

Research Article

Scale Expansion of Community Investigations and Integration of the Effects of Abiotic and Biotic Processes on Maintenance of Species Diversity

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Information on the maintenance of diversity patterns from regional to local scales is dispersed among academic fields due to the local focus of community ecology. To better understand these patterns, the study of ecological communities needs to be expanded to larger scales and the various processes affecting them need to be integrated using a suitable quantitative method. We determined a range of communities on a flora-subregional scale in Yunnan province, China (383210.02 km²). A series of species pools were delimited from the regional to plot scales. Plant diversity was evaluated and abiotic and biotic processes identified at each pool level. The species pool effect was calculated using an innovative model, and the contribution of these processes to the maintenance of plant species diversity was determined and integrated: climate had the greatest effect at the flora-subregional scale, with historical and evolutionary processes contributing ~11%; climate and human disturbance had the greatest effect at the local site pool scale; competition exclusion and stress limitation explained strong filtering at the successional stage pool scale; biotic processes contributed more on the local community scale than on the regional scale. Scale expansion combined with the filtering model approach solves the local problem in community ecology.

1. Introduction

The maintenance of biodiversity patterns is a core issue in community ecology due to the high extinction rate of global biodiversity [1–3]. However, in researching the influence of various processes on plant diversity, traditional community ecology is generally limited to local processes such as competition, predation, local environment, and mutualism in communities [4–7]. Community ecologists do not consider the regional processes, such as long-distance biogeographical migration, speciation, large-scale extinction, buildup and sorting of species, and climatic differences, among communities [2, 4]. Other ecologists and conservationists have conducted much recent research on the maintenance of plant community diversity, focusing on assessing the relative importance of regional and local processes [8–10]. These studies generally make use of statistical approaches, such as multiple regression or structural equation modeling, and

experimental approaches linking species pool theory, to study the importance of local and regional processes [11].

Regional and local processes are a series of abiotic and biotic processes defined by scale. The community ecologist works to explain species coexistence on a local scale. In contrast, those ecologists and conservationists who consider multiple-scale processes have greatly improved our ability to explain variation in diversity [12]. Community ecologists rarely focus on obtaining an integrated view of how the local- and regional-scale processes affect biodiversity. Studies of multiple-scale processes also lack a systematic integration of those processes based on interdisciplinary knowledge on the different scales. However, to understand the maintenance of biodiversity patterns, there is a need for integration of interdisciplinary theories, research, and approaches [3–13]. Many ecologists have indicated that due to its overwhelming emphasis on the local scale, traditional community ecology has not been able to come up with many patterns, rules,

or a workable continent theory [2, 6, 14–19]. Ricklefs [20] also suggested that the patterns of diversity represent the regional buildup, loss, and sorting of species within a region and that considering the community as a local, interacting assemblage of species that cannot be inclusive of the populations of its component species has hindered progress toward understanding plant diversity on local to regional scales.

Although ecologists have addressed this issue, to date, no specific studies have focused on it. To obtain an integrated view from local to regional scales, the basic premise is clearly expansion of the studied scale in describing an ecological community. Furthermore, the influence of various abiotic and biotic processes on the diversity pattern within the expanded ecological community need to be integrally analyzed using a suitable quantitative method.

A flora subregion is an area delimited by botanists based on the origin of the flora, climate, vegetation pattern, evolution, history, and geography [21–23]. Defining a plant community as a unit on the flora subregional scale allows ecologists to conduct various studies on how regional and local processes shape plant diversity within this expanded community. The expanded community unit includes populations of its component species which are only distributed in that particular flora subregion and are important for the buildup of the zonal plant community. On this larger scale, a filter model approach linked to species pool theory can be used as a tool for the integration of various processes within the expanded community. A species pool is the set of species occurring on a particular scale and the geographical extent of that scale [8, 24, 25]. A series of species pools are nested and linked in terms of species composition. The level of diversity at the smaller pool level is dictated by the selection or filtering by abiotic and biotic processes on species immigrating from its neighboring larger pool level. Strong filters result in low diversity at the smaller species pool level [11, 25].

In this study, we first established the expanded communities on the flora subregional scale in Yunnan province, China, a region which has been recognized as a center of the origin of global plant diversity and a natural laboratory for studies on plant diversity [26–28] (Figure 1). The series of species pools were delimited from regional to successional stage scales in the expanded communities. Plant diversity was evaluated at each pool level, and abiotic and biotic processes, including land area, climate, landform, vegetation, succession stages, density, and biomass, were identified by geographical information system (GIS) 9.2 and direct survey. We established a model based on that of Rajaniemi et al. [11] to quantify the filter effects on species between two neighboring species pools, to assess the contributions of these abiotic and biotic processes to the maintenance of plant diversity pattern, and to integrate these processes from regional to local scales. We addressed three questions. (1) What characteristics will emerge when the local scale ecological community is expanded to a larger-scale (flora subregion) plant community? (2) Can the different contributions of abiotic and biotic processes to the maintenance of plant diversity be identified based on the application of the filter model method? (3) Can this method integrate the abiotic

and biotic processes from regional to local scales to explain plant diversity pattern and solve local problems in traditional community ecology?

2. Materials and Methods

2.1. Assumption. Eleven flora subregions within the Yunnan flora region (Figure 1) were delimited by botanists based on the ecological geographical distribution of flora elements, endemic species, edifiers and dominant species in the zonal vegetation, and the relative similarity in the formation of flora and vegetation [21, 23, 29]. Comparatively, Flora district (a smaller unit than flora subregions) and the Yunnan flora region (a larger unit than flora subregions), as corresponded to administrative division: county and province, were arbitrarily delimited based on the administrative borders of county and province. Thus, we hypothesized the range of the ecological community expanded to a flora subregional scale delimited by natural and ecological processes in Yunnan province ($21^{\circ}8'32'' - 29^{\circ}15'8''$ N, $97^{\circ}31'39'' - 106^{\circ}11'47''$ E, Figure 1). We started with two hypotheses. (1) Provided that we could determine plant diversity, species composition, and various processes affecting plant diversity in each expanded community, that is, each flora subregion in the Yunnan flora region, the characteristics of the scale-expanded plant community relative to the local ecological community (Question 1 in the introduction) could be described. (2) The expanded community included the flora subregion itself, a local site, and a traditional community. These hierarchical ecosystems were defined as flora subregion, local site, and community species pools; the plant species in the flora subregional pool immigrated from the Yunnan flora region pool, those in the local pool from the flora subregional pool, and those in a specific community from the local site pool according to species pool theory [8, 24, 25]. The size of a species pool was dictated by the number of plant species capable of reaching the pool from its larger neighboring pool and selection or filtering by various abiotic and biotic processes at the pool level on these species (Figure 2). Fewer far-reaching species and a stronger filter would lead to a smaller species pool. The difference between a species pool and its larger neighboring pool in species richness and composition due to the filtering by these abiotic and biotic processes on the immigrating species was defined as the species pool effect [11]. If we could determine the actual species number in each pool and the number of plant species capable of reaching it, the species pool effect at each pool level could be quantified. Furthermore, if a measure of these abiotic and biotic processes at each pool level could be determined, using regression of the effect of species pool on these measures, we could identify their different contributions to the buildup of the species pool, that is, the maintenance of plant diversity (Question 2). Based on quantification of the species pool effect and the different contributions of the abiotic and biotic processes to this effect, we could obtain an integration of these abiotic and biotic processes from regional to local scales to explain plant diversity pattern (Question 3).

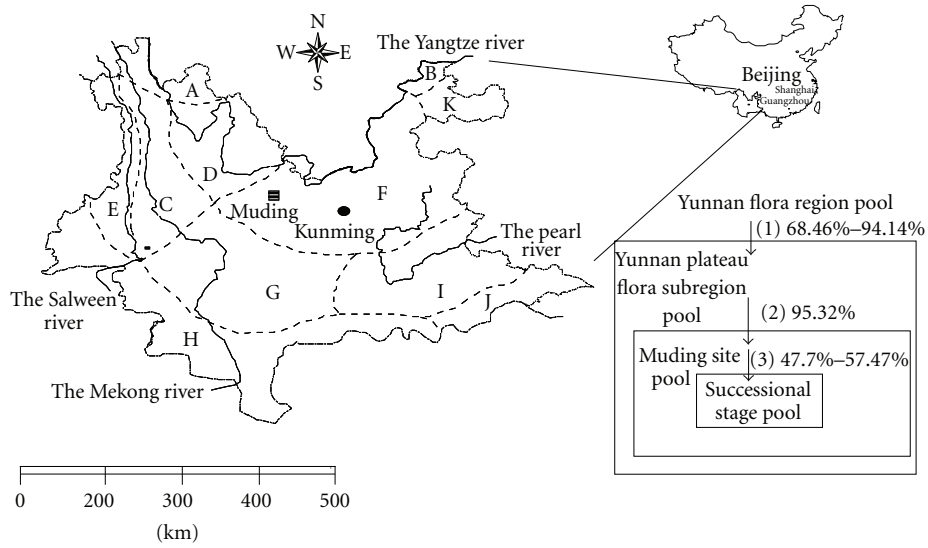


FIGURE 1: Map of the flora region of Yunnan province in China. On the map, all flora subregions are determined as scale-expanded communities. A: Kang-Tibet flora subregion; B: Big-small Liangshang flora subregion; C: Western Yunnan gorge flora subregion; D: Jingshaji river flora subregion; E: Eastern-Himalaya flora subregion; F: Yunnan plateau flora subregion; G: Middle Liangcan-Honghe river flora subregion; H: Yunnan-Burma-Laos border flora subregion; I: Eastern-south Yunnan flora subregion; J: Yunnan-Viet Nam border flora subregion; K: Eastern Yunnan flora subregion. The hierarchical species pools and filters eliminating species from each are summarized in the bottom right-hand corner of the figure. (1) Filter between the Yunnan flora region pool and the 11 flora subregion pools. (2) Filter between Yunnan plateau flora subregion F and the Muding site pool (local pool). (3) Filter between the Muding local pool and successional stage pools. Percentage beside each arrow shows the filter ratio of species between neighboring pools.

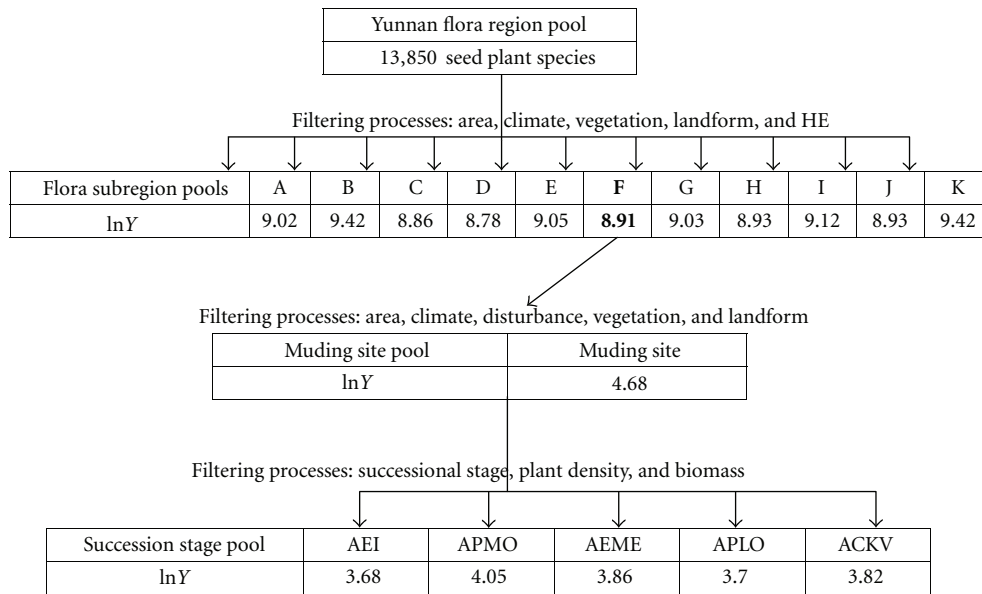


FIGURE 2: Filtering effects (ln Y) on plant species of neighboring large species pool at the Yunnan flora-subregion level, the Muding site pool level, and the successional stage pool level.

2.2. Plant Diversity and the Measures of Different Abiotic and Biotic Processes at Each Pool Level

Yunnan Flora Subregional Pool. In the past ten decades, botanists have extensively researched the flora of Yunnan and recorded 13,850 species of seed plants (nearly 98% of the

estimated species number for the province) and their distribution in *The Inventory of Seed Plants of Yunnan, Yunnan Flora, Yunnan Vegetation* [26, 28]. We first drew up a table with the names of 11 flora subregions (Table 1) and then identified the distribution of each of these 13,850 species across each flora subregion by searching the literature. If

TABLE 1: Calculation of the number of plant species in each expanded ecological community (flora subregion).

Expanded ecological communities ^a	A	B	C	D	E	F	G	H	I	J	K
Species 1	1	0	0	1	0	1	1	0	1	1	0
Species 2	1	0	1	0	0	1	1	0	0	1	0
Species 3	0	0	1	1	0	1	1	0	1	0	1
—	—	—	—	—	—	—	—	—	—	—	—
Species 13,850	0	1	1	0	1	1	0	1	0	0	1
The sum of species number											

^a See legend to Figure 1 for definition of subregions A–K.

TABLE 2: Some characteristics of expanded ecological communities at the flora subregion scale.

Expanded ecological communities ^a	A	B	C	D	E	F	G	H	I	J	K	Total
Species number ^b	3,150	769	3,962	4,368	2,994	3,720	3,085	3,602	2,607	3,597	812	32,666 ^a
Land area (10 ³ km ²)	11.96	4.31	32.62	32.68	16.94	81.63	64.41	67.44	47.18	14.63	10.32	383.21
Climate diversity	4	1	5	5	4	3	3	3	2	3	1	7
Landform diversity	3	3	4	6	2	5	3	6	4	2	3	11
Vegetation diversity	12	6	12	19	12	16	18	31	17	11	7	71

^a See legend to Figure 1 for definition of subregions A–K.

^b Species number includes common species among all flora regions. Excluding this overlap, the number of species is 13,850. We used the number of climate type, landform type, and formation under vegetation type to express climate, landform diversity, and vegetation diversity, respectively.

a certain species was distributed in a flora subregion, it was assigned “1” in the corresponding cell in Table 1; if it was not, it was assigned “0”. Once all 13,850 plant species had been identified, the number of seed plants in each flora subregion, indicating plant diversity in these expanded-scale communities, was summed. Past studies have shown that the overall province has seven climate types (north tropical zone, south subtropical zone, central subtropical zone, north subtropical zone, south temperate zone, central temperate zone, and north temperate zone), 11 landform types (alpine, mid-mountain, low mountain, hill, plain, basin, gorge, asphalt, lake, karst peak cluster, and volcanic landform), and 71 formations among 29 subvegetation types [26, 28–30]. Each expanded-scale community (flora subregion) had different types of climate, landform, and vegetation. We defined the number of climate types, landforms, and vegetation in each expanded community as climate, landform, and vegetation diversity affecting plant diversity (Table 2). To assess these diversities, we digitized a climate delimitation map, landform delimitation map, and vegetation type map of Yunnan province (all different climate, landform, and vegetation types were marked on these maps), superposed them on the Yunnan flora map using GIS 9.2, and determined the number of climate, vegetation, and landform types in each expanded community on the output map from GIS 9.2. We also used the information on flora obtained from our investigation of the literature to demonstrate some of the characteristics of these expanded communities. Among the 11 flora subregions, the Yunnan plateau flora subregion (subregion F in Figure 1) was selected to quantify the species pool effect between the flora subregional pool and the Muding site pool. Flora subregion F has 3,720 seed plants (Table 2). The natural zonal vegetation in the subregion is semihumid evergreen broadleaf forest. Due to intense human disturbance in the 1960s and 1970s, many of the

zonal forests have disappeared, having been replaced by secondary successional stages of the zonal forest, including a shrub-herb community, *Pinus yunnanensis* needleleaf forest, *P. yunnanensis* needle-broadleaf forest, cultivated forests, and fragmented semihumid evergreen broadleaf forests [27, 31, 32].

Muding Site Pool. The set of plant species occurring across all plant communities in the Muding site. The site (101°28′18″E 25°24′09″N) is a local ecosystem within Yunnan plateau flora subregion F, about 200 km from Kunming (Figure 1). All secondary successional stages of semihumid evergreen broadleaf forest are present within the site. These successional stages include AEI (Ass. *Elsholtzia fruticosa* + *Imperata cylindrica*, a typical shrub-herb community), APMO (Ass. *Pinus yunnanensis* + *Myrsine africana* + *Oplismenus compsitus*, a needleleaf forest), APLO (Ass. *P. yunnanensis* + *Lithocarpus confines* + *O. compsitus*, a needle-broadleaf forest), AEME (Ass. *Eucalyptus smith* + *M. africana* + *Eupatorium adenophorum*, a cultivated forest), and ACKV (Ass. *Cyclobalanopsis glaucoides* + *Keteleeria evelyniana* + *Viola duelouxii*, a fragmented semihumid evergreen broadleaf forest). The number of plant species in the pool was determined by vegetation survey: three 10 × 40 m plots were established in representative stands for each successional stage. We recorded all arboreal species and counted the number of individuals of each species. In each plot, four equally spaced 4 × 4 m subplots in the shrub layer and four equally spaced 1 × 1 m subplots in the herb layer were established along a diagonal line bisecting the plot. Species in these subplots were also recorded and the number of individuals of each species counted. The above-ground biomass of each herb layer subplot was harvested, dried in the laboratory, and weighed. The total area sampled in the vegetation survey was 7,020 m². We recorded a total of 252 seed plant species. The

land area at the site is 3.21 km², with one-third of it being arable land. The site is dominated by one climatic type and one landform type, and the climate and landform diversities are 1.

Successional Stage Pools. The set of plant species occurring in each of the secondary successional stages within the Muding local site pool. The data for the measure of filter processes are presented in Table 3.

2.3. Assessing the Effect of Species Pool and Analysis. We established (1) to quantify the effect of species pool between any two neighboring pools

$$\ln Y = \frac{\ln (X_i - X_{pi})^2}{X_{pi}}, \quad (1)$$

where $\ln Y$ is the effect of species pool; X_i is the observed richness of the i th species pool at a given species pool level; X_{pi} is the predicted richness of the i th species pool, that is, the number of species theoretically capable of reaching the i th species pool from its larger neighboring species pool. Plant species in the Yunnan flora region are able to reach all flora subregions, the Muding site, and successional stages by immigration, because they are all linked, without sea or obvious geographical isolation although high mountains and deep valleys may, to some extent, limit long-distance emigration [26, 27]. Thus, we used the number of species in the larger neighboring species pool from which the i th species pool was built by immigration of plant species to express X_{pi} . Large $\ln Y$ indicated a strong effect of species pool or a strong filter; that is, there are a large number of plant species that do not colonize at the given pool level due to limitation by various processes, simultaneously indicating low diversity. In the equation, X_{pi} is always greater than X_i , because there are always abiotic and biotic processes filtering species from the larger neighboring pool, causing a decrease in plant species richness at the smaller pool level. Thus, $\ln Y > 0$. X_i at a particular species pool level is a group of stochastic variables that are independent of each other. They obey a normal distribution $N(0, 1)$. So, we can transform (1) into (2) to assess the difference between observed species number, X_i , and predicted species number, X_{pi} , based on a statistical goodness of fit test [33, 34]

$$X^2 = \sum \ln Y = \frac{\sum \ln (X_i - X_{pi})^2}{X_{pi}}, \quad (2)$$

where X^2 is a X^2 function. Generally, the X^2 function is of the form $X^2 = \sum (X_i - X_{pi})^2 / X_{pi}$. Log transformation of $(X_i - X_{pi})^2 / X_{pi}$ can produce a calculated X^2 within a reasonable range. The X^2 test can be conducted with small samples even a single sample to test the observed versus predicted difference [33, 34]. The significance level based on X^2 and n was determined by consulting a quantile table. A confidence level of 0.95 ($\alpha = 0.05$) was selected as the indicator of significance.

All abiotic and biotic processes occurring at the smaller pool level commonly contribute to the filtering of plant

species from its larger neighboring pool (Figure 2). We considered that the filtering between the Yunnan flora region pool and the Yunnan flora subregion pools was dictated by land area, diversity of climate, landform, vegetation, and HE (historical and evolutionary) processes at the Yunnan flora subregional level to create the different diversities in these flora subregions (Table 2 and Figure 2). Human disturbance (such as land reclamation in historical farming) and biological interaction (such as invasion at the regional scale) were taken as parts of HE processes, because they had a long-term effect on diversity. Therefore, regression between $\ln Y$ and the measure of each process was used to identify the relative importance of that process in the maintenance of diversity. However, although land area, and diversity of climate, landform, and vegetation could be quantified (Table 2), HE could not. Statistical theory shows that if a system is controlled by known and defined processes, the total variance of the regression of the dependent variable on all processes equals 1 [34]. Past studies have shown that land area, climate, landform, vegetation, and HE constitute nearly all of the processes impacting plant diversity on a regional scale [8, 9, 11, 35, 36]. Thus, the total variance of the regression of $\ln Y$ on all of these processes can be determined as 1. The variance of the regression of $\ln Y$ on those processes, not including HE, must, therefore, be less than 1. The contribution of HE to the total variance must be that part making the total variance less than 1. Thus, (3) can be used to assess the role of HE in the maintenance of plant diversity

$$\text{HE}(\%) = (1 - R^2) \times 100, \quad (3)$$

where R^2 is the regression coefficient (multivariable) of $\ln Y$ on land area, diversity of climate, landform, and vegetation at the flora subregional pool level.

The filter on plant species of the Yunnan plateau flora subregion pool at the Muding site pool level might be mainly due to land area, diversities of climate, vegetation and landform, and disturbance, under the conditions of the similar HE; the filter on plant species of the Muding site pool at the successional stage pool level might be mainly due to different successional stages, plant density, and biomass under the conditions of the same survey area, climate, landform, and soil type [8, 9, 11, 35, 36]. Similarly, the regression analysis between $\ln Y$ and the measure of each process at the two species pool levels can identify the relative importance of these processes in the explanation of diversity pattern. Analysis of variance (ANOVA using SPSS V15) was used to test the significance of the regression relationship. A greater R^2 and high degree of variability in the regression indicates higher contribution to explaining the effect of species pool. Among these processes, successional stage was a qualitative index. We assigned 1, 2, 3, 4, and 5, respectively, to stages AEI, APMO, AEME, APLO, and ACKV, to quantitatively conduct the regression of $\ln Y$ on the measure of successional stage as a filtering process; $\ln Y$ at a particular stage corresponded to the value assigned to that stage.

TABLE 3: Parameters reflecting the measures of filter processes in successional-stage species pools.

Successional stage pool	AEI	APMO	AEME	APLO	ACKV	F-value	P value
Species richness ^a							
Tree	5 ± 2	10 ± 3	9 ± 3	24 ± 5	36 ± 5	2.98	0.040*
Shrub	21 ± 7	14 ± 5	21 ± 6	24 ± 9	19 ± 6	2.43	0.006**
Herb	46 ± 10	30 ± 7	27 ± 8	25 ± 9	23 ± 5	3.15	0.005**
Plant density (stem·m ⁻²)							
Tree	0.05 ± 0.01	0.38 ± 0.18	0.15 ± 0.03	0.34 ± 0.09	0.66 ± 0.17	11.70	0.001***
Shrub	2.15 ± 0.34	2.08 ± 0.52	3.15 ± 0.47	2.55 ± 0.28	2.87 ± 0.39	2.46	0.003**
Herb	152.1 ± 32.50	208.3 ± 28.77	215.2 ± 29.16	199.3 ± 31.82	72.09 ± 9.27	3.72	0.001***
Above-ground biomass of herb plants (kg·m ⁻²)	161.6 ± 97.90	26.59 ± 8.71	32.01 ± 6.68	12.80 ± 4.51	50.54 ± 14.96	3.05	0.002**

^a Species richness, plant density, and biomass are expressed as $\mu \pm$ s.d. Species richness is the number of plant species in the plots, and the number of different species in each successional stage for the calculation of the effect of species pools, ln Y, are 152 (AEI), 132 (APMO), 143 (AEME), 151 (APLO), and 142 (ACKV).

*,**,*** Significantly different among succession stages at α levels of 0.05, 0.01, and 0.001, respectively.

3. Results

3.1. Characteristics of Scale-Expanded Plant Community.

Once the flora subregions had been determined as expanded ecological communities, there were 11 ecological communities in Yunnan province of China. Each community had a different number of plant species (Table 2). These seed plants belonged to 266 families, 2,047 genera, making up 88.3% and 68.5%, respectively, of the total number of families and genera in China. Among them, 108 genera and more than 1,000 plant species were endemic to Yunnan. These endemic plants were found mainly in flora subregions A, C, D, E, and J. Land area obviously differed among these flora subregion communities, and there were different numbers of climate types and landform types in each. Vegetation diversity is high in Yunnan province: ecologists have recorded 29 subvegetation types and 71 formations. These subvegetation types include some typical vegetation, such as humid tropical rainforest, seasonal rainforest, mountain rainforest, deciduous monsoon forest, semihumid evergreen broadleaf forest, needleleaf forest, and shrub-herb vegetation. Form. *Parashorea chinensis* and Form. *Dipterocarpus tonkinensis*, *Hopea mollissima*, and *Crypteronta paniculata* were recognized as the mark of a tropical forest. Flora composition presented contrasting differences among these expanded ecological communities (see Supplemental materials, which is available online at doi:10.115/2011/596508). There were many endemic species and some geographical substitutions in species distribution. Here, we define flora composition, the number of families and genera, the number of plant species, and natural geography and environment as community characteristics aside from the local community characteristics such as individual density, frequency of species occurrence, biomass and production, and degree of importance of each species once the local community has been defined on the flora subregion scale.

3.2. Contributions of Ecological Processes to the Effect of Species Pool. The filter of land area, climate, vegetation, landform, and HE processes on species in the Yunnan flora region

pool created 11 Yunnan flora subregional pools. The filter effects (ln Y) from the Yunnan flora region pool to each of the flora subregion pools ranged from ca. 8.78 to 9.42 (Figure 2), leading to a 68.46% to 94.14% reduction in species (Figure 1). The difference between observed and predicted species number at that level was very significant based on X^2 test ($X^2 = 99.47$, $n = 11$, and $P < 0.0001$). Among them, the big-small Liangshang flora subregion (Figure 1 (B)) and the Eastern Yunnan flora subregion (Figure 1 (K)) underwent a much greater filter effect than others (Figure 2), reducing species richness by 94.45% and 94.14% (Figure 1), respectively, relative to the expected richness if no filters had been operating. Conversely, the Western Yunnan gorge flora subregion, C, and Jingshaji river flora subregion, D, underwent a weaker filtering effect. The contribution of the various processes to filtering differed (Table 4). Climate made the greatest contribution according to the regression analysis. Vegetation and land area played an intermediate role in the filtering, and landform played the smallest role. The multivariable regression of ln Y on land area, climate, and vegetation diversity presented $R^2 = 0.893$, and HE processes amounted to 10.70% (Table 4). This indicated that land area, climate, and vegetation diversity explain more than 80% of the variation in the maintenance of plant diversity and HE only explains about 11%.

The filter effect, ln Y, between Yunnan plateau subregional pool F and the Muding site pool (subregion pool to local pool) was 4.68, significantly smaller than that from the Yunnan flora region pool to each of the flora subregional pools (Figure 2), but the difference between observed and predicted species numbers at that level was still significant ($X^2 = 4.68$, $n = 1$, $P < 0.05$). The filter reduced species richness by 95.32% (Figure 1). There was only one climate type and one kind of landform within the Muding site and one-third of the land was arable at the local site pool level. Diversity of climate and landform was much lower than that at the subregion pool level, but human disturbance was strong (regression analysis could not be conducted at the level).

TABLE 4: The respective regression of species pool effect, $\ln Y$, from Yunnan flora region pool to flora subregion pools, on land area, climate, vegetation, and landform diversity in these subregion species pools, the multivariable regression, and HE.

Process impacting filter	Regression model ^a	<i>n</i>	<i>R</i> ²	<i>F</i> -value	<i>P</i> value
Land area (x_1 , km ²)	$y = -0.147 \ln(x_1) + 9.515$	11	0.428	6.726	0.029
Climatic diversity (x_2)	$y = -0.344 \ln(x_2) + 9.389$,	11	0.861	55.554	0.000
Vegetation diversity (x_3)	$y = -0.326 \ln(x_3) + 9.887$	11	0.522	9.841	0.012
Landform diversity (x_4)	$y = -0.215x_4 + 9.312$	11	0.156	1.659	0.230
x_1, x_2, x_3	$y = 9.549 - 0.002x_1 - 0.120x_2 - 0.004x_3$	11	0.893	19.406	0.001

^a $y = \ln Y$, $x =$ process impacting filter. Climatic diversity, vegetation diversity, and landform diversity are indicated by the number of each type of climate, vegetation, and landform in an expanded community, that is, flora subregion. In multivariable regression model, landform diversity was excluded due to low R^2 . HE (%) = $(1 - 0.893) \times 100 = 10.70$.

The $\ln Y$ from the Muding site pool to the successional stage pools was low, only reducing Muding site species richness by 47.70% to 57.47%. The $\ln Y$ was greatest in APMO and smallest in AEI (Figure 2). X^2 test also demonstrated the difference between observed and predicted numbers of species ($X^2 = 19.11$, $n = 4$, $P < 0.01$, but if we, resp., tested the filter on plant species of local Muding site pool at AEI, APMO, APLO, AEME, or ACKV, X^2 corresponding to AEI, APLO, and ACKV was less than 3.841, no significant at 0.05 level, Figure 2). These successional stages within the Muding site presented the same abiotic conditions, such as sample area, climate, and soil type. However, the biotic conditions, such as successional stage, plant density, and biomass, differed among successional stages. The regression analysis presented a quadratic relationship between $\ln Y$ and plant density in different layers along these successional stages and between $\ln Y$ and above-ground biomass in the herb layer (Table 5). However, the relationship between $\ln Y$ and successional stages showed a liner decreasing trend except for the herb layer. Successional stages in the tree layer and plant density in all layers were most important in explaining plant diversity.

4. Discussion

Ecologists define communities as units, generally populations of different species living within a specified location in space and time [2]. These units are fixed in the hierarchy organism-population-community-ecosystem-landscape-biosphere [37]. However, traditional community ecology mainly pays attention to the influence of species interactions, such as competition, predation, and mutualism on diversity on a local scale [6, 7], leading to communities which do not encompass most of the populations of their component species [2]. The scale expansion of ecological community to flora subregion allows the inclusion of most of the populations of component species and is fixed in the organism-population-community-ecosystem-landscape-biosphere hierarchy, constituting a complete system of ecology. Similarly, the scale expansion of ecological community to flora subregion sets community ecologists' studies on an objective scale delimited according to identical or similar flora, endemic species, geographical and climatic regions, vegetation, HE processes, and so on [21–23, 29]. In the

expanded community, ecologists can study elements of the flora, endemic phenomena, evolutionary history, species composition, vegetation, climate, and topographical diversities, or fully use findings from the literature, as well as species interactions, such as competition, predation, and mutualism on a local scale to explain plant diversity pattern on different scales. All these can demonstrate community characteristics after the local-scale ecological community is expanded to a larger-scale (flora subregion) plant community.

We identified climatic diversity as making a greater contribution to the maintenance of plant diversity on the flora subregional pool level than land area, vegetation, or landform diversities using the filter model method following scale expansion of the ecological community. The effect of climate can be explained by interspecific competition theory: some species win under a particular climate type in interspecific competition and other species win under other climatic types in a flora subregion; if there are diverse climates in that region, it can hold more species [38–42]. In essence, this is because unsuitable climate can cause plants to die, thus changing species composition and richness in plant communities [13]. Increases in land area can result in high diversity if each flora subregion is regarded as a separate island [38]. However, an increase in land area alone, with no parallel increase in resource diversity such as climate type, cannot lead to higher diversity: this becomes clear when comparing flora subregions A, C, D, and J with E, G, H, and I for these two processes (Table 2). Thus, climatic diversity is a more important factor than land area. Honnay et al.'s [43] local study also presented, for most of the species groups, patch area, which is usually a redundant variable in explaining species richness relative to resource diversity. The relationship between plant diversity and vegetation diversity is identical with that between plant diversity and climatic diversity, because diverse climate can facilitate the development of different vegetation types, containing different species. Diverse landform represents complex landform. Complex landform theoretically limits the long-distance immigration of species, leading to a decrease in plant diversity [44, 45], but regression showed a weak negative relationship between $\ln Y$ and landform diversity. This may be because complex landform changes the climatic regime occurring in a range of longitudes and latitudes and creates climatic diversity, which is advantageous

TABLE 5: The regression relationship between $\ln Y$ and, respectively, plant density, herb above-ground biomass, and successional stages at the plot level.

Process impacting filter	Regression model ^a	<i>n</i>	<i>R</i> ²	<i>F</i> -value	<i>P</i> value
Plant density (stem · ha ⁻¹)	$y = 8.80E - 006x^2 - 0.008x + 3.619$ (tree layer)	15	0.506	6.157	0.014
	$y = 0.015x^2 - 0.231x + 3.216$ (shrub layer)	60	0.340	14.456	0.000
	$y = 4.63E - 006x^2 - 0.003x + 3.805$ (herb layer)	60	0.325	10.602	0.000
Above-ground biomass (g · m ⁻²)	$y = 1.07E - 005x^2 - 0.003x + 3.608$ (herb layer)	60	0.135	3.347	0.045
Successional stages	$y = -0.4569x + 3.7729$ (tree layer)	15	0.5664	16.994	0.001
	$y = -0.2632x + 1.7585$ (shrub layer)	60	0.033	1.531	0.222
	$y = 0.0439x^2 - 0.1889x + 2.8064$ (herb layer)	60	0.0913	2.209	0.122

^a $y = \ln Y$, $x =$ process impacting filter.

for plant diversity. A similar impact of landform on plant diversity of managed grasslands was reported in the Alps and in an Ecuadorian mountain rainforest [46, 47].

Ecological systems are dynamic on evolutionary scales of time and space and the processes on all temporal and spatial scales contribute to shaping ecological systems at all levels [2, 48, 49]. It is difficult to precisely quantify the contribution of HE processes [2, 50]. We tried using a simple statistical model for this purpose. Results showed that HE could explain about 11% of the variance in the filtering effect at the flora subregion scale. HE processes reflect the impact of past ecological processes (on a geological time scale) on current plant diversity [20, 51]. Theoretically, their contribution to the maintenance of plant diversity is expected to be greater than 11%, perhaps 20% to 30% of the total. However, this is still small based on the result calculated using (3). This shows that relatively similar HE processes among flora subregions may be playing a role in the formation of plant diversity pattern. This may be because the different species assemblies and flora in the previous regions corresponding to these flora subregions evolved similarly due to the impact of identical changes in geographical pattern. After all, all subregions' geographical patterns were shaped by the rise of the Himalayan mountain system dating back about five hundred million years, and there are a large number of common species among the 11 flora subregions (Table 2). The similar long-term anthropogenic activities, that is, identical production and culture methods, among these flora subregions may also be related to the small contribution of HE processes [28]. Due to their complexity, HE processes are usually ignored in attempts to explain the maintenance of plant diversity [52, 53]. However, an integral assessment of the role of various processes in the maintenance of plant diversity requires that ecologists quantitate the effect of HE processes, as was attempted here. Such an assessment also highlights the greater importance of climate, vegetation diversity, and land area, as key processes in the maintenance of the current diversity pattern in a regional ecosystem [14, 25, 50].

The filter between the Yunnan plateau flora subregion pool and the Muding site pool is related to the diversity of climates, vegetation and landforms, land area, and disturbances. High climate diversity must lead to the coexistence of many species that can adapt to different climatic types.

High vegetation and landform diversity can create high habitat heterogeneity, bringing about plant diversity, but the diversities of climate, vegetation, and landform at the Muding site pool level are much lower than those at the flora subregion pool level. Land area is also much smaller, and thus holds few species. In addition, one-third of the Muding site was covered by arable land. By comparison, Xishan reserve in Kunming city, next to the Muding site, which is similar to the latter in land area, climate, vegetation type, and landform but has not been subjected to any obvious human disturbance, contains about 1,000 species, four times the number at the Muding site pool and one-third of the species found in Yunnan plateau flora subregion pool F with its three climatic types [28]. This indicates the great effect of climate diversity and disturbance on the filtering of species. With respect to the filtering process between the Muding site pool and the successional stage pool, it may be driven by microenvironmental effects, stress limitation, and competition exclusion, because successional stages and plant density had the major impact in the species pool effect under the conditions of the same survey area, climate, landform, and soil type (Table 5). Key and dominant species were different among the successional stages, causing changes in the microenvironment [54, 55]. The different microenvironments, such as shading, soil water, and nutrient conditions, are closely related to the filter on immigrating species from larger species pools [25]. In addition, a strong filter at high plant density may be related to increasing density of the dominant species, excluding subordinate species in interspecific competition [56]. However, a strong filter at low plant density may be due to environmental stress, for example, unproductive lands [55], in which many species cannot endure and are, therefore, excluded, and the abundance of plant individuals in the plant community is low [57]. The relationship between the species pool effect and biomass is identical to that between the effect and plant density in low and high plant density stages, because competition and stress equally occur in high and low biomass stages [58].

The above-mentioned findings and analyzes indicate that the different contributions of abiotic and biotic processes to the maintenance of plant diversity can be identified based on the application of the filter model method in species pool theory. Species pools are related to the number of species,

the scale of the ecosystems containing these species, the similarity in habitat, and HE processes [8, 24, 25]. Pärtel et al. [25] defined species pools as regional, local, and community pools (traditional community), that is, the set of species existing, respectively, in the region, the local landscape, and the target community. Abiotic and biotic processes can filter species from a large pool to create the next smallest neighboring pool [9, 59, 60]. Plant diversity is closely related to environmental resources, but other processes also play a large role [38–40]. A convincing interpretation of plant diversity pattern requires the integration of various aspects. In scale-expanded communities, the filter model can be used to analyze the relationship between the filtering effect on plant species and each abiotic or biotic process at different species pool levels, from regional to local, to reveal the mechanism underlying the diversity. This method provides a vertical link between different species pools so that these abiotic and biotic processes can be integrated to explain plant diversity pattern at all different scales (Figure 2). This combines the understanding of diversity maintenance on regional and intermediate scales with the traditional studies performed on a local scale by community ecologists. Thus, the scale expansion of ecological community to flora subregion and the application of a filter model solve the problem of “localness” that exists with the traditional communities. Ecologists are able to completely explore the mechanism explaining plant diversity, to generate a variety of patterns, processes, rules, and a workable continent theory [18].

5. Conclusions

The number of plant species, the quantitation of abiotic and biotic processes, and the effect of species pool at different species pool levels can be determined to integrate the abiotic and biotic processes affecting plant diversity. We found that the processes that are important for one pool level are not important at another pool level in the maintenance of species diversity. Effects of abiotic processes gradually weaken with decreasing scale. The scale expansion of ecological community and the application of the filter model provide an integrated view of the local- and regional-scale assessment of abiotic and biotic processes on the maintenance of ecological diversity. A community at a regional scale and an interdisciplinary integration using floristics, GIS, vegetation ecology, and geography reveal more about the processes that lead to diversity patterns than a local community.

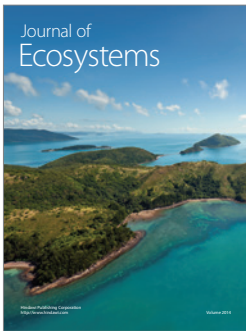
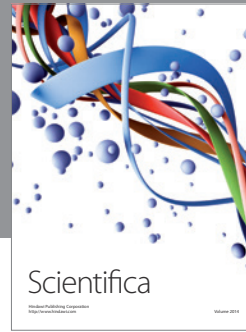
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