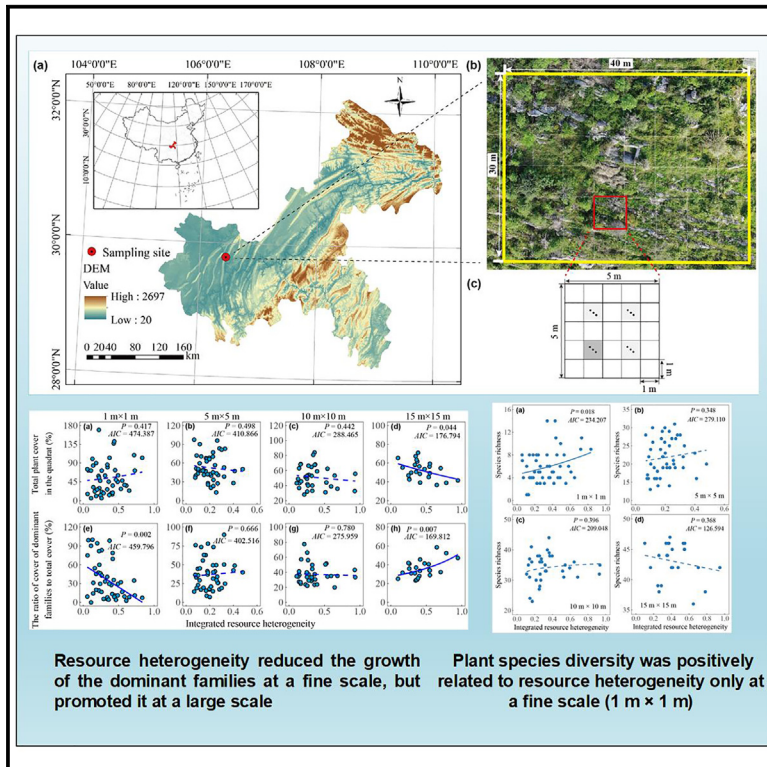


Soil resource heterogeneity promotes species richness only at a fine scale at the early restoration of karst abandoned farmland

Graphical abstract



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In brief

Environmental science; Ecology; Plant ecology

Highlights

- Species richness was spatially scale dependent
- Species diversity was positively related to resource heterogeneity only at a fine scale
- Resource heterogeneity reduced overall plant growth at a large scale
- It highlights the importance of fine-scale ecological information in karst areas



Article

Soil resource heterogeneity promotes species richness only at a fine scale at the early restoration of karst abandoned farmland

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SUMMARY

The relationship between heterogeneity and plant diversity remains unclear in low-resource karst. We made *in situ* observations at different spatial scales within a fixed plot on abandoned farmland that had been enclosed for 4 years. Species richness was spatially scale dependent, while species evenness remained consistently low across all scales. Species diversity was positively related to resource heterogeneity only at a fine scale (1 m × 1 m), mainly driven by an increase in the species richness of non-dominant groups. Resource heterogeneity reduced overall plant growth at a large scale. However, it reduced the growth of the dominant families (Asteraceae and Poaceae) at a fine scale, but promoted it at a large scale. Our results suggest that soil resource heterogeneity exerts a scale-dependent positive impact on species richness during the early restoration of abandoned farmland by low resource availability and highlight the importance of fine-scale ecological information in karst areas.

INTRODUCTION

The relationship between habitat heterogeneity and vascular plant diversity is important but still controversial.^{1–4} The widely accepted “environmental heterogeneity hypothesis” posits that variation in resources promotes species coexistence.⁵ Mechanisms underlying the opportunity for species to exploit resource heterogeneity mainly include two aspects. First, highly heterogeneous habitats provide multiple ecological niches for species occurrences, which can reduce interspecific competition and allow more species to coexist.^{6,7} Second, habitat heterogeneity can also provide more shade or refuge for more organisms.⁸ The “environmental heterogeneity hypothesis” has been confirmed in many ecosystems.^{7,9,10} However, recent studies, including those by Ben-Hur and Kadmon¹¹ and Heidrich et al.,¹² have reported negative or hump-shaped relationships between heterogeneity and diversity. Resource availability level and spatial scale are important variables influencing the heterogeneity-diversity relationship.¹³ The question of what shape heterogeneity-diversity relationships take under specific resource and scale conditions remains worth exploring.¹²

The positive relationship between habitat heterogeneity and biodiversity may be modulated by environmental stressors, e.g., low resource availability.¹⁴ For instance, Scott and Baer⁵ found that light heterogeneity exhibited a positive correlation

with the effective number of plant species under low light availability, but no correlation was observed under high light availability. A reduction in available resources may increase the types of restricted resources and relatively increase the niche dimensions, thus promoting the positive relationship between habitat heterogeneity and species diversity.¹⁵ Conversely, as restricted resources become abundant and homogenized, niche dimensions may be reduced, resulting in a decrease in species diversity.¹⁵ However, excessive habitat heterogeneity can lead to habitat fragmentation, shifting the relationship between habitat heterogeneity and species richness from positive to negative as fragmentation intensifies.¹⁶ In a previous study, Phouthavong et al.¹⁷ found a comparatively lower diversity of fern species in karst areas with high habitat heterogeneity when contrasted to non-karst areas with lower habitat heterogeneity. Habitat fragmentation can negatively impact species richness by isolating habitats and reducing resource availability. This isolation restricts the ability of species, especially rare species, to disperse and access necessary resources, leading to a decline in their populations.¹⁶ Consequently, the overall community species richness may decrease. Liu et al.¹⁸ found a decrease in resource availability within the karst shrub community as resource heterogeneity increased. This decrease limited the survival and reproduction of several plant species, ultimately resulting in a negative impact on biodiversity.¹⁸ Given these conflicting empirical



findings, further research is needed to determine whether the relationship between resource heterogeneity and species diversity supports the positive correlation advocated by the “environmental heterogeneity hypothesis” in resource-limited environments.

Numerous studies suggested that the relationship between habitat heterogeneity and plant diversity is scale dependent.^{8,13,19–21} Positive heterogeneity-diversity relationships are frequently observed at larger scales,²² due to the presence of a greater variety of microhabitats, which enables more species to reach their optimal microhabitats in the region.²³ However, insignificant or negative heterogeneity-diversity relationships often occur at fine scales. For example, Bergholz et al.²⁴ found that environmental heterogeneity had no significant impact on species α -diversity in a semi-arid environment at fine scales (0.06 and 1 m²). Similarly, in a simulation experiment, Xue et al.²¹ demonstrated that soil heterogeneity and nutrient heterogeneity at the block scale (40 cm) did not affect the richness and diversity, and even had a significant negative effect on the richness at the patch scale (30 cm). However, resource variability, such as soil depth, can be particularly strong in fine-scale habitats in some regions,^{25,26} accommodating the coexistence of multiple species with different resource gradient preferences. Therefore, the heterogeneity-diversity relationship may be positive at a fine scale.

Coexisting species in a community respond differently to soil resource heterogeneity.²⁷ For example, increasing soil heterogeneity at a fine scale is more conducive to the growth and competitiveness of invasive plants compared to native species.^{28,29} Many common invasive plants may thrive in patches with high resource heterogeneity characterized by rapid growth rates and high water use efficiency.^{30–32} Due to their higher root foraging precision, dicotyledons may be more responsive to resource heterogeneity compared to monocotyledons, whose root foraging precision is limited by a large number of adventitious roots.³³ At the community level, the effect of soil heterogeneity may be neutralized because different plants may respond differently to soil heterogeneity.³⁴ Dominant groups may also have stronger and faster responses to environmental stress.³⁵ In addition, plants have been demonstrated to enhance the utilization of heterogeneous nutrients by increasing root growth with more efficiency at the community level as compared to the individual level.³⁶ Currently, there is a lack of research on the responses of functional groups to resource heterogeneity and plant growth at the community level in karst regions.

Compared with other subtropical ecosystems, karst ecosystems are dominated by low resource availability and high habitat heterogeneity.³⁷ The natural karst soil layer is shallow due to a slow soil formation rate³⁸ and severe soil erosion. Drought is also the most obvious characteristic of the karst ecosystem due to the extensive development of rock fissures, sinkholes, and a large proportion of shallow soil, featuring low water retention capacity and a high water loss rate.^{39,40} Simultaneously, the extremely fragmented topography and mosaic distribution of rocks, coupled with a limited amount of soil, have given rise to various microhabitats such as rocky trenches and crevices.⁴¹ These habitats exhibit high heterogeneity in water and soil resources both horizontally and vertically.^{42,43} Therefore, low

resource availability and high habitat heterogeneity are important selection pressures for local vegetation growth and community construction currently and in the future.^{44–46}

In recent years, abandoned land has been increasing due to the conversion of farmland to grassland and forest^{47–49} and emigration of the rural labor force from karst areas. The natural restoration of abandoned land is considered the preferred solution for resolving ecological and environmental challenges in vulnerable karst ecosystems. Ecologists are consistently striving to enhance biodiversity and community complexity.^{50,51} It should be noted that the species diversity and community composition during the early restoration stage of abandoned land play a crucial role in the later successional processes.⁵² Therefore, this study focused on the early natural restoration stage of abandoned farmland to investigate species diversity, soil resources (heterogeneity and availability), and their relationship. The aim was to answer four scientific questions: (1) Are there positive heterogeneity-diversity relationships in a karst region with low soil resources? (2) Are these relationships scale dependent? (3) How does plant growth at the community level respond to resource heterogeneity? and (4) Do dominant plant groups react more positively to resource heterogeneity? This study is expected to further elucidate the formation and maintenance mechanism of species diversity during the early restoration stage of abandoned farmland and provide a scientific basis for dynamic analyses of community succession and vegetation restoration in the karst ecosystem.

RESULTS

Soil resource availability and resource heterogeneity

Soil resource availability was low and there was no obvious difference among different scales (Table 1). As the spatial scale expanded from 1 m × 1 m–15 m × 15 m, the heterogeneity of each soil resource increased. Notably, soil depth exhibited considerable heterogeneity, with a coefficient of variation consistently exceeding 36% across all scales (Table 1).

Species composition and species diversity

A total of 65 herbaceous plant species, belonging to 29 families and 61 genera, were identified in the sample plots. Asteraceae with 14 species and Poaceae with 12 species accounted for 40% of all the species identified. Apiaceae had five species and Ranunculaceae had three species. The remaining 25 families, including Crassulaceae, Fabaceae, Lamiaceae, Oxalidaceae, Rosaceae, and others, only had one or two species each.

The importance values of *Daucus carota*, *Sedum emarginatum*, and *Medicago sativa* were among the top 4 at all scales, with values $\geq 5\%$. Over ten species in Poaceae or Asteraceae were among the top 20 plants in terms of importance value at all scales. These two families had significantly higher family importance values than other families (trait values are shown in Tables S1 and S2). With the increase of scale, the importance values of *Miscanthus sinensis* and *Bromus japonicus* in Poaceae increased, from 5th to 2nd and 4th to 9th, respectively. The rankings of *Senecio scandens* and *Bellium minutum* in Asteraceae also increased, from 15th to 7th and 20th to 12th, respectively (Figure S1).

Table 1. Basic statistics of soil resource availability and soil resource heterogeneity

Scales	pH	SWC (%)	SD (cm)	AN (mg kg ⁻¹)	TN (g kg ⁻¹)	TC (g kg ⁻¹)
Resource availability (Mean ± standard deviation)						
1 m × 1 m	5.99 ± 0.64	26.54 ± 3.64	22.40 ± 14.07	29.50 ± 10.43	2.56 ± 0.63	21.07 ± 7.43
5 m × 5 m	6.03 ± 0.57	27.03 ± 3.93	20.05 ± 10.03	35.44 ± 14.34	2.89 ± 0.77	24.84 ± 8.70
10 m × 10 m	5.92 ± 0.41	26.41 ± 2.81	20.60 ± 6.60	35.89 ± 8.39	2.82 ± 0.50	24.03 ± 5.84
15 m × 15 m	5.83 ± 0.24	25.81 ± 1.75	21.05 ± 4.40	35.43 ± 5.62	2.75 ± 0.32	23.23 ± 3.82
Resource heterogeneity (Mean ± standard deviation)						
1 m × 1 m	3.18 ± 1.93	10.93 ± 7.42	49.22 ± 37.59	23.53 ± 12.81	10.34 ± 8.05	13.83 ± 9.98
5 m × 5 m	9.30 ± 12.74	16.17 ± 13.43	61.99 ± 29.86	37.86 ± 17.11	25.99 ± 19.37	32.66 ± 21.19
10 m × 10 m	13.24 ± 9.59	20.27 ± 8.78	63.44 ± 11.90	50.99 ± 14.43	34.77 ± 13.30	44.00 ± 16.18
15 m × 15 m	16.90 ± 7.37	23.79 ± 5.94	67.13 ± 8.11	56.96 ± 7.98	39.82 ± 10.52	50.83 ± 13.69

Soil resource availabilities are average values and soil resource heterogeneities are coefficients of variation. SWC, soil water content; SD, soil depth; AN, available nitrogen; TN, total nitrogen; TC, total carbon.

Both species richness ($R^2 = 0.880$, $p < 0.001$) and the Shannon-Wiener index ($R^2 = 0.359$, $p < 0.001$) exhibited a positive but asymptotic relationship with increasing spatial scales (Figures 1A and 1B; Table S3). The plateau in species richness was observed at the 15 m × 15 m scale, while the Shannon-Wiener index approached an inflection point at the 5 m × 5 m scale, marking the transition to a plateau. However, species evenness did not show a significant trend with spatial scale ($R^2 = 0.001$, $p = 0.395$) (Figure 1C; Table S3).

Contribution of single soil resource heterogeneity to richness

Resource variables that contributed to the variation of species richness varied by scale. At 1 m × 1 m scale, soil depth heterogeneity had the highest contribution to changes in species richness (60.29%), followed by soil available nitrogen heterogeneity (22.90%). At the 5 m × 5 m scale, soil pH heterogeneity had the highest contribution (42.26%), followed by soil depth heterogeneity (26.99%). At the 10 m × 10 m scale, soil pH heterogeneity had the highest contribution (35.24%), followed by soil moisture heterogeneity (31.59%). At the 15 m × 15 m scale, soil total nitrogen heterogeneity had the highest contribution (37.59%), followed by soil total carbon heterogeneity (32.21%) (Table 2).

The effect of integrated resource heterogeneity on species richness

Integrated resource heterogeneity had a significant positive effect on herbaceous species richness only at 1 m × 1 m scale ($p < 0.05$) (Figure 2). Although integrated resource heterogeneity was not significantly correlated to the abundance of the dominant families (Asteraceae and Poaceae) ($p > 0.05$), it was signif-

icantly positively correlated to the richness of non-dominant families ($p < 0.01$) (Figure S2A). There was no significant correlation between integrated resource heterogeneity and species richness across the 5 m × 5 m, 10 m × 10 m, and 15 m × 15 m spatial scales, with p values exceeding the 0.05 threshold for all tested models ($p > 0.05$) (Figure 2; Table S4).

The effect of integrated resource heterogeneity on total plant cover and cover ratio of dominant families

At 1 m × 1 m scale, the total plant cover did not exhibit a significant trend with increasing integrated resource heterogeneity ($p > 0.05$). However, the cover ratio of the two major families, Asteraceae and Poaceae, showed a significant decrease ($p < 0.01$). At the 5 m × 5 m and 10 m × 10 m scales, neither total plant cover nor the cover ratio of the dominant families (Asteraceae and Poaceae) responded significantly to integrated resource heterogeneity across all tested models. At the 15 m × 15 m scale, the total plant cover decreased significantly ($p < 0.05$) with increasing integrated resource heterogeneity, while the cover ratio of dominant families significantly increased ($p < 0.01$) (Figure 3; Tables S5 and S6).

DISCUSSION

It is an important challenge to determine changes in species diversity and species composition at different spatial scales in ecology.^{53–55} Species richness was spatially scale dependent in the early restoration stage of abandoned farmland with high soil resource heterogeneity and low resource availability. However, species evenness was low at any scale as a result of a large number of rare species. Integrated resource heterogeneity had a positive effect on species diversity only at a fine scale, mainly by increasing the species richness of non-dominant taxa. In addition, the growth responses of all plants and dominant families to resource heterogeneity exhibited spatial scale dependence. Resource heterogeneity reduced overall plant growth at a large scale. Resource heterogeneity reduced the growth of dominant families (Asteraceae and Poaceae) at a fine scale, but promoted it at a large scale. With these findings, this study provides specific implications for planning karst restoration efforts, emphasizing the importance of focusing on the fine scales. In addition, this study contributes valuable field data across multiple spatial scales, supporting the validation of the “environmental heterogeneity hypothesis” in the early stages of karst restoration. The findings advance both the theoretical understanding and practical approaches within the field of karst restoration, and for ecosystem restoration more broadly.

Spatial scale dependencies in species richness and species evenness

In our study, we discerned distinct patterns in species diversity indices across varying spatial scales. Notably, species richness increased with spatial scale. The species richness-area relationship is one of several well-established ecological laws that can explain the well-known scale dependence of richness.⁵⁶ It is evident that larger areas with larger soil volume and total nutrient pool can support larger plant populations, reducing the extinction probability due to stochastic events and the occurrence

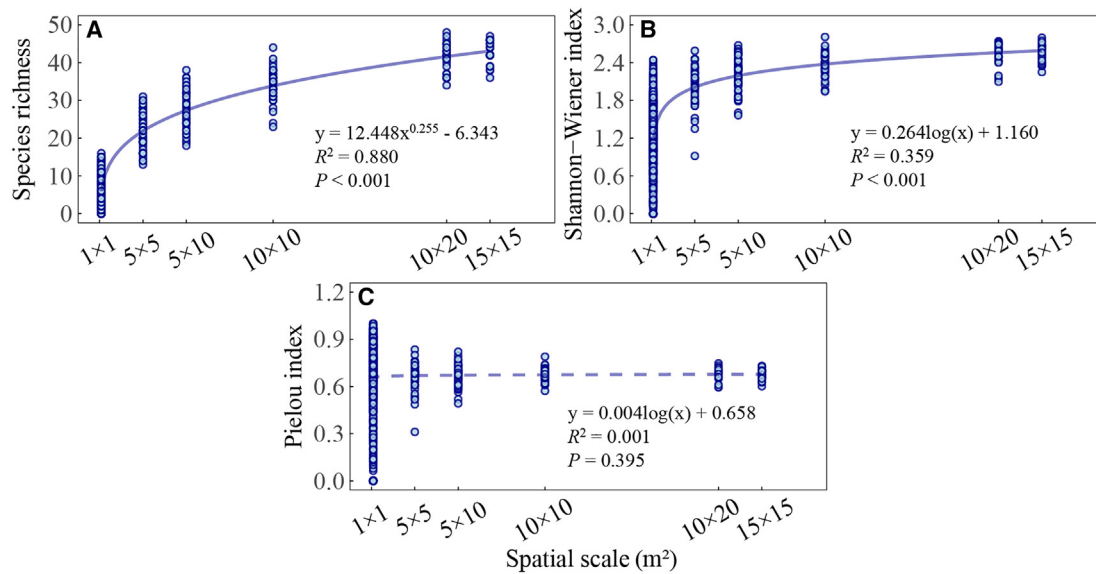


Figure 1. Species richness and the Shannon-Wiener index exhibited a positive but asymptotic relationship with increasing spatial scales
Relationships between spatial scale (m^2) and species richness (A), Shannon-Wiener index (B), and Pielou index (C).

probability of all species increased with habitat size.^{18,57} Generalist species may profit more from high habitat heterogeneity at large spatial scale compared to habitat specialists, thereby increasing total species richness in the community.⁵⁸ However, although species richness increased as a power function with spatial scale, species evenness was not scale dependent among different species across scales. This contrasts the commonly observed negative correlation between species richness and evenness at the same scale.⁵⁹ Our results indicated that the spatial scale regulated the population distribution among multiple species. Furthermore, the average evenness of species at all scales was lower than that found in semi-natural grasslands,⁶⁰ likely because of the large number of rare species in our study. In karst areas, high heterogeneity provides diverse habitats, offering numerous ecological niches for different species to exploit. However, due to low soil resource availability, most species that reach this area cannot become dominant. This may explain why the species evenness in this study was similarly low at all scales. Thus, spatial scale is the key factor in shaping species richness but not species evenness. To enhance our comprehension of species diversity, it is necessary to understand various diversity indicators (both evenness and richness) at different spatial scales.⁶¹

Spatial scale dependencies in heterogeneity-diversity relationships

Positive heterogeneity-diversity relationships were only observed at the fine scale ($1 \text{ m} \times 1 \text{ m}$), at which soil resource heterogeneity was relatively high, indicating strong microhabitat complexity.^{62,63} Strong microhabitat complexity, while providing more habitats for plant colonization, also reduces competition through the differentiation of resource requirements between species.^{64,65} Previous controlled experiments have suggested that within heterogeneous patch sizes smaller than the root

span of some plant species, those with larger root systems may outcompete others, potentially diminishing diversity.^{27,66} However, the $1 \text{ m} \times 1 \text{ m}$ sample area exceeded the root span of all species present, allowing for a more equitable utilization of resources. In addition, the high spatial heterogeneity at the small scale of this study was reflected in the strong soil depth variability rather than the presence of isolated patches that might reduce habitat area.¹³ The herbaceous plants under investigation possessed flexible root systems that enabled them to effectively colonize both deep and shallow soils.⁶⁷ The highly heterogeneous environment at small scales did not limit the establishment of new plant individuals and populations to reduce richness, so no neutral or negative heterogeneity-diversity relationships were observed.

However, as the scale extends, resource heterogeneity increases rapidly and may lead to habitat fragmentation, potentially altering the positive relationship between habitat heterogeneity and species richness.¹⁶ The positive influence of habitat heterogeneity on species richness depends on the availability of suitable habitats and the connectivity that allows for species movement and gene flow. Fragmentation can counterbalance this effect by isolating populations and reducing habitat size, particularly impacting rare species. This isolation can lead to increased vulnerability to local extinction, reduced recolonization rates, and diminished genetic diversity, which in turn negatively affects overall species richness.

At the large scale ($15 \text{ m} \times 15 \text{ m}$), we did not observe a significant heterogeneity-diversity relationship, which may be due to the fact that all samples at this scale exhibited high environmental heterogeneity. Each sample at the $15 \text{ m} \times 15 \text{ m}$ scale contained 225 $1 \text{ m} \times 1 \text{ m}$ subsamples with substantial variability in soil depth, suggesting that soil depth variability was no longer the primary contributor to species richness at this scale. Instead, variability in total carbon (TC) and total nitrogen (TN) became

Table 2. Contribution of soil resource heterogeneity to species richness

Soil resources	Contribution to species richness (%)			
	1 m × 1 m	5 m × 5 m	10 m × 10 m	15 m × 15 m
SWC	1.34	13.94	30.33	5.57
SD	60.29 ^a	26.99	20.87	11.06
TC	2.91	6.36	3.48	32.21
TN	5.35	6.59	5.69	37.59 ^a
AN	22.90	3.97	2.93	4.10
pH	7.19	42.23 ^a	36.71 ^a	9.47
Sum	100	100	100	100

SWC, soil water content; SD, soil depth; AN, available nitrogen; TN, total nitrogen; TC, total carbon.

^aThe maximum contribution value of the primary soil resource to species richness at each spatial scale is highlighted in bold.

more influential. The interlocking and mosaic distribution of karst soils and rocks in natural karst habitats implies that homogeneous habitats are only possible at small scales.⁶⁸ At larger scales, the heterogeneity of resources, such as TC and TN, was high across all the samples. Consequently, richness was not sensitive to integrated resource heterogeneity at 15 m × 15 m spatial scale.

Our study showed that the positive heterogeneity-diversity relationships were primarily driven by the increase of non-dominant rather than the dominant families (Asteraceae and Poaceae). In terms of life history, Poaceae are dominant species that are often perennial and can expand rapidly by tillering, allowing for long-term colonization.⁶⁹ Annuals of non-dominant species have shorter lifespans and are relatively more inclined to establish by occupying vacant ecological niches in heterogeneous habitats. In terms of plant specialization to ecological niches, dominant species, such as those in several Asteraceae, have a wider ecological niche and can establish at different levels of environmental heterogeneity,⁷⁰ and thus the richness of dominant families did not increase significantly with increasing heterogeneity. However, the majority of non-dominant species exhibit limited resource utilization,⁷¹ and the greater the environmental variability at the fine scale, the higher the possibility of non-dominant species meeting the required resource level.

Growth responses of all plants and dominant families to integrated resource heterogeneity

Plant cover reflects their growth.⁷² At the 1 m × 1 m scale, integrated resource heterogeneity inhibited the growth of dominant Asteraceae and Poaceae, resulting in a decreased cover ratio. However, at the 15 m × 15 m scale, these families showed an opposite trend in response to integrated resource heterogeneity, likely because the essential environmental drivers of biological processes vary across spatial scales.^{73–75} At a fine scale, soil depth variation accounts for the highest weight in integrated resource heterogeneity. Some dominant families are usually limited to a specific soil depth,^{76,77} which leads to a lower cover ratio compared to non-dominant families.

At a large scale, the overall plant growth in high heterogeneous habitats was weakened, mainly because there was a significant

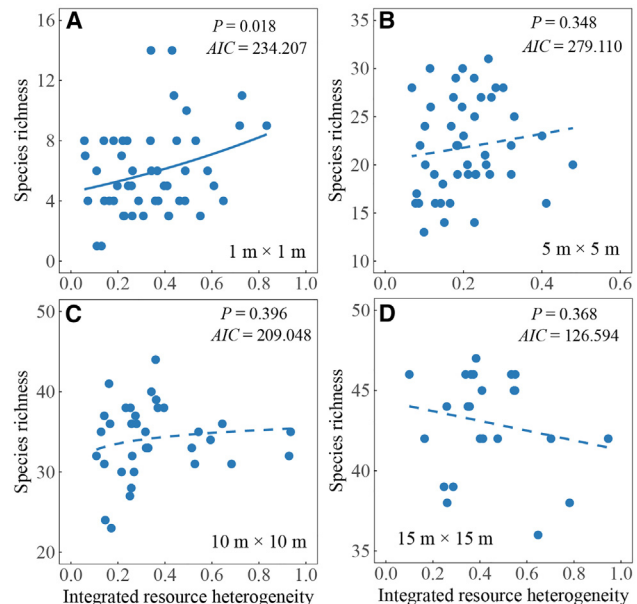


Figure 2. Integrated resource heterogeneity had a significant positive effect on herbaceous species richness only at 1 m × 1 m scale

The relationships between integrated resource heterogeneity and species richness at spatial scales of 1 m × 1 m (A), 5 m × 5 m (B), 10 m × 10 m (C), and 15 m × 15 m (D). A significant relationship is observed only at the 1 m × 1 m scale ($p < 0.05$).

positive correlation between bare rock rate and integrated resource heterogeneity. The increase in rock area meant a decrease in herbaceous plant survival space. Although some studies have indicated that soil nutrients can be found in well-developed fissures in limestone areas,⁷⁸ herbaceous plants with shallow roots in the early stage of restoration struggle to effectively utilize resources in deep rock fissures.⁷⁹ Therefore, the lack of surface soil limited overall plant growth in the highly heterogeneous habitat at a large scale. However, the cover ratios of Asteraceae and Poaceae increased significantly along the heterogeneous gradient. At a larger scale, the variation of TC and TN accounted for a higher weight in integrated resource heterogeneity, indicating that plants from the two families demonstrate greater fitness compared with other families in an environment of high soil nutrient variability and high bare rock rate. This fitness was likely aided by their tall stature large leaves and large specific leaf area, which reflect competition for light resources.^{80,81} Further, invasive species of the Asteraceae family exhibit a greater capacity for sexual and asexual reproduction, as well as water and nutrient use efficiency.^{82,83} The ranking of importance values of some Asteraceae and Poaceae species increased with the increase of scale, which further emphasized their dominant position in the community at a larger scale.

Conclusions

We found that species richness was particularly responsive to environmental heterogeneity at the 1 m × 1 m scale, but was not observed at the larger scale we assessed. This finding highlights the necessity of incorporating habitat and soil heterogeneity when selecting scales for monitoring the restoration of

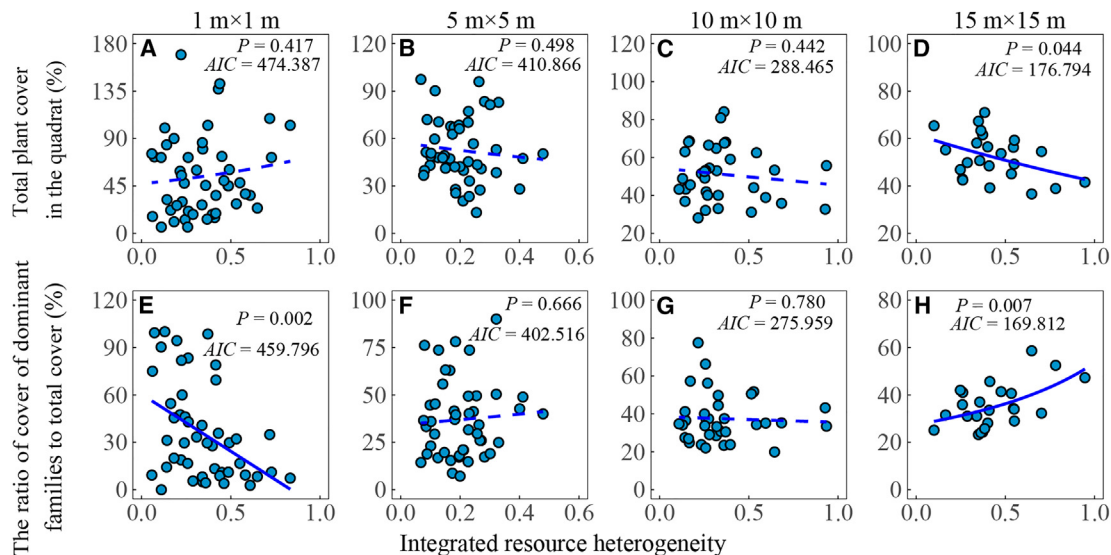


Figure 3. The total plant cover and the cover ratio of the dominant families had the different trends with increasing integrated resource heterogeneity

The relationships for integrated resource heterogeneity with total plant cover in the quadrat (A–D) and cover ratio of dominant families (E–H) at 1 m × 1 m, 5 m × 5 m, 10 m × 10 m, and 15 m × 15 m. Dominant families: Asteraceae and Poaceae.

degraded lands. Moreover, environmental heterogeneity at a fine scale deserves special attention in karst areas with fragmented topography. This study can provide a theoretical basis for the conservation of biodiversity at a fine scale under the environmental changes faced by karst ecosystems.

Limitations of the study

In the present study, we only checked the relationships between heterogeneity and vascular plant diversity at short-term and smaller scales. However, the species diversity, community structure, intraspecific and interspecific relationships, and ecological processes will vary with the community succession and increasing spatial scale. It is necessary to focus on species coexistence theories, such as niche differentiation, interspecific competition and facilitation, to investigate the mechanisms of community species coexistence and diversity maintenance under different environmental and microhabitat gradients at long-term and bigger scales. Also, the ecosystem function and stability are needed to take into consideration in the fragile karst in the future.

RESOURCE AVAILABILITY

Lead contact

Further information and requests for reagents should be directed to and will be fulfilled by the lead contact, Jinchun Liu (jinchun@swu.edu.cn).

Materials available

This study did not generate new unique reagents.

Data and code availability

- All data will be shared by the [lead contact](#) upon request.
- This paper does not report original code.
- Any additional information required to reanalyze the data reported in this paper is available from the [lead contact](#) upon request.

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AUTHOR CONTRIBUTIONS

X.G.: conceptualization, data curation, funding acquisition, formal analysis, investigation, and writing – original draft; J. Luo: investigation and writing – review and editing; W.L.: formal analysis and writing – review and editing; H.D.: investigation and writing – review and editing; Y.Z.: investigation and writing – review and editing; W.T.: methodology and writing – review and editing; Z.L.: investigation, validation, and writing – review and editing; K.S.: writing – review and editing; J.T.: conceptualization and writing – review and editing; J. Liu: conceptualization, data curation, funding acquisition, investigation, methodology, project administration, and writing – original draft.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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 - Plot setting and plant survey
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- [QUANTIFICATION AND STATISTICAL ANALYSIS](#)
 - Species diversity index-spatial scale curve

- Species importance value
- Resource heterogeneity
- Statistical analysis

SUPPLEMENTAL INFORMATION

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STAR★METHODS

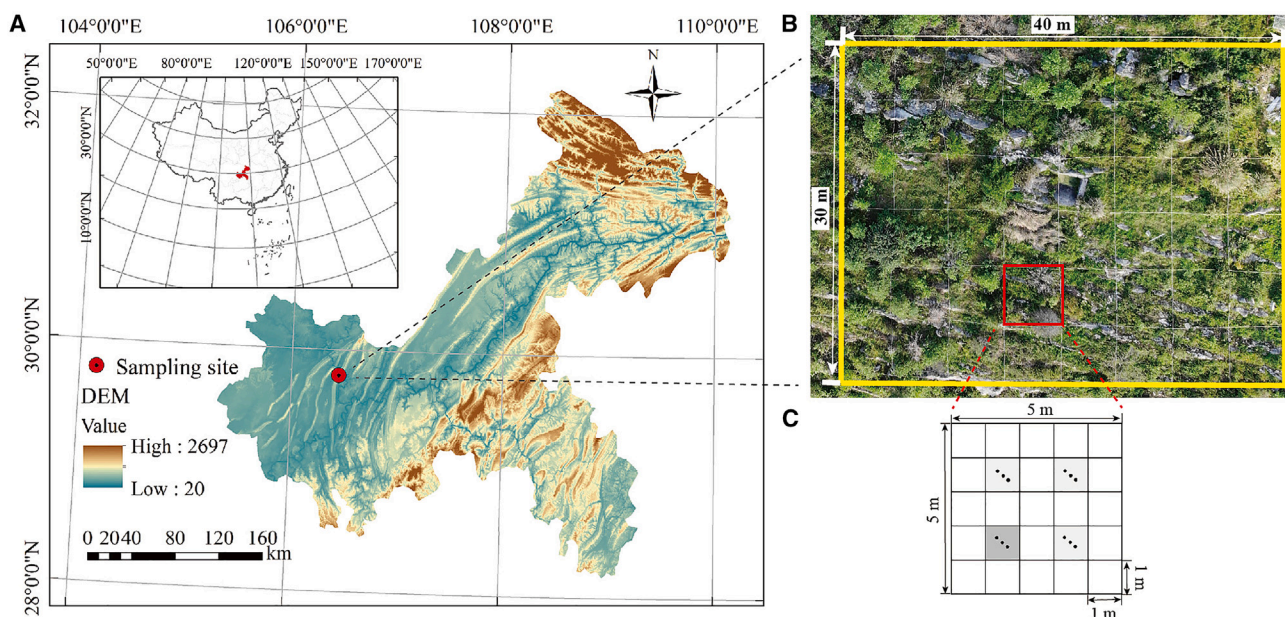
KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Biological samples		
186 soil samples	Chongqing Jinfo Mountain Karst Ecosystem National Observation and Research Station, Caoshang, Beibei, Chongqing, China	N/A
Deposited data		
Source data	This study	N/A
Source code	This study	N/A
Software and algorithms		
R v.4.3.0	R Core Team	https://www.R-project.org/
GS+9.0	Gamma Design Software, LLC	https://gs.software.informer.com/9.0/

METHOD DETAILS

Study site

This research was conducted at the Caoshang Observation and Research Site ($106^{\circ}27'10''$ E , $29^{\circ}47'26''$ N) of the Chongqing Jinfo Mountain Karst Ecosystem National Observation and Research Station, located 5 km south of Beibei, Chongqing, China (see below figure). The study site was located in a karst trough valley, which was an agricultural field before restoration. In 2018, this field was abandoned and enclosed as the Caoshang Observation and Research Site. This area experiences a subtropical humid monsoon climate with an average annual temperature of approximately 18.3°C and an average annual precipitation of about 1250 mm.



Geographic location (A) and aerial photo (B) of the study site in a karst trough valley in Chongqing, China, as well as the soil collection protocol (C) used at the site. The four gray cells ($1\text{ m} \times 1\text{ m}$) represented the four soil sampling quadrats. The soil was sampled separately at three points in one quadrant (dark gray), and the three soil samples were mixed into one in each of the three quadrants (light gray).

Plot setting and plant survey

In March 2022, a $30\text{ m} \times 40\text{ m}$ fixed plot that had been restored for four years was established. The plot was divided into 48 subplots ($5\text{ m} \times 5\text{ m}$) using steel pipes and steel cables. Each subplot was subdivided into 25 quadrats ($1\text{ m} \times 1\text{ m}$) (Figures 4B and 4C). To maximize the number of quadrats for scales exceeding $5\text{ m} \times 5\text{ m}$, we employed a spatial sampling design that incorporated partial

overlap among quadrats ⁸⁴, enhancing the representation of the environmental gradient within our study area. Each quadrat served as a virtual sample plot, allowing for a detailed analysis of species diversity at varying spatial scales. Specifically, we identified and delineated 35 quadrats at 10 m × 10 m scale (a) and 24 quadrats at 15 m × 15 m scale (b) within the overarching 30 m × 40 m study plot (Figure S3). During May–June 2022, we recorded all herbaceous plant species along with their species names, heights and cover across each 1 m × 1 m quadrat (total of 1200 quadrats).

Soil sampling and analysis

After finishing the plant survey, we collected topsoil (0–10 cm) in 4 quadrats (1 m × 1 m) of each subplot (5 m × 5 m) (Figure 4C). In each subplot, the soil was sampled separately at three points, as for the 1 m × 1 m scale soil nutrients test in one quadrat. In the other three quadrats, we mixed the soil samples from three points and took 1/3 of them back to determine soil nutrient levels at other scales (Figure 4C). Since two sampling quadrats were completely covered by rocks, a total of 286 soil samples were collected.

Soil chemical properties including pH, total carbon (TC), total nitrogen (TN), and available nitrogen (AN), were analyzed for each quadrat using standard soil test methods.⁸⁵ Soil water content (SWC) was quantified by an oven-dry method. Soil available nitrogen ($\text{NO}_3^- \text{N} + \text{NH}_4^+ \text{N}$) was determined by potassium chloride leaching spectrophotometry using fresh soil samples. The air-dried soil was collected using a plastic sieve with different pore sizes. After passing through a 2 mm sieve, soil pH was determined at 20°C in the ratio of soil and deionized water 1:2.5 (w/w). After passing through a 100-mesh sieve, both total carbon (TC) and total nitrogen (TN) concentrations in the soil were measured using a Vario EL cube CN Elemental Analyzer (Elementar Analysen Systeme GmbH).

To minimize the damage to the naturally restored vegetation, soil depth was measured with a steel brazier at three sites in each soil sampling quadrat in late October 2022. A total of 576 soil depth values were measured. Further, the bare rock rate of each soil sampling quadrat was estimated by two observers. The average of the two estimated values was recorded as the bare rock rate for that sampling quadrat. The average bare rock rate of four sampling quadrats was taken as the bare rock rate for each 5 m × 5 m subplot.

We considered spatial autocorrelation in soil variables, a prevalent characteristic of *in situ* plot inventory data.⁸⁶ We applied a square-root transformation to the data, making them more normally distributed for spatial autocorrelation analysis. Subsequently, we conducted spatial autocorrelation analysis using GS+9.0 software, successfully fitting the optimal semi-variance function theoretical model for each soil variable (Figure S4; Table S7). Spatial dependence was evaluated by the ratio of nugget to total semi-variance, expressed as a percentage. This metric classified the degree of spatial dependence: <25% indicated strong, 25–75% moderate, and >75% weak spatial dependence. Our findings categorized soil depth, soil water content, pH, total nitrogen, and total carbon as moderately spatially dependent, while available nitrogen showed weak spatial dependence (Table S7).

QUANTIFICATION AND STATISTICAL ANALYSIS

Species diversity index-spatial scale curve

We systematically assessed species diversity across six spatial scales to generate species diversity index–spatial scale curves: 1 m × 1 m ($n = 1200$), 5 m × 5 m ($n = 48$), 5 m × 10 m ($n = 48$), 10 m × 10 m ($n = 35$), 20 m × 10 m ($n = 25$), and 15 m × 15 m ($n = 24$). Species diversity index -spatial scale curves were tested using logarithmic function and power function models.

In this study, we employed three species diversity indices to assess ecological variation across different spatial scales: the species richness index (S), Shannon–Wiener index (H'), and Pielou evenness index (E). The species richness index (S) refers to the number of species in the grid cells at each scale. In addition, the Shannon–Wiener index (H') is an index for the comprehensive evaluation of species richness and evenness (0–1 scale) in a community, measuring dominance concentration.⁸⁷

$$H' = - \sum_{i=1}^s \frac{N_i}{N} \log_2 \frac{N_i}{N} \quad (\text{Equation 1})$$

$$E = \frac{H'}{\ln s} \quad (\text{Equation 2})$$

where S is the species richness, N_i is the cover of species i in the community, and N is the sum of the covers of all species.

We selected four representative scales (1 m × 1 m, 5 m × 5 m, 10 m × 10 m, 15 m × 15 m) for subsequent analysis based on species diversity index - spatial scale curves. Given the similar trends between the Shannon–Wiener index and species richness along spatial scales, and considering the directness and ease of measuring species richness, our study focused on this metric for analyzing the relationship between heterogeneity and richness at different spatial scales.

Species importance value

We used the following formula to estimate the importance value (IV) for each species in the quadrats⁸⁸ at the four different spatial scales (1 m × 1 m, 5 m × 5 m, 10 m × 10 m, and 15 m × 15 m). This calculation is specific to each species and is derived as follows:

$$IV = \frac{Hr+Cr+Fr}{3} \quad (\text{Equation 3})$$

where IV is the importance value. Hr , Cr and Fr are the relative height, cover and frequency of each species, respectively, which were calculated using the following formulas:

$$Hr = \frac{Ha}{Hs} \quad (\text{Equation 4})$$

$$Cr = \frac{Ca}{Cs} \quad (\text{Equation 5})$$

$$Fr = \frac{Fa}{Fs} \quad (\text{Equation 6})$$

where Ha is the average height of a species, Hs is the sum of the average heights of all species; Ca is the coverage of a species, Cs is the sum of the coverage of all species; Fa is the frequency of a species, Fs is the sum of frequency of all species.

Resource heterogeneity

At the $1\text{ m} \times 1\text{ m}$ scale, three samples from each of the 48 three-point independent sampling quadrats were taken as independent measurements, whereas at scales above $1\text{ m} \times 1\text{ m}$, the mean of the three-point independent sampling quadrats was taken as the measurement for that cell. The mean and heterogeneity of each variable were calculated using the measurements (3, 4, 16 and 36) contained in each scale grid cell ($1\text{ m} \times 1\text{ m}$, $5\text{ m} \times 5\text{ m}$, $10\text{ m} \times 10\text{ m}$ and $15\text{ m} \times 15\text{ m}$), and the coefficient of variation (CV) of the measurements was used to express resource heterogeneity.

We calculated integrated resource heterogeneity based on the complex resource gradient framework established by Xu et al.⁸⁹ To ensure the comparability of heterogeneity across samples, all environmental variable values were normalized to $[0, 1]$ range. This normalization was crucial for the calculation of the integrated resource heterogeneity (IRH) score, as it allows the heterogeneity of different samples at the same spatial scale to be directly comparable. The IRH score was determined by weighting each environmental variable according to the results of variance partitioning analysis, which quantified the relative importance of each variable in influencing species richness. The variance partitioning analysis was conducted using the *hier.part* package.⁹⁰ The formula for calculating integrated resource heterogeneity (IRH) is as follows:

$$IRH = X_1 \times [CV(SWC)]_n + X_2 \times [CV(SD)]_n + X_3 \times [CV(TC)]_n + X_4 \times [CV(TN)]_n + X_5 \times [CV(pH)]_n + X_6 \times [CV(AN)]_n \quad (\text{Equation 7})$$

where X_1, X_2, X_3, X_4, X_5 and X_6 are the contributions of each soil resource heterogeneity (coefficient of variation) to species richness at each spatial scale, respectively, and the sum of the values of X_1, X_2, X_3, X_4, X_5 and X_6 is 100%. $[Y]_n$ is the normalized value of each variable.

Statistical analysis

The relationship between integrated resource heterogeneity score and species richness was assessed by generalized linear models, linear regression and non-linear models. We removed two anomalous outliers at the $5\text{ m} \times 5\text{ m}$ scale applying Cook's distance.⁹¹

To investigate the effects of resource heterogeneity on the growth of overall plants and dominant families, the relationships between integrated resource heterogeneity score and both the total plant cover and cover ratio of dominant families (Asteraceae and Poaceae) were assessed by generalized linear models, linear regression and non-linear models.