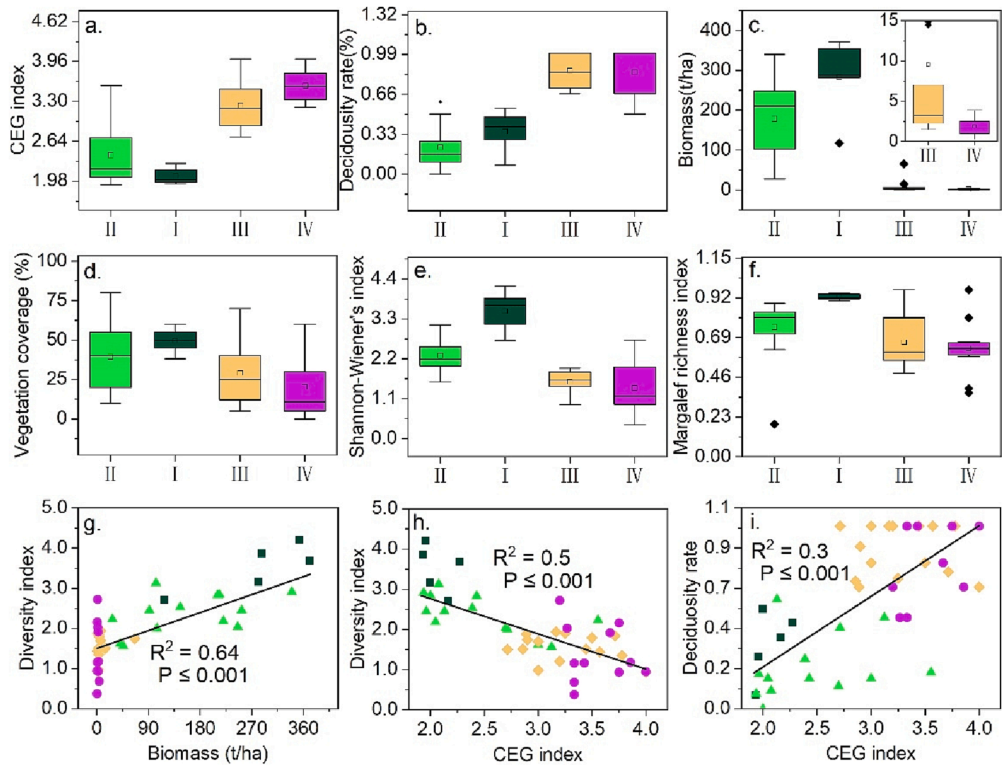

Fig. 4. The change in different vegetation sample types (I~IV) of the community ecological gradient index (CEG index, a), deciduosity rate (b), biomass (c), vegetation coverage (d), Shannon-Wiener's index (e), Margalef richness index (f), and the relationship between diversity index and biomass (g), CEG index and deciduosity rate and (h), diversity index (i).

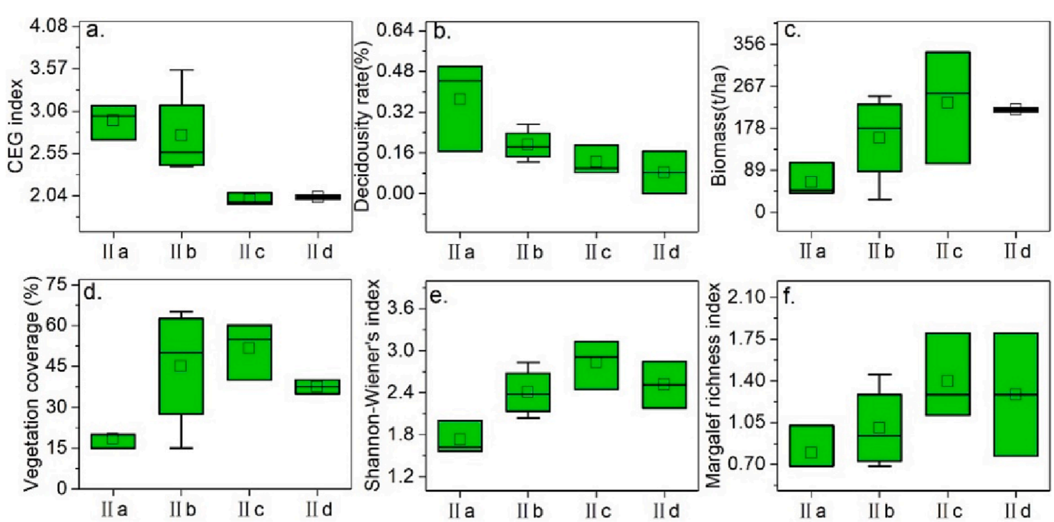

Fig. 5. The change in different ages of *Masson pine* plantation forests (the recovery years of IIa~IId from 10 to 30 years).

Table 2
The litter amount and allocation in various community types.

Vegetation types	Average Amount (g/m^2)	Allocation of litter mass (%) Branches	Decidousity	Evergreen	Shrub	Xerophyte
I. Pri	630	43.75	31.1	25.15	—	—
II. Pla	452	41.89	45.84	13.27	—	—
III. SG	147.23	41.7	—	—	29.93	41.79
IV. Xer	88.79	—	—	—	—	100
Ib. Pri*	510	41.76	32.87	19.37	4.64	1.74
IIb. Pla*	490	38.5	23.84	—	18.83	18.83
IIIb. SG*	36.8	—	—	—	—	100

3.3. Soil properties under community sequence

The soil quality tends to experience drought, strong alkalinity, and loose texture from primary forests to scrubs and xerophytes. The soil pH value, water content, density, and soil texture can effectively indicate these trends (Fig. 6). The soil environment changed from neutral to strongly alkaline as the surface vegetation decreased. The average pH value increased from 7.26 in primary forests to 8.96 in badlands. Notably, plantation forests hold acidic soil with a pH of 5.14, which is equal to the acidic soil sample (Fig. 6-a). An increased pH value is accompanied by a rapid loss of soil water content. SG had the highest soil water content, reaching more than 13%, followed by primary forests at approximately 12%. The average water contents of the xerophyte and badland were only 7.73% and 5.64%, respectively (Fig. 6-b). Xerophyte soil had the highest soil density, at approximately 1.7 g/cm^3 (Fig. 6-c). The primary forests have the highest proportion of sand (5–50 μm), at 40% and 60%, respectively, while the proportion of coarse sand (greater than50 μm) in scrub grassland and xerophytes is over 70%. For badlands, the proportion of coarse sand is more than 80% (Fig. 6d).

The soil nutrients showed that the available nitrogen content in alkaline soil was significantly lower than those in other acidic purple soil, karst, or red soil and tended to be enhanced with the reduction in surface vegetation (Table 3). The SOC and TN of the alkaline soil under different vegetation types were similar to those of the acidic soil samples but much higher than those of the karst soil and red soil, which showed a faster soil formation rate and organic matter accumulation. Despite abundant TN, AN represents a low N-use efficiency in alkaline soil, which is only 65% and 74% of the karst and red soil, respectively. Xerophyte soil only had 40% AN of primary forests, while the content further decreased to 10.96 ± 1.41 mg/kg in badland. This trend can also be reflected by more detailed community classifications (Table S4). TN in litter shows an opposite trend to soil nitrogen limitation. The litter TN in scrub grassland and xerophytes was significantly higher than that in the primary and plantation forests (Table S5). The APH content was also significantly lower than that in karst and red soil but higher than that in primary and plantation forests in acidic soil. The APH in primary and plantation forests was approximately 2.81 and 2.87 mg/kg, respectively, much higher than that in shrubs and xerophytes. APO contents in scrub grassland and badland, approximately 168.67 ± 62.62 mg/kg and 117.21 ± 28.24 mg/kg, respectively, indicate that potassium may come from soil parent materials. The trends of TPH and TPO in the litter are largely consistent across primary forests to scrub-grassland and xerophytes but have a clear trough in plantation forests. The acidic environment may be more favorable for the loss or transformation of these two elements. Therefore, the soil SOC and TN contents are mainly from litter matter, while TPO and TPH may be affected by both soil parent material and litter decomposition.

3.4. Plant-soil correlations by RDA

Redundancy analysis (RDA) showed that environmental factors explained 87.8% and 36.03% of the total variation in 19 communities and 45 species, respectively. Axis 1 explains 82.09% of the aggregated variation in plant communities and 23.4% of the species scale (Fig. 7-a, b). These results can be verified by the Monte-Carlo test (Table 4). Among the environmental variables, soil water content, pH, and AN provided the greatest explanatory power, accounting for 42.9%, 20.8%, and 20.5% of the total variation, respectively (Fig. 7a, Table 4). The arrow direction of the soil water content is consistent with biomass, litter amount, richness, and diversity, dominance, which show a significant positive correlation with each other ($R^2 > 0.3$) (Fig. 7-c). The soil pH arrow also has the same direction as the CEG and deciduosity rate of plant communities and exhibits a strong positive correlation with each other (R^2 = 0.63, 0.49). AN was significantly correlated with biomass, litter amount, richness, and diversity (R^2 greater than 0.4). A dry-wet environmental gradient was also found in Axis 1 for the positive correlation with soil water content and AN and the negative correlation with pH. Despite the insignificance of the F test, available potassium

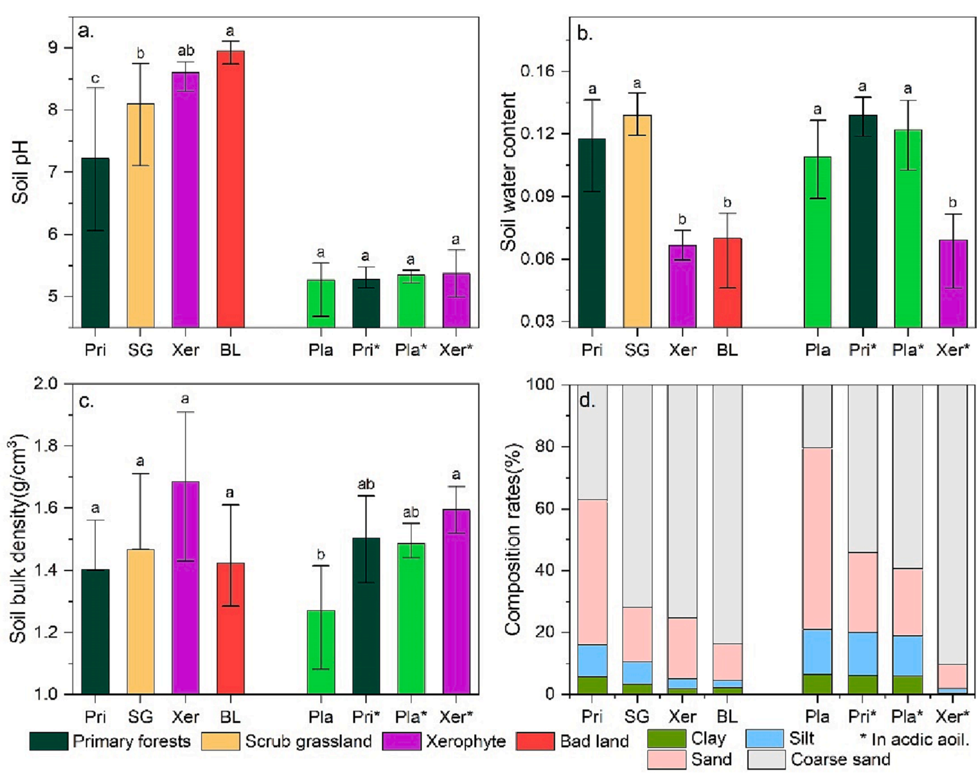

Fig. 6. The soil pH, water content, density, and composition ratio at different vegetation types. (The soil texture: clay: less than2 μm, silt: 2–5 μm, sand: 5–50 μm, coarse sand: greater than50 μm; according to USDA (USDA 2017).

Table 3
The nutrient properties of soil among different community types.

Variable*	Units	Alkaline soil**					Acidic soil			Default***	
		Pri	Pla	SG	Xer	BL	VIR	Pla	Xer	KS	RS
SOM	g/kg	14.19 ± 5.54	15.68 ± 4.1	11.28 ± 6.11	12.9 ± 9.2	3.18 ± 1.72	18.01 ± 6.58	11.63 ± 3.41	16.43 ± 6.57	2.79 ± 0.48	3.09 ± 0.37
TN	g/kg	1.18 ± 0.46	0.71 ± 0.09	0.78 ± 0.26	0.69 ± 0.29	0.36 ± 0.07	0.77 ± 0.22	0.57 ± 0.07	1.23 ± 0.1	0.14 ± 0.02	0.12 ± 0.01
AN	mg/kg	62.21 ± 21.6	39.33 ± 8.52	30.96 ± 19.3	31.25 ± 13.15	10.96 ± 1.41	47.66 ± 17.89	33.3 ± 9.52	73.58 ± 16.15	103.7 ± 10.39	115 ± 12.22
APH	mg/kg	2.81 ± 1.23	0.6 ± 0.41	2.87 ± 2.01	1.02 ± 0.94	1.38 ± 1.78	0.88 ± 1.07	0.82 ± 0.38	4.86 ± 2.08	4.7 ± 2.72	6.2 ± 1.48
APO	mg/kg	104.53 ± 22.93	36.35 ± 11.35	168.67 ± 62.62	98.29 ± 19.02	117.21 ± 28.24	17.5 ± 5.57	42.28 ± 4.28	31.46 ± 0.28	74.8 ± 5.87	78.5 ± 14.53

* SOM: soil organic matter, TN: total nitrogen, AN: available nitrogen, APH: available phosphorous, APO: available potassium, LB: litter biomass, OC: organic carbon.
**Pri: primary forest, Pla: plantation forest, SG: scrub grassland, XER: xerophyte, BL: badland.
*** KS: karst soil, RS: red soil;

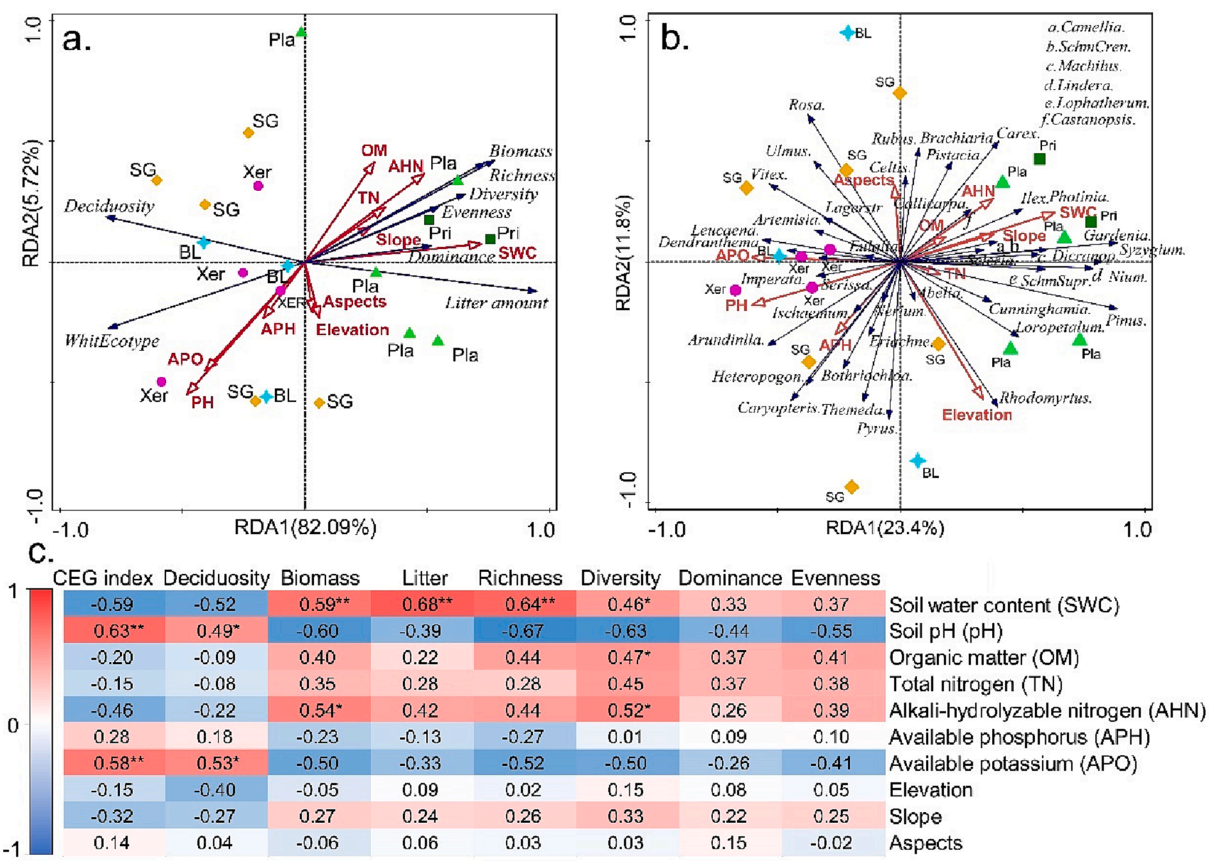

Fig. 7. The redundancy analysis ordination maps are based on the 19 quadrats with soil indicators (a) and 45 species with an importance value of 10% (b) and the Pearson coefficient matrix (c) of soil indicators and community characteristics. Plant community indices and species (solid arrows), environmental variables (hollow arrows), and sampling sites are shown in plots a and b. The full names of the species are shown in Table S6. ** indicates that the correlation is significant at the 0.01 level (2-tailed) in plot c, and * indicates significance at the 0.05 level.

showed a negative relationship with the biomass and richness of plant communities ($R^2 < -0.5$).

Although the species distribution was disturbed by biotic and abiotic factors on a small scale, RDA still found that slope, elevation, and AN were the significant factors in the distribution of 45 species, which together explained 35.8% of the total variation (Table 4, Fig. 7b). Terrain factors explained 14.2% of the slope and 11.3% of the altitude of the total variation. Only AN explained 10.3% of the total variables with a significance value less than 0.5. The above results were also confirmed by research at other regional scales (Yilmaz et al. 2017, Zhang et al. 2021). Another key finding of the species distribution RDA is that xerophyte species, such as *Themeda*., *Heteropogon*., *Ischaemum*., and *Eriachne*., are distributed on the left, while primary forest species such as *Photinia* and *Castanopsis* are concentrated on the right, which is consistent with the results of the quadrat RDA. Therefore, the RDA from the species level also confirmed the dry to wet environment gradient in DCA and key factors of community succession.

a. %Var is the percentage of variance in 19 samples or 45 species explained by the variable.

** Significant at the 0.01 level (2-tailed).

* Significant at the 0.05 level (2-tailed).

Table 4
Redundancy analysis (RDA) of the ecological stoichiometry and soil properties using forward selection with a Monte Carlo permutation test.

Name	% Var	F-ratio	P-value	Axis	1	2
RDA for plant communities scale: 19 quadrats						
Soil water content (SM)	42.9	12.8	0.002**	Eigenvalues	82.09	5.7
pH value	20.8	4.5	0.054	Cumulative percentage variance	82.09	87.8
Available nitrogen (AN)	20.5	4.4	0.034*	Species data		
Available potassium (APO)	14.7	2.9	0.084	Species-environment relation		
Total nitrogen (TN)	9.2	1.7	0.174	Summary of Monte Carlo test	For all axes	
Organic matter (OM)	7.7	1.4	0.242	F-ratio	36.7	5.8
Slope	6.2	1.1	0.294	p-Value	0.006	0.006
Available phosphorus (APH)	2.6	0.5	0.536	Species-environment correlations	0.964	0.7
Elevation	0.6	0.1	0.848			
Aspects	0.3	0.1	0.92			
RDA for species scale: 45 species (Importance value > 10%)						
Slope	14.2	2.1	0.058	Eigenvalues	19.36	16.68
Elevation	11.3	1.8	0.026*	Cumulative percentage variance	19.36	36.03
AN	10.3	1.8	0.054	Species data		
APH	7.7	1.4	0.146	Species-environment relation		
Soil pH	5.9	1.1	0.424	Summary of Monte Carlo test	For all axes	
Aspects	6.1	1.1	0.386	F-ratio	1	1.3
TN	5.3	1	0.484	p-Value	0.268	0.068
OM	6.9	1.3	0.264	Species-environment correlations	0.982	0.94
APO	4.3	0.8	0.646			
SM	4.9	0.9	0.578			

4. Discussion

4.1. Species adaptation in alkaline soil of humid red beds

Adaptation to seasonal drought by adjusting plant ecotype and deciduous ratios has been validated in China's karst and Mediterranean climate regions (Cerda et al. 2010, Xiong et al. 2017). Previous comparative studies found that arid and deciduous species in alkaline soil have a higher composition of 35.29% than other zones at the same latitude, as documented by Oliveira-Filho (Oliveira-Filho et al. 2003). In this research, the deciduous composition of the primary forests was over 40%, while the default sample only had 7.4%. The average CEG in scrub grassland was 22.6% higher than that in primary forests and over 50% higher than that in deciduous components. All plants were strong xerophytic and perennial herbs in the xerophyte stage. More deciduous species in communities can maintain water in the dry season by falling leaves and making full use of water in the rainy season, which indicates the arid environment in the subtropics (Tomlinson et al. 2013). All of the above results indicate an adaptation to seasonal drought. Therefore, seasonal drought in alkaline environments of purple soil is crucial for community structure and species composition.

We interpret the extreme seasonal drought of plant communities in the humid region as a combined effect of a monsoon climate and alkaline soil. In southern China, precipitation is mainly concentrated in summer, while there is relative drought in winter for broad-leaved evergreen forests (Yuanliang et al., 2015). In addition, the high pH value formed by the calcareous reaction leads to a low humification process compared with other acidic soils, which leads to a rough soil texture (Strom et al. 2005). Soil with rough texture generally exhibits higher permeability, resulting in greater moisture loses and a drier soil condition. Related studies have shown that the soil pH value negatively correlates with total nitrogen because additional NO_2 is formed by the soil OH-ions integrated with nitrogen, reducing the nitrogen content (Wrage et al. 2001). Soil AN in the red beds soft rock area is significantly lower than those in the default samples and background values. Therefore, an arid environment, coarse texture, and N limitation widely exist in alkaline soil.

An unfavorable soil environment will influence plant community dynamics. For poor and loose soil on a steep slope, the community stability is influenced mainly by soil erosion and other factors (Cerda et al. 2010). In deciduous forests, a high-density scrub-grassland community is usually constructed to prevent erosion (Gilliam 2007). However, the herbaceous layer in scrub-grassland communities will experience a dynamic process of declining and growing with the change in deciduous and evergreen composition during succession (Augusto et al. 2015). *Ulmus parvifolia Jacq.* and *Xylosma racemosum (Sieb. et Zucc.) Miq* is a native species in alkaline soil, adapting to the dry season through winter fallen leaves. Most species are deciduous or thorny trees and vines, accounting for more than 30%. The CEG value of this community was approximately 0.27 larger than that of the climax vegetation. Arid ecotype species increased by 12.5% (Table S7). *Pinus massoniana.* and *Schima superba.* species usually invade the primary forest under human interference. Virginal broadleaf forests can transition to a new structure of broadleaved mixed forest with coniferous species to adapt to the unfavorable soil environment. The native tree species reoccupied the position after the invaded species died, forming a dynamic process over time. With the accumulation of litter, the soil pH value gradually decreases to a neutral level due to the neutralization effect of fulvic acid in litter matter (Sayer 2006). A relatively stable community is formed with the accumulation of organic matter, nitrogen, phosphorus, and potassium at the same time. A dynamic and stable process in natural communities is formed by adjusting the community structure and species renewal to adapt to the changing environment. Therefore, primary forests have a special adaptation mechanism to alkaline soil by adjusting the community structure and species composition.

4.2. Cause of degradation sequence of primary forest

Strong alkalinity, drought, and N deficiency are ubiquitous in the plant-soil system formed in red beds. The soil pH of primary forests is generally neutral to slightly alkaline due to long-term soil-vegetation interactions. The effect of desiliconization and aluminum enrichment is usually not apparent during alkaline soil formation, emerging as neutral to strongly alkaline by soil-forming time (Brady and Weil 2002). The community's environment becomes extremely dreary along the gradient from primary forests to scrub-grassland and xerophyte. Compared with primary forests, the change rate of the CEG of scrub grassland increased by 38.4% on average. When degraded to xerophytes, it increased by 80.8%. At the same time, the average nitrogen decreased by approximately 10.96 ± 1.41 mg/kg, which was only 14% of the native plant community. Soil nutrients become poor with the inverse succession of primary forests, which may have a limiting effect on the restoration of the plant community (De Graaf et al. 2009). Primary forests will transition into shrubs and grasses and xerophytes and further form badland landscapes with the influence of human disturbances such as lumbering, firewood, and reclamation.

In general, native species seeds stored in the soil and saplings will develop after the removal of the arboreal layer in the primary forest. The seedlings will reoccupy the dominant layer and form a complete community for a long enough time (Guariguata and Ostertag 2001). However, the shrub community habitat tends to be dry when the understory shrub is exposed to the surface because it accelerates the evaporation of soil moisture and the soil becomes dry. The shrub community adapts to arid habitats by increasing the deciduous species to 75%. According to Caldeira's research, a similar mechanism in which habitat drought caused by the destruction of the arboreal layer limits community restoration was found in Mediterranean oaks (Caldeira et al. 2014). Under steep slope conditions, organic matter and nutrients such as nitrogen, phosphorus, and potassium are quickly lost with the erosion of surface soil and plant litter. At the same time, with nutrient loss, many alkaline substances from the soil parent material are further released, leading to an increase in soil pH (Yan et al., 2019b).

Many studies have shown that parent material and climate conditions are the key factors affecting soil pH changes because the exchangeable cations that determine the pH value, such as Ca+, N+, and Mg+, are mainly derived from the parent material and are controlled by precipitation leaching (Angiolini et al. 2013, Hou et al. 2022). Soil degradation caused by increasing the soil pH and the loss of nutrient elements further reduces the absorption of soil nutrients by plant roots (Paula et al., 2008). Therefore, the shrub plants in alkaline soil have short aboveground parts with developed root systems, similar to the shrub communities in arid and semiarid areas (Kizito et al. 2006). For xerophyte communities, the ground surface is occupied by dry perennial herbs after shrub cutting, and deciduous shrubs disappear (Tárrega et al., 2009). Compared with scrubs and grasses, the xerophyte community experienced strong drought and alkalinity as the soil moisture content in the xerophyte community decreased by 23%, and the soil pH increased by 11%. In addition, plantation forests widely exist in the target area, which accounted for 33% of the total survey. Many studies have shown that *Pinus massoniana* has a significant "acidification" effect on the soil environment (Ste-Marie and Paré 1999, Kuang et al. 2008). Our research shows that the average pH value of the soil in plantation forests is only 5.14, which is close to the default acidic soil sample and consistent with related research (Xue et al. 2014, Vazquez et al. 2020).

The surface soil of the xerophyte community is prone to erosion. Accompanied by erosion, nutrients are lost, and alkaline substances are released, so degradation will occur under intensified environmental stress (Chen et al. 2019, Zhao et al. 2019). The land may be degraded to badland if xerophyte communities are reclaimed for agricultural use under steep slope conditions. In addition, the alkaline soils in the study are developed from the weathering fragments of purple mudstone, which are rich in calcareous materials. $CaCO_3$ released by the newly formed soil is much higher than the total amount of erosion loss under erosion conditions. Therefore, the soil alkalinity tends to be enhanced under hydration conditions. The strong water erosion of the badland exposed the bedrock, and a large amount of calcium release led to the soil pH rising to 9, while the water content decreased rapidly. The extreme soil environment in badlands makes it difficult for plants to survive, forming a desert-like landscape.

Therefore, the physical and chemical properties of soil play a vital role in plant community degradation (Fig. 8). The reasons are as follows: (1) the poor water retention capacity and high soil temperature that existed in alkaline soil after vegetation destruction on the surface significantly restricted the restoration of vegetation; (2) with the revised succession of plant communities, a higher pH value led to the increasing environmental stress of root nutrient absorption while weakening the soil acidity regulation capacity of plants. The soil pH is as strong as approximately 9 in the badland, where no plants can survive in this landscape as an extreme form of degradation. (3) N limitation widely exists in calcareous soil and will be exacerbated with decreasing soil erosion and plant nitrogen fixation capacity.

4.3. Competitions of bedrock erosion and scrub invasion in badland areas

The badlands formed in red beds soft rocks feature the absence of vegetation, rugged surfaces, even gullies, thin weathering regolith on slope surfaces and high erosion rates (Yan et al., 2018). A high erosion rate was highlighted in the Nanxiong badlands due to the rapid weathering caused by considerable daily surface temperature variation and wetting–drying cycles (Yan et al. 2019a). The absence of vegetation has been discussed in many works. Seed removal is not the cause of the lack of vegetation on the slopes of badlands (Garciafayos et al. 1995). Estela Nadal-Romero suggested that topographic thresholds of plant colonization exist in humid badland environments (Nadal-Romero et al. 2014). In this contribution, we think the unfavorable environment of badland for plant growth is represented as poor soil texture, low soil water retention, nitrogen deficiency, and a pH value greater than 9.0. Secondary vegetation is also difficult to recover from primary forests under natural conditions because there is no species source and strong

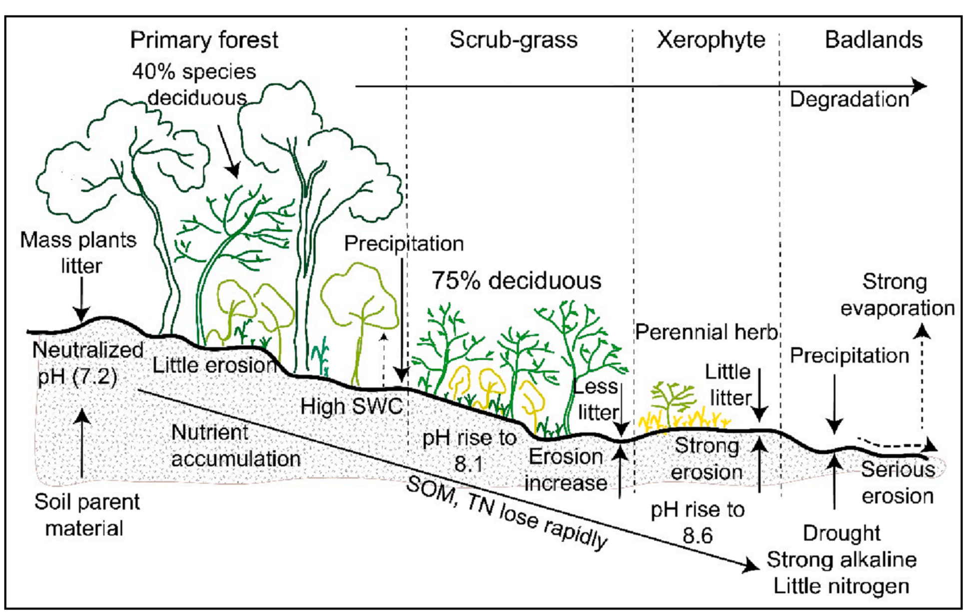

Fig. 8. The conceptual model of soil degradation from primary forests to scrub-grassland communities in red bed soft rock. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

alkaline stress for plant growth.

For the areas with a gentle slope under the erosion area, detrital material accumulates and is generally more than 20 cm. The accumulated regolith material in a gentle slope has a higher water content than the area with dense gullies. The gentle slope areas of badlands compete with weathering debris accumulation and surrounding shrub invasion because of the suitable habitats of plant communities and possible seeds from surrounding communities. In the case of intensified erosion, herbaceous plants are easily flooded by accumulated parent materials, which leads to invasive species of small shrubs with extremely developed root systems (Ovalle et al., 2021). Regolith on the surface can be fixed and accelerate soil development as erosion stops, forming relatively stable scrub-grassland communities. Observations of abandoned plowing and artificial forest deforestation show that under-forest shrubs and grasses developed after planting, but the coverage was below 40%. Soil N limitation will gradually ease and nutrient accumulation will increase under long-term soil–plant interactions. Therefore, it is difficult to draw explicit conclusions from the perspective of species connections. In addition, some species that adapt to the alkaline environment cannot survive in acidic soil.

5. Conclusion

Our study explores plant secondary succession and soil degradation in humid red beds areas. A general trend of higher arid habitats was found in plant communities, which represents an elevated community ecological gradient (CEG) and deciduous rate. Even in the primary forests, the CEG and deciduosity rates were much higher than those in other forests at the same latitude, leading to different species compositions. This type of forest has a special mechanism for adapting to the dry season climate by regulating species ecotypes and leaf litter ratios and neutralizing pH through accumulating litter. Therefore, forests developed in alkaline environments need special attention. Our study also found a succession sequence of the alkaline environment from primary forest to scrub grassland to xerophyte by DCA ordination. In addition to aridification, this succession sequence was accompanied by soil pH elevation and N deficit exacerbation. The significant reduction in the amount of litter suggests less vegetation coverage and intensification of surface erosion due to vegetation destruction. Areas, where steep slopes are conducive to erosion development, may form severely eroded badland landscapes, resulting in environmental disasters. Restoring forests on badlands is difficult due to strong alkalinity, rapid erosion, and nitrogen deficiency. Therefore, protecting and restoring forests in the alkaline environment of humid regions requires special patience and professional research to maintain this unique diversity on earth.

CRediT authorship contribution statement

Yuanliang Jin: Conceptualization, Investigation, Software, Writing – original draft. **Yuewu Xiang:** Methodology, Investigation, Data curation. **Chengshuai Liu:** Writing – review & editing. **Luobin Yan:** Writing – review & editing. **Jingxian Li:** Investigation, Data curation. **Zhen Li:** Investigation, Data curation, Writing – review & editing. **Bin Zhao:** Visualization, Validation. **Shengqi Qi:** Supervision.

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.

Data availability

The data that has been used is confidential.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2023.110504.

References

Angiolini, C., Landi, M., Pieroni, G., Frignani, F., Finoia, M.G., Gaggi, C., 2013. Soil chemical features as key predictors of plant community occurrence in a Mediterranean coastal ecosystem. Estuar. Coast. Shelf Sci. 119, 91–100.
Augusto, L., De Schrijver, A.n., Vesterdal, L., Smolander, A., Prescott, C., Ranger, J., 2015. Influences of evergreen gymnosperm and deciduous angiosperm tree species on the functioning of temperate and boreal forests. Biol. Rev. 90 (2), 444–466.
Bai, Z.G., Dent, D.L., Olsson, L., Schaepman, M.E., 2008. Proxy global assessment of land degradation. Soil Use Manag. 24 (3), 223–234.
Barbeta, A., Mejía-Chang, M., Ogaya, R., Voltas, J., Dawson, T.E., Peñuelas, J., 2015. The combined effects of a long-term experimental drought and an extreme drought on the use of plant-water sources in a Mediterranean forest. Glob. Chang. Biol. 21 (3), 1213–1225.
Baribault, T.W., Kobe, R.K., Rothstein, D.E., 2010. Soil calcium, nitrogen, and water are correlated with aboveground net primary production in northern hardwood forests. For. Ecol. Manage. 260 (5), 723–733.
Brady, N.C., Weil, R.R., 2002. The nature and properties of soils. J. Range Manag. 5, 333.
Bussotti, F., Pollastrini, M., 2020. Opportunities and Threats of Mediterranean Evergreen Sclerophyllous Woody Species Subjected to Extreme Drought Events. Appl. Sci.-Basel 10, 1–13.
Caldeira, M.C., Ibáñez, I., Nogueira, C., Bugalho, M.N., Lecomte, X., Moreira, A., Pereira, J.S., Brando, P., 2014. Direct and indirect effects of tree canopy facilitation in the recruitment of Mediterranean oaks. J. Appl. Ecol. 51 (2), 349–358.
Casper, B.B., Bentivenga, S.P., Ji, B., Doherty, J.H., Edenborn, H.M., Gustafson, D.J., 2008. Plant-soil feedback: Testing the generality with the same grasses in serpentine and prairie soils. Ecology 89 (8), 2154–2164.
Cerda, A., Lavee, H., Romero-Diaz, A., et al., 2010. Soil erosion and degradation in mediterranean-type ecosystems preface. Land Degrad. Dev. 21, 71–74.
Chao, A., Colwell, R.K., Lin, C.-W., Gotelli, N.J., 2009. Sufficient sampling for asymptotic minimum species richness estimators. Ecology 90 (4), 1125–1133.
Chen, J., Xiao, H., Li, Z., Liu, C., Wang, D., Wang, L., Tang, C., 2019. Threshold effects of vegetation coverage on soil erosion control in small watersheds of the red soil hilly region in China. Ecol. Eng. 132, 109–114.
Crouzeilles, R., Curran, M., Ferreira, M.S., Lindenmayer, D.B., Grelle, C.E.V., Rey Benayas, J.M., 2016. A global meta-analysis on the ecological drivers of forest restoration success. Nat. Commun. 7 (1).
De Graaf, M.C.C., Bobbink, R., Smits, N.A.C., Van Diggelen, R., Roelofs, J.G.M., 2009. Biodiversity, vegetation gradients and key biogeochemical processes in the heathland landscape. Biol. Conserv. 142 (10), 2191–2201.
Diwediga, B., Wala, K., Folega, F., Dourma, M., Woegan, Y.A., Akpagana, K., Le, Q.B., 2015. Biophysical and anthropogenous determinants of landscape patterns and degradation of plant communities in Mo hilly basin (Togo). Ecol. Eng. 85, 132–143.
El-Sherbeny, G. A., M. A. Dakhil, E. M. Eid, et al., 2021. Structural and Chemical Adaptations of Artemisia monosperma Delile and Limbarda crithmoides (L.) Dumort. in Response to Arid Coastal Environments along the Mediterranean Coast of Egypt. Plants-Basel 10:481.
Farneda, F. Z., R. Rocha, A. Lopez-Baucells, et al., 2018. Functional recovery of Amazonian bat assemblages following secondary forest succession. Biological Conservation 218:192-199.
Frouz, J., Prach, K., Pižl, V., Háněl, L., Starý, J., Tajovský, K., Materna, J., Balík, V., Kalčík, J., Řehounková, K., 2008. Interactions between soil development, vegetation and soil fauna during spontaneous succession in post mining sites. Eur. J. Soil Biol. 44 (1), 109–121.
Garciafayos, P., Recatala, T.M., Cerda, A., Calvo, A., 1995. Seed population-dynamics on badland slopes in southeastern spain. J. Veg. Sci. 6, 691–696.
Gibson, L., Lee, T.M., Koh, L.P., Brook, B.W., Gardner, T.A., Barlow, J., Peres, C.A., Bradshaw, C.J.A., Laurance, W.F., Lovejoy, T.E., Sodhi, N.S., 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. Nature 478 (7369), 378–381.
Gilliam, F.S., 2007. The ecological significance of the herbaceous layer in temperate forest ecosystems. Bioscience 57, 845–858.
Guariguata, M.R., Ostertag, R., 2001. Neotropical secondary forest succession: changes in structural and functional characteristics. For. Ecol. Manage. 148 (1-3), 185–206.
Gunn, J.S., Ducey, M.J., Belair, E., 2019. Evaluating degradation in a North American temperate forest. For. Ecol. Manage. 432, 415–426.
Hosseinpur, A.R., Samavati, M., 2008. Evaluation of chemical extractants for the determination of available potassium. Commun. Soil Sci. Plant Anal. 39 (9-10), 1559–1570.

Hou, R., Li, T., Fu, Q., Liu, D., Li, M.o., Zhou, Z., Li, Q., Zhao, H., Yu, P., Yan, J., 2020. Effects of biochar and straw on greenhouse gas emission and its response mechanism in seasonally frozen farmland ecosystems. Catena 194, 104735.
Hou, R., Qi, Z., Li, T., Fu, Q., Meng, F., Liu, D., Li, Q., Zhao, H., Yu, P., 2022. Mechanism of snowmelt infiltration coupled with salt transport in soil amended with carbon-based materials in seasonally frozen areas. Geoderma 420, 115882.
Hüttl, R.F., Schneider, B.U., 1998. Forest ecosystem degradation and rehabilitation. Ecol. Eng. 10 (1), 19–31.
Kardol, P., Bezemer, T.M., van der Putten, W.H., 2006. Temporal variation in plant-soil feedback controls succession. Ecol. Lett. 9, 1080–1088.
Kerley, S.J., Shield, I.F., Huyghe, C., 2001. Specific and genotypic variation in the nutrient content of lupin species in soils of neutral and alkaline pH. Aust. J. Agr. Res. 52, 93–102.
Kirk, P.L., 1950. Kjeldahl-method for total nitrogen. Anal. Chem. 22 (2), 354–358.
Kizito, F., Dragila, M., Sène, M., Lufafa, A., Diedhiou, I., Dick, R.P., Selker, J.S., Dossa, E., Khouma, M., Badiane, A., Ndiaye, S., 2006. Seasonal soil water variation and root patterns between two semi-arid shrubs co-existing with Pearl millet in Senegal, West Africa. J. Arid Environ. 67 (3), 436–455.
Kuang, Y.W., Sun, F.F., Wen, D.Z., Zhou, G.Y., Zhao, P., 2008. Tree-ring growth patterns of Masson pine (Pinus massoniana L.) during the recent decades in the acidification Pearl River Delta of China. For. Ecol. Manage. 255 (8-9), 3534–3540.
LeBauer, D.S., Treseder, K.K., 2008. Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. Ecology 89 (2), 371–379.
Li, S., 2021. Classification and reference of purple soil in ST and WRB. Southwest University, Chongqing.
Liao, K.F., Hu, C., Hu, X.J., et al., 2021. A study on plant diversity evaluation in Danxia Wutong Nature Reserve in Nanxiong City. Ecol. Sci. 40, 156–164.
Lima, T.T.S., Miranda, I.S., Vasconcelos, S.S., 2010. Effects of water and nutrient availability on fine root growth in eastern Amazonian forest regrowth, Brazil. New Phytol. 187, 622–630.
Lin, DunMei, Lai, JiangShan, Mi, Xiang Cheng, Ren, HaiBao, Ma, KePing, 2013. Spatial variation in community structure of a subtropical evergreen broad-leaved forest: Implications for sampling design. Chin. Sci. Bull. 58 (10), 1181–1186.
McArdle, B.H., Anderson, M.J., 2001. Fitting multivariate models to community data: A comment on distance-based redundancy analysis. Ecology 82 (1), 290–297.
Miki, N.H., Sasaki, S., Yang, L., Ogasa, M.Y., 2017. Effects of soil nutrient conditions on water transport properties and recovery from severe drought stress in Pinus densiflora saplings. J. For. Res. 22 (3), 177–184.
Montanarella, L., 2007. In: Environmental Science and EngineeringClimate and Land Degradation. Springer Berlin Heidelberg, Berlin, Heidelberg, pp. 83–104.
Moss, J.P., Bailey, N., Cipollini, M.L., 2020. Survey of Rare Plants Within a Calcareous Flatwoods Community and Analysis of Plant-Environmental Relationships. Castanea 85, 205–222.
Mulvaney, R.L., Khan, S.A., 2001. Diffusion methods to determine different forms of nitrogen in soil hydrolysates. Soil Sci. Soc. Am. J. 65 (4), 1284–1292.
Nadal-Romero, E., Petrlic, K., Verachtert, E., Bochet, E., Poesen, J., 2014. Effects of slope angle and aspect on plant cover and species richness in a humid Mediterranean badland. Earth Surf. Proc. Land. 39 (13), 1705–1716.
Newbold, T., Hudson, L.N., Hill, S.L.L., et al., 2015. Global effects of land use on local terrestrial biodiversity. Nature 520 (7545), 45–50.
Oliveira-Filho, A. T., L. A. Jarenkow, and M. J. N. Rodal. 2003. Floristic relationships of seasonally dry forests of Eastern South America based on tree species distribution patterns. Pages 159-192 *in* Meeting on Tropical Savannas and Seasonally Dry Forests, Edinburgh, SCOTLAND.
Ovalle, P.E.R., Bisigato, A.J., Campanella, M.V., 2021. Soil erosion facilitates shrub encroachment in Patagonian herbaceous steppes. Land Degrad. Dev. 32 (11), 3377–3385.
Paula, D.M., Julia, M., Sonia, F., 2008. Plant limiting nutrients in Andean-Patagonian woody species: Effects of interannual rainfall variation, soil fertility and mycorrhizal infection. For. Ecol. Manage. 255 (7), 2973–2980.
Peng, H., L. Yan, Z. Chen, et al., 2015. A preliminary study of desertification in red beds in the humid region of Southern China (in Chinese). Acta Geographica Sinica 70: 1699-1707.
Piraino, S., Camiz, S., Filippo, A., Piovesan, G., Spada, F., 2013. A dendrochronological analysis of Pinus pinea L. on the Italian mid-Tyrrhenian coast. Geochronometria 40 (1), 77–89.
Poorter, L., Markesteijn, L., 2008. Seedling traits determine drought tolerance of tropical tree species. Biotropica 40, 321–331.
Rigling, A., Bigler, C., Eilmann, B., Feldmeyer-Christe, E., Gimmi, U., Ginzler, C., Graf, U., Mayer, P., Vacchiano, G., Weber, P., Wohlgemuth, T., Zweifel, R., Dobbertin, M., 2013. Driving factors of a vegetation shift from Scots pine to pubescent oak in dry Alpine forests. Glob. Chang. Biol. 19 (1), 229–240.
Robinson, S. 2016. Land Degradation in Central Asia: Evidence, Perception and Policy. Pages 451-490 *in* R. H. Behnke and M. Mortimore, editors. End of Desertification?: Disputing Environmental Change in the Drylands.
Roleček, J., Tichý, L., Zelený, D., Chytrý, M., 2009. Modified TWINSPAN classification in which the hierarchy respects cluster heterogeneity. J. Veg. Sci. 20 (4), 596–602.
Sayer, E.J., 2006. Using experimental manipulation to assess the roles of leaf litter in the functioning of forest ecosystems. Biol. Rev. 81, 1–31.
Silva, T.L., Vale, C.G., Godinho, R., Fellous, A., Hingrat, Y., Alves, P.C., Abáigar, T., Brito, J.C., 2017. Ecotypes and evolutionary significant units in endangered north African gazelles. Biol. J. Linn. Soc. 122 (2), 286–300.
Slessarev, E.W., Lin, Y., Bingham, N.L., Johnson, J.E., Dai, Y., Schimel, J.P., Chadwick, O. A., 2016. Water balance creates a threshold in soil pH at the global scale. Nature 540 (7634), 567–569.
Souza, D.M.d., Morais, P.A.d.O., Matsushige, I., Rosa, L.A., 2016. Development of Alternative Methods for Determining Soil Organic Matter. Revista Brasileira De Ciencia Do Solo 40 (0).
Ste-Marie, C., Paré, D., 1999. Soil, pH and N availability effects on net nitrification in the forest floors of a range of boreal forest stands. Soil Biol. Biochem. 31 (11), 1579–1589.
Ström, L., Owen, A.G., Godbold, D.L., Jones, D.L., 2005. Organic acid behaviour in a calcareous soil implications for rhizosphere nutrient cycling. Soil Biol. Biochem. 37 (11), 2046–2054.
Tang, J., Tang, XiaoXin, Qin, YangMei, He, QiuShun, Yi, Y., Ji, ZhiLiang, 2019. Karst rocky desertification progress: Soil calcium as a possible driving force. Sci. Total Environ. 649, 1250–1259.
Tárrega, R., Calvo, L., Taboada, Á., García-Tejero, S., Marcos, E., 2009. Abandonment and management in Spanish dehesa systems: Effects on soil features and plant species richness and composition. For. Ecol. Manage. 257 (2), 731–738.
Taubner, H., Roth, B., Tippkötter, R., 2009. Determination of soil texture: Comparison of the sedimentation method and the laser-diffraction analysis. J. Plant Nutr. Soil Sci. 172 (2), 161–171.
Timm, L.C., Pires, L.F., Reichardt, K., Roveratti, R., Oliveira, J.C.M., Bacchi, O.O.S., 2005. Soil bulk density evaluation by conventional and nuclear methods. Aust. J. Soil Res. 43 (1), 97.
Tomlinson, K.W., Poorter, L., Sterck, F.J., Borghetti, F., Ward, D., de Bie, S., van Langevelde, F., Cornelissen, H., 2013. Leaf adaptations of evergreen and deciduous trees of semi-arid and humid savannas on three continents. J. Ecol. 101 (2), 430–440.
Turner, K.G., Anderson, S., Gonzales-Chang, M., Costanza, R., Courville, S., Dalgaard, T., Dominati, E., Kubiszewski, I., Ogilvy, S., Porfirio, L., Ratna, N., Sandhu, H., Sutton, P.C., Svenning, J.-C., Turner, G.M., Varennes, Y.-D., Voinov, A., Wratten, S., 2016. A review of methods, data, and models to assess changes in the value of ecosystem services from land degradation and restoration. Ecol. Model. 319, 190–207.
Usda, 2017. Soil survey manual sand, USDA Handbook 18th. Government Printing Office, Washington, D.C.
van Loon, W.M.G.M., Walvoort, D.J.J., van Hoey, G., Vina-Herbon, C., Blandon, A., Pesch, R., Schmitt, P., Scholle, J., Heyer, K., Lavaleye, M., Phillips, G., Duineveld, G. C.A., Blomqvist, M., 2018. A regional benthic fauna assessment method for the Southern North Sea using Margalef diversity and reference value modelling. Ecol. Ind. 89, 667–679.
Vazquez, E., Benito, M., Espejo, R., Teutscherova, N., 2020. Response of soil properties and microbial indicators to land use change in an acid soil under Mediterranean conditions. Catena 189, 1–10.
Whittaker, R.H. (Ed.), 1978. Classification of Plant Communities. Springer Netherlands, Dordrecht.
Wrage, N., Velthof, G.L., van Beusichem, M.L., Oenema, O., 2001. Role of nitrifier denitrification in the production of nitrous oxide. Soil Biol. Biochem. 33 (12-13), 1723–1732.
Xin, C., Li, Z., Dong, H., 1990. The vegetation of Neilingding island in Zhujiang river mouth(in Chinese). Ecological science:23–34.
Xiong, K., Chi, Y., Shen, X., 2017. Research on Photosynthetic Leguminous Forage in the Karst Rocky Desertification Regions of Southwestern China. Pol. J. Environ. Stud. 26 (5), 2319–2329.
Xue, L., Li, Q.J., Chen, H.Y., 2014. Effects of a Wildfire on Selected Physical, Chemical and Biochemical Soil Properties in a Pinus massoniana Forest in South China. Forests 5, 2947–2966.
Yan, L. B., H. Peng, S. Y. Zhang, et al., 2019a. The Spatial Patterns of Red Beds and Danxia Landforms: Implication for the formation factors-China. Scientific Reports 9.
Yan, P., H. Peng, L. B. Yan, et al., 2019b. Spatial variability in soil pH and land use as the main influential factor in the red beds of the Nanxiong Basin, China. Peerj 7.
Yan, L., Liu, P., Peng, H., Kašanin-Grubin, M., Lin, K., 2018. Laboratory study of the effect of temperature difference on the disintegration of redbed softrock. Phys. Geogr. 40 (2), 149–163.
Yelenik, S.G., Levine, J.M., 2011. The role of plant-soil feedbacks in driving native-species recovery. Ecology 92 (1), 66–74.
Yilmaz, H., O. Y. Yilmaz, and Y. F. Akyuz. 2017. Determining the factors affecting the distribution of Muscari latifolium, an endemic plant of Turkey, and a mapping species distribution model. Ecology and Evolution 7:1112-1124.
Yuanliang, J.I.N., H. P., Luobin YAN,, et al., 2015. Discussion on desertification of humid region in southern China. Prog. Geogr. 34, 772–780.
Zhang, J.Y., Dai, M.H., Wang, L.C., Zeng, C.F., Su, W.C., 2016. The challenge and future of rocky desertification control in karst areas in southwest China. Solid Earth 7, 83–91.
Zhang, Q.P., Wang, J., Wang, Q., 2021. Effects of abiotic factors on plant diversity and species distribution of alpine meadow plants. Eco. Inform. 61, 1–8.
Zhao, A.Z., Zhang, A.B., Liu, J.H., Feng, L.L., Zhao, Y.L., 2019. Assessing the effects of drought and "Grain for Green" Program on vegetation dynamics in China's Loess Plateau from 2000 to 2014. Catena 175, 446–455.