Although many studies have focused on the effects of the environment and area on local patterns of species richness, few studies have demonstrated how to reconcile the availability of more niches with smaller habitat areas in heterogeneous localities. Here, the environmental range that a species prefers was defined as a niche; a space was defined as an available space if the environmental range of the space matches a niche; and the metric ‘environmental range per unit space (ERUS)’ was presented to describe the heterogeneity of localities. Because the spaces with stressful environmental ranges, outside the niche, increased with increasing heterogeneity, available spaces did not continue to indefinitely increase, but the proportion of available spaces in spaces was low at high heterogeneous localities. Consequently, the probability of species occurring in their respective available spaces was unimodal. Due to the presence of large spaces in homogenous localities and more spaces in heterogeneous localities, the interval distances between nonadjacent spaces were large in these localities. Together, the changes in the number and proportion of available spaces and distance between spaces determined the unimodal probability of species dispersing into their respective available spaces. Thus, the probability of species coexisting was unimodal because it is important for coexisting species to grow in their respective available spaces. The probability of population extinction increased with increasing heterogeneity because the available spaces became narrower. In this way, the ERUS strongly influence species richness: a unimodal richness along the heterogeneity gradient occurred in suitable, suboptimal and stressful environments and a unimodal algae richness occurred in a lake and river. These results challenge the viewpoint that richness increases with heterogeneity, providing information about the conservation of richness in very homogeneous and heterogeneous regions, and highlighting the importance of balancing the roles of environment and space in understanding and predicting richness.

Keywords: available space, coexistence, dispersal, extinction, heterogeneity
Introduction

Local species richness patterns reflect the influences of environmental attributes on species coexistence and population distributions (Allouche et al. 2012, Frid et al. 2018, Gong et al. 2019, Liu et al. 2019). Many previous studies have tested the effects of environmental heterogeneity and homogeneity on species richness, and showed that heterogeneity can enhance species richness by allowing the coexistence of more species with different niches (Mellard et al. 2012, Stein et al. 2014, Mandal et al. 2018, Fournier et al. 2020). However, the advantages of heterogeneity often come at the costs of smaller habitat areas and higher impairments to movement and dispersal, which conversely increase local extinctions and decrease richness (Nogues-Bravo et al. 2008, Allouche et al. 2012, He 2012, Hart et al. 2017, Fournier et al. 2020). Because the two metrics of heterogeneity and habitat area (i.e. the number of habitat types and the area of each habitat, respectively) effectively capture different aspects of environmental and spatial influences on species richness (Allouche et al. 2012, Frid et al. 2018, Fournier et al. 2020), balancing these two metrics is crucial to understand, predict and conserve species richness.

Species richness is represented as the number of species per unit space, and the metric that explains the local species richness patterns is often the range of values of one or some environmental factors (e.g. water content of soil from 35% to 45%, air temperature from 25°C to 28°C, salinity of water from 0‰ to 20‰) (Rahbek 1995, Levine and HilleRisLambers 2009, Ben-Hur and Kadmon 2019, Cooper et al. 2020). Based on this, we present the metric of environmental range per unit space (ERUS) to link environment to space, and the environmental range that a particular species prefers is defined as a niche. Here, the environmental range is the difference between maximum value and minimum value of environmental factor. The ERUS and the niche in a study can be determined by the primary environmental factor (e.g. the range of salinity for explaining and predicting the distribution and growth of less- and more-saline tolerant species in a salt marsh), or can be determined by the combination of ranges of some factors. Meanwhile, an actual physical space is defined as an available space when the environmental range of the space matches a niche (i.e. the spaces where the niches are realized). Therefore, the term ‘available space’ is herein considered an actual physical area that constitutes an appropriate habitat for a species. In contrast, some spaces are unavailable when the environmental ranges of these spaces are highly stressful and thus do not match niches (i.e. spaces with stressful environments, outside the niche). With this, the metric ERUS not only describes the heterogeneity but also denotes the relevant information regarding the environmental and spatial features present.

A large ERUS value reflects environmental heterogeneity, a wide environmental range, small available spaces and a high number of available spaces. Note, however, that the number of available spaces does not necessarily continue to increase with increasing values of ERUS because a large environmental range may include acutely stressful environmental conditions, and thus, the proportion of available spaces in spaces should be low at localities with very high levels of ERUS. The interval distances between two nonadjacent spaces for a given species is large in heterogeneous localities because the number of spaces between two nonadjacent spaces is high. A low ERUS reflects environmental homogeneity, a narrow environmental range, large available space and few available spaces. The interval distances between two nonadjacent spaces are also large in homogeneous localities because of the large available spaces.

In this way, the ERUS value reflects the relationship among the number of available spaces, the proportion of available spaces in spaces, the size of the available spaces and the distances between spaces. These factors substantially influence dispersal, population sizes and coexistence of species, which makes ERUS useful for revealing the ecological mechanisms that determine species richness. As such, we predict that when the gradient of heterogeneity is established with increasing ERUS value, species richness will initially increase but subsequently decrease along this gradient, suggesting that both very homogeneous and heterogeneous localities should be the focus of conservation efforts.

Environmental conditions in aquatic environments profoundly impact algal richness (Mellard et al. 2012, Passy and Larson 2019). Nevertheless, environmental parameters in aquatic ecosystems often follow predictable spatial patterns. For example, dissolved oxygen decreases with depth, whereas the concentration of nutrients increases with depth (Muluk and Beklioglu 2005, Mellard et al. 2012). Moreover, the values of aquatic environmental parameters are continuous (Yeager et al. 2011, Massicotte et al. 2015). Consequently, metrics such as environmental range, the spatial frequency of niches, habitat type and environmental fragmentation are not useful for describing aquatic heterogeneity. We argue that inferences regarding the importance of ERUS should be made while considering the potential effects of aquatic heterogeneity on the local species richness patterns of algae.

In this study, a model that reveals the effects of ERUS on species richness was developed to study the general pattern of species richness along the heterogeneity gradient, and the algal richness and ERUS values in a lake and a river were examined to test whether this general pattern occur in real ecosystem or not. The aim was to highlight the importance of linking the environment and space to understand, predict and conserve species richness, and to demonstrate that ERUS is a measurable attribute of growth conditions that provides a spatial dimension to environmental heterogeneity.

Material and methods

Model

Reducing either the number of available spaces or the proportion of available spaces decreases the probability that species occur in their respective available spaces (Chave et al. 2020). Based on this, we present the metric of linking the environment and space to understand, predict and conserve species richness. The aim was to highlight the importance of ERUS should be made while considering the potential effects of aquatic heterogeneity on the local species richness patterns of algae.

In this study, a model that reveals the effects of ERUS on species richness was developed to study the general pattern of species richness along the heterogeneity gradient, and the algal richness and ERUS values in a lake and a river were examined to test whether this general pattern occur in real ecosystem or not. The aim was to highlight the importance of linking the environment and space to understand, predict and conserve species richness, and to demonstrate that ERUS is a measurable attribute of growth conditions that provides a spatial dimension to environmental heterogeneity.
Having fewer available spaces overall, lower proportions of available spaces, and/or larger distances between spaces are strong environmental filters that decrease the probability of species dispersing into their respective available spaces (Bar-Massada 2015, Blanchard et al. 2020). According to the niche theory, it is important for coexisting species to grow in their respective available spaces (Gravel et al. 2006, Levine and HilleRisLambers 2009, Bar-Massada 2015). Thus, fewer available spaces overall, lower proportions of available spaces and larger distances between spaces reduce the probability that species coexist and thereby reduce species richness. Small available spaces increase the probability that populations become extinct (He 2012, Hart et al. 2017, Schuler et al. 2017). Although there may be an exception to the inverse relationship between the number of niches and niche size for small homogeneous localities, which instead have few available spaces and large available spaces, these characteristics still determine the low species richness in such localities. Therefore, unimodal species richness along the heterogeneity gradient established with increasing ERUS value should be the general pattern for local species richness.

Based on previous studies (Chesson and Warner 1981, Chave et al. 2002, McKane et al. 2004, Hubbell 2006, Chisholm and Lichstein 2009, Rybicki and Hanski 2013, Bar-Massada and Wood 2014, Ben-Hur and Kadmon 2019), 10 equations were used to construct the model.

A locality is randomly set. The spaces are in the locality, and the sites are in spaces. One individual occupies a site. Thus, the spatial hierarchy is site-space-locality. The ERUS of a locality is represented by the equation:

\[
\text{ERUS} = \frac{\sum_{j=1}^{n} \frac{|x_j - \bar{x}_i|}{D_{ij}}}{n}
\]

(1)

where \(i\) is a site, \(j\) is the site adjacent to site \(i\), \(x_j\) and \(x_i\) are the environmental values of sites \(i\) and \(j\), respectively; here, the environmental values can be the levels of an important environmental factor or the integration of levels of multiple factors; \(D_{ij}\) is the distance between site \(i\) and \(j\); and \(n\) is the number of sites adjacent to site \(i\).

To be concise, the area of a locality is fixed, and the area is equal among the localities. The environmental minimum and maximum are at opposite ends of the locality, respectively. Thus, the ERUS can be simplified by the following equation:

\[
\text{ERUS} = E_{\text{max}} - E_{\text{min}}
\]

(2)

where \(E_{\text{max}}\) and \(E_{\text{min}}\) are the environmental maximum and the environmental minimum of the locality, respectively.

The number of spaces and the size of a space in a locality is represented by the equation:

\[
E_k = E_{\text{min}} + \frac{v_k}{K} (E_{\text{max}} - E_{\text{min}})
\]

(3)

where \(k\) is a random space in the locality; \(E_k\) is the environmental range of space \(k\); \(v_k\) is the relative location of space \(k\) in the locality and coded 1, 2, 3,……, \(K\). \(K\) is the number of spaces.

When the individuals in space \(k\) die or emigrate from space \(k\), vacant sites are created in space \(k\). Besides the offspring of individuals in space \(k\), immigrants from other spaces could migrate into space \(k\) and colonize the vacant sites. The other spaces and space \(k\) can be in the same locality or different localities. The species composition in space \(k\) over time is represented by the equation:

\[
N_{k,t+1} = (1-m)N_{k,t} + B_{k,t} + I_{k,t}
\]

(4)

where \(N_{k,t}\) and \(N_{k,t+1}\) are arrays of species and individual number. The sequence number of array element is the reference number of species (i.e. a sequence number corresponds to a species), and the value of an array element is the individual number of the species that corresponds to the sequence number of this element. At the end of the simulation, the species richness that immigrants survive in space \(k\) at time \(t\), and thus \(m\) is the proportion of vacant sites in the total number of sites. The term in the brackets is a floor function, and the number of individuals is an integer. \(B_{k,t}\) is the individual number of offspring from time \(t\) to time \(t+1\). \(I_{k,t}\) is the individual number of immigrants from time \(t\) to time \(t+1\).

\[
B_{k,t} = m(1-p_k)N_{k,t}
\]

(5)

\[
I_{k,t} = \max_{m_{ps}} R_{s,k}
\]

(6)

where \(p_k\) is the potential proportion of immigrant individuals in the total individuals in space \(k\) (Eq. 7). The potential number of vacant sites that will be occupied by immigrants is \(m_{ps}\), and the potential number of vacant sites that will be occupied by the offspring is \(m(1-p_k)\). \(R_{s,k}\) is the probability that immigrants survive in space \(k\) (as calculated by Eq. 8–10), \(m\) represents the species with the highest survival probability among the immigrants that disperse into space \(k\), and thus reflects the environmental filter.

The potential proportion of immigrants in space \(k\) is represented by the equation:

\[
p_k = \frac{c}{c + r(J_k / J)}
\]

(7)
where $c$ is the immigration rate, and $r$ is the birth rate of resident species in space $k$; $J$ is the number of sites in the locality, $J_{s_k}$ is and the number of sites in space $k$. A site in a space accommodates one individual.

The survival probability of immigrants in space $k$ is represented by the equation:

$$R_{s,k} = \frac{\left(\sum_{x=1}^{S} D_{s,k}N_{s,k,x} + \sum_{j=1}^{L} D_{s,k}N_{s,j,k}\right)}{\sum_{x=1}^{S} \sum_{j=1}^{L} \left( D_{s,k}N_{s,k,x} + D_{s,k}N_{s,j,k}\right)}F_{s,k}$$  (8)

where $D_{s,k}$ is the probability that a random species $s$ disperses from space $x$ into space $k$, with $x$ and $k$ being in the same locality. $N_{s,k,x}$ is the abundance of species $s$ in space $x$. If some or one individual of species $s$ are/is in a particular locality at time $t$, the movement of the individual(s) in the locality does not change the species richness of this locality at time $t+1$. Thus, $D_{s,k}$ is set as 100%. The random species $s$ may be able to disperse into space $k$ from other localities. $L$ is the number of such localities, and $l$ is a random one of such localities. $D_{s,j}$ is the probability of the random species $s$ dispersing from locality $l$ into space $k$ (as calculated by Eq. 9). $N_{s,j,k}$ is the abundance of species $s$ in the locality $l$. $F_{s,j}$ is the match between the niche of species $s$ and the environment of space $k$ (as calculated by Eq. 10).

The probability of an immigrant $s$ dispersing into space $k$ from the locality $l$ is represented by the equation:

$$D_{s,j} = e^{-\frac{-\left(l-j\right)^2}{2\theta^2}}$$  (9)

where $\theta$ is the migration breadth of species $s$.

The match between the niche of species $s$ and the environment of space $k$ is represented by the following equation:

$$F_{s,j} = e^{-\frac{-\left(c - e_{s,j}\right)^2}{2\sigma^2}}$$  (10)

where $e_{s,j}$ is the niche of species $s$. $\sigma$ is the niche breadth of species $s$.

Two simulation methods were used. We set the maximum ERUS to 10. In the first method, the three levels of ERUS were 7, 4 and 1. According to the ERUS levels, the localities were sorted into heterogeneous, intermediate and homogeneous. There were three environmental stress levels within each locality: suitable, suboptimal and stressful (Table 1). In the second method, the eight levels of ERUS were 0.01, 1, 2, 3, 4, 5, 6 and 7, which indicated that the environments changed from homogenous to heterogeneous. The environmental minimum ($E_{min}$) of each locality was a random value between 0 and 3, and the stress level increased with increasing $E_{min}$. This simulation included random combinations of ERUS levels and stress levels.

The species in each locality were randomly sampled when the model started to run. $J$ was set at 300, and the abundance of individuals in a locality was 300. The species richness $S$ in the simulated ecosystem was also set at 300. The relationship between the number of spaces in a locality ($K$) and the ERUS value was $K=100 \times$ ERUS. Birth rate $r$ was 10, mortality and emigration rate $m$ was 0.25, immigration rate $c$ was 0.2, niche breadth $\sigma$ was 0.3 and migration breadth $\theta$ was 10. Because most species perform well in moderate (suitable) environments (Rohde 1992, Mellard et al. 2012, Mandal et al. 2018), the number of available spaces decreased with increasing environmental stress levels. Moderate environmental ranges were set between 0 and 2, with the range 0–1 containing the highest number of available spaces. The model was run over 1000 time-steps, such that the species richness stabilized by the end of the run. Each ERUS and all possible environmental stress levels from the second method were randomly combined, and therefore more replications were needed to determine the average richness at each ERUS level. Therefore, the number of replications for the first and second methods were 10 and 30, respectively.

R ver. 3.5.1 (<www.r-project.org>) was used to run the simulation. The R code used to run simulations is available as supplementary material. Then, the effect of ERUS on species richness was tested. For the first method, a two-way ANOVA followed by a Tukey's HSD test was used to analyze the effects of ERUS and environmental stress level on species richness. For the second method, a negative binomial regression was used to analyze the relationship between ERUS and species richness. We used a significance level of 0.05 ($p < 0.05$). The statistical analyses were performed using SPSS 19.0 (IBM, USA).

**Investigation**

Ankang Lake (32°36′6.11″N, 108°53′21.26″E), also known as Yingu Lake, is located in Ankang, Shaanxi Province, China, and is in the upper reaches of the Hanjiang River, China, and is in the upper reaches of the Hanjiang River, China.
which is the largest tributary of the Yangtze River. The area of the lake is 38,625 km², and its total capacity is 25.8 × 10⁸ m³, with a mean annual discharge of 190 million m³, a mean annual water temperature of 14–16°C, and a mean annual rainfall of 800–1100 mm. This lake was created by an artificial dam, and our investigation was conducted in the lake and in the river downstream of the dam. The river passes through Ankang city, and the distance between the dam and Ankang city is about 15 km.

Water samples were collected in mid-July from 17 sampling locations in the lake. The distance from the sampling locations to the dam was 1–33 km, with 2 km between each location. Samples were taken from five depth levels at each location, which were epilimnion (0.5 m), metalimnion (2.5, 5 and 10 m) and hypolimnion (20 m). There were 85 sampling sites in the lake. Additionally, nine sampling locations were located in a river downstream of the dam. The distance from the sampling locations in the river to the dam was 1–17 km, with 2 km between each location. The river water samples were taken at 0.5 and 2.5 m depth levels at each location. There were 18 sampling sites in the river. From each sampling site, 1 l of water was fixed with 1% Lugul's solution to identify the algal species, while 500 ml of water was refrigerated at 4°C for subsequent nutrient analyses in our laboratory. Each sample was replicated in triplicate.

Temperature, pH, dissolved oxygen and salinity were measured with a portable water quality analyzer (Hydrolab DS5). Total nitrogen and total phosphorus were measured using a spectrophotometer. The 1 l of water collected for algal species analysis was allowed to settle for 48 h, and then the upper 950 ml of water was removed. Then, 0.1 ml of water was taken from the remaining 50 ml to identify algal species under a microscope.

Principal component analysis (PCA) was used to test the variation in the six measured environmental variables. The first two axes explained 82.67% of the variation in the environmental variables of the lake (PC1 = 58.89% and PC2 = 23.78%) and 81.10% of the variation in the environmental variables of the river (PC1 = 54.46% and PC2 = 26.65%). The PC1 and PC2 values were taken as the weight of each PCA score. The value of the PCA score for each axis was multiplied by its weight, and the two products were added to determine the environmental value for each site.

Each sampling site was treated as the center to construct a locality, and Eq. 1 was used to calculate the ERUS values of 85 localities and 18 localities in the lake and the river, respectively. A cluster analysis was used to sort the localities into three groups in the lake and river. According to these groups, the lake and river were divided into homogeneous, intermediate and heterogeneous parts. The proportion of low-ERUS localities was high in homogeneous parts, the proportion of medium-ERUS localities was high in intermediate parts, and the proportion of high-ERUS localities was high in heterogeneous parts.

A negative binomial regression test was used to evaluate the relationship between ERUS values and algal richness in the lake and river. An ANOVA followed by a Tukey’s HSD test was used to analyze the difference in algal richness among the three regions in the lake and the river. The significance level was set at 0.05. These analyses were performed using SPSS 19.0 (IBM, USA).

### Results

The first simulation showed that the effects of ERUS on species richness were significant (Table 2, Fig. 1). Low, medium and high ERUS values reflected the homogeneity, intermediate and heterogeneity of the environments, respectively. Species richness was highest in the intermediate localities, followed by the heterogeneous localities, and was lowest in the homogeneous localities (Fig. 1). The effects of environmental stress on species richness were significant (Table 2, Fig. 1).

The interactions of ERUS and environmental stress on species richness were significant (Table 2). A medium ERUS intensifies the positive effects of suitable environments on species richness. Mean species richness across homogeneous, intermediate and heterogeneous localities was 100 when the environments were suitable, and this value was 26.58% and 78.57% higher than the mean species richness for suboptimal and stressful environments, respectively (Fig. 1). In comparison, at the intermediate localities, the species richness of suitable environments was 35.23% and 95.08% higher than those of the suboptimal and stressful environments, respectively (Fig. 1). Although species richness was low in stressful environments, the richness of intermediate localities was significantly higher than that of homogeneous and heterogeneous localities, respectively (Fig. 1).

A gradient of heterogeneity was constructed with increasing ERUS values, and the second simulation method revealed a unimodal pattern of species richness along the gradient (Fig. 2). The eight levels of ERUS represented eight localities, and the environmental stress level of each locality was random. When the stress levels were similar among localities, the unimodal pattern of species richness embodied the effects of ERUS on species richness shown by the first method, regardless of whether the stress levels were low, medium or high. When the stress levels were different among localities, however, the unimodal pattern of species richness was the main effect of ERUS on species richness, and the main effects were very strong and were uncorrelated with the effects of environmental stress.

Table 2. Summary of two-way ANOVA of the effects of the environmental range per unit space (ERUS) and environmental stress level on species richness in the first simulation method.

| Source                        | df | F    | p    |
|-------------------------------|----|------|------|
| ERUS                          | 2  | 132.24 | < 0.001 |
| Environmental stress level    | 2  | 484.51 | < 0.001 |
| ERUS × Environmental stress level | 4  | 37.93 | < 0.001 |

Note: p < 0.05 is taken to be significant.
A unimodal pattern of algal richness along the gradient of aquatic ERUS was observed in Ankang Lake (Fig. 3). Because 94% of the hypolimnion sampling localities had low ERUS values that were clustered into the low ERUS level, and because the ERUSs of 97% sampling localities of the metalimnion were clustered into the high ERUS level, the heterogeneity of water in the metalimnion of the lake was the highest, followed by that of the epilimnion, and lastly, that of the hypolimnion (Fig. 4). The algal richness values in the heterogeneous metalimnion and homogeneous hypolimnion were approximately 11.85% and 16.14% lower, respectively, than that of the intermediate epilimnion.

A unimodal pattern of algal richness along the gradient of aquatic ERUS was also observed downstream (Fig. 3). Because the ERUS values of 100% sampling localities in the

Figure 1. The effects of ERUS (environmental range per unit space) and environmental stress level on the species richness. The capital letters indicate significant differences in the species richness among the low, medium and high ERUS localities; the lowercase letters indicate significant differences in species richness among different environmental stress levels. Error bars indicate standard errors and \( p < 0.05 \) is taken to be significant.

A unimodal pattern of algal richness along the gradient of aquatic ERUS was observed in Ankang Lake (Fig. 3). Because 94% of the hypolimnion sampling localities had low

Figure 2. The unimodal pattern of species richness with increasing the ERUS (environmental range per unit space).

Figure 3. The relationship between algal richness and aquatic ERUS values (environmental range per unit space) of localities in a lake (top) and a river (bottom).
section of the river passing through the city (13–17 km from the dam) were clustered into the low level, and because the ERUS values of 100% sampling localities in the river section close to the city (9–11 km from dam) were clustered into the high level, the heterogeneity of the section close to the city was the highest, followed by that of the section close to the dam and, lastly, that of the section passing through Ankang city (Fig. 4). The algal richness in the heterogeneous and the homogeneous sections was approximately 10% and 31% lower, respectively, than that in the intermediate section.

Discussion

In this study, we investigated links between a gradient of environmental heterogeneity and species richness. The environmental heterogeneity simulations with ERUS showed a unimodal pattern of species richness along the gradient. The observations demonstrated that this unimodal relationship occurred between algal richness and heterogeneity gradient of aquatic ecosystem. These results challenge the previous idea that species richness increases with increasing environmental heterogeneity (Mellard et al. 2012, Massicotte et al. 2015, Mandal et al. 2018).

The environmental range that a particular species prefers was defined as a niche; correspondingly, an actual physical space was defined as an available space if the environmental range of the space matches the niche of a species. Thus, when a particular species grows in its available space and the available space is large, the population of the species will also be large and the contribution of the species to the species richness is definite (He 2012, Stein et al. 2014, Hart et al. 2017). When species grow in the spaces where the environment is unsuitable, mortality is high due to environmental stress and competitive exclusion; when the spaces are small, the probability of population extinctions are high. In these cases, the species’ contribution to the species richness is accidental (Tilman 2004, Schwilk and Ackerly 2005, Levine and HilleRisLambers 2009). On the other hand, the basis
for species coexistence is that species grow in their respective available spaces, and coexistence is crucial to species richness in localities (Gravel et al. 2006, Levine and HilleRisLambers 2009, Bar-Massada 2015).

Surprisingly, both high environmental heterogeneity and high environmental homogeneity hinder species growth in their respective available spaces. Because most species prefer moderate (suitable) environments (Rohde 1992, Tilman 2004, Mellard et al. 2012, Mandal et al. 2018), in our study the environmental range continues to increase with increasing values of ERUS, but the number of available spaces may not continue to increase as the proportion of extreme environments increases. Thus, in highly heterogeneous localities, the proportion of available spaces in the total spaces is low. The lower number of available spaces in homogeneous environments and the lower proportion of available spaces in heterogeneous environments both reduce the probabilities that species occur in their respective available spaces. Moreover, the probability that migrants disperse into their respective available spaces declines as the number and proportion of available spaces decrease and the interval distances between spaces increase. Because the distance which individuals can migrate is limited in nature (Chave et al. 2002, Schwilk and Ackerly 2005, Chisholm and Lichstein 2009), the number of individuals of a particular species that disperse into its available space declines with increasing interval distances between its available space and the spaces it presently occupies. Except for in small homogeneous localities, available spaces are large in homogeneous localities, whereas the number of available spaces between two particular spaces is large in heterogeneous localities, both of which can lead to large interval distances between spaces.

In addition to the degree of fit between the environment and the niche requirements of a species, another aspect of available space is the size of the available space because the size profoundly influences the rate of population extinction (He 2012, Hart et al. 2017, Schuler et al. 2017). When the size of the available space is large enough, the population density of the species can reach a saturated (equalized) level. Random environmental fluctuations, emigrations and deaths decrease population density, but the lower the population density, the higher the restoration rate (Tilman 2004, Hubbell 2005). When the space size decreases, the probability of extinction increases because of low population density (He 2012, Hart et al. 2017, Schuler et al. 2017). The available spaces are small in both heterogeneous localities and small homogeneous localities, and therefore, the probability of population extinction is high in those localities.

Soberón and Peterson (2020) define the fundamental niche as the set of environmental conditions for which values of fitness are capable of sustaining populations. They also define the existing niche as the subset of the conditions of the fundamental niche that is actually available to a species, being within its dispersal reach at a given time. Soberón and Nakamura (2009) define the realized niche as the part of the potential niche that the species would actually use, after the effects of competitors and predators are taken into account. In this study, niches are the result of random interactions and interspecific competition, and species compete for space and resources including nutrient, water and light. According to the niche theory, the regular spacing of niches wherein the differences among niches exceeds a threshold, as with limiting similarity created by competitive exclusion, supports the coexistence of competitive winners (Gravel et al. 2006). If the differences of niches between immigrants and residents are high, immigrant niches can exist in the intervals between the niches of resident species; if the degree of niche overlap between immigrants and residents is high, competitive exclusion occurs (Tilman 2004, Gravel et al. 2006). The winner species definitively and stably contribute to species richness. Conversely, if a species is competitively excluded in the spaces in which its niche is realized, the species need not be considered in the ERUS model because such species can only trigger a fluctuation of richness. In this way, the ERUS model implies interspecific competition, niche overlap and resource limits.

Our observations showed that the distribution of the local species richness of algae was unimodal along the gradient of aquatic heterogeneity. Because the gradient of aquatic heterogeneity was constructed according to the aquatic ERUS, the heterogeneity gradient reflected the balanced effects of environment and space. Bar-Massada (2015) defined heterogeneity as the diversity of habitat types, which implies that the size of each habitat type decreases with increasing habitat types. Allouche et al. (2012) defined heterogeneity as the difference in elevation in a locality and showed the environment-related chain of causation from wide differences in elevation to wide environmental ranges, small available spaces and thus high extinction probability. This chain of causation is known as the area-heterogeneity tradeoff. Their results also showed a unimodal species richness distribution along the heterogeneity gradient. Some studies have shown that interactions between environmental gradients and space size drive such unimodal patterns in zooplankton, fish and plants (Paxton et al. 2017, Frid et al. 2018, Gong et al. 2019, Liu et al. 2019). Allouche et al. (2012) conducted a meta-analysis and discovered that empirical data better fit such unimodal patterns than the positive pattern predicted by classical niche theory. These studies demonstrate that when the heterogeneity metric integrates both environment and space, the increase and then decrease of species richness along the heterogeneity gradient should be the general spatial pattern of species richness.

The ERUS integrates environmental factors with spatial ones by linking the levels of an important environmental factor or combination of multiple factors of sampling sites with the relative distances among the sites. A system can be objectively divided into different regions according to the difference between the ERUS values. The differences in ERUS among regions reflect the environmental fragmentation or continuity of the defined ERUS values. ERUS is directly proportional to the environmental range. Together, the ERUS and environmental values reflect the spatial frequency of niches. Thus, the ERUS gives the heterogeneity more context.
In this study, the aquatic ecosystems were divided into homogeneous, intermediate and heterogeneous parts according to their ERUS values and the locations of the sampling localities, a methodological approach that could be useful in the conservation of species richness. There were more low-ERUS localities in homogeneous parts and more high-ERUS localities in heterogeneous parts. Because Ankang Lake suffers little human disturbance, our results should reflect a general pattern for habitat heterogeneity (or homogeneity) among different depths in lakes. The ERUS of the section of the river passing through the city was low, and the ERUS of the river section close to the city was high. This suggests that humans create homogeneous regions and adjacent heterogeneous regions, which decrease species richness. Thus, in addition to the regions with intense human disturbance, the monitoring and management of regions adjacent to human settlements is necessary to conserve species richness.

The effects of the ERUS on local species richness is very strong. The gradient of environmental heterogeneity can be constructed by increasing the ERUS values. While the number of available spaces does not continue to increase along the gradient of heterogeneity, the proportion of available spaces in total spaces and the size of available spaces continue to decrease, and the distances over which species disperse into their respective available spaces first decrease and then increase along the gradient. In this way, the ERUS determines a unimodal pattern of species richness along a heterogeneity gradient in suitable, suboptimal and stressful environments.

Metrics that balance environmental and spatial effects on species richness help elucidate spatial patterns of species richness and indicates that preserving very homogeneous and heterogeneous regions is important for the conservation of species richness more broadly because such metrics can substantially influence dispersal, extinction and coexistence by influencing the number of available physical spaces in which niches are realized, the proportion of available spaces in total spaces, the size of available spaces and the distance between physical spaces.

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Author contributions

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Zong Cheng Ma: Data curation (equal); Methodology (equal); Project administration (equal); Software (equal). Long Tang: Conceptualization (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (equal); Resources (equal); Supervision (equal); Validation (equal); Writing – original draft (equal); Writing – review and editing (equal).

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Data availability statement

All data used in the manuscript are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.h18931zkp> (Zhou et al. 2021).

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