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The Process of Patchy Expansion for Bamboo (*Phyllostachys edulis*) at the Bamboo–Broadleaf Forest Interface: Spreading and Filling in Order

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Abstract: Bamboo (*Phyllostachys edulis*) expansion to native adjacent forests has become an increasingly serious problem; however, expansion patterns of bamboo are still lacking research, especially at a community scale. Quantitative research on bamboo expansion patterns plays a significant role in understanding the bamboo expansion process, as well as expansion prevention and control. We analyzed the change in expansion pattern, expansion index, and expansion rate of bamboo in the bamboo-broadleaf transition zone sample plots, specifically from 2017 to 2021 and from the bamboo forest (representing the late stage of bamboo expansion) to the bamboo expansion front (representing the early stage of bamboo expansion). We found that the expansion of bamboo is a patchy expansion, including inner filling patch, boundary expanding patch, transboundary leaping patch, expansion–infill mixed patch, and stationary patch. From the early stage of bamboo expansion (year 2017 and bamboo expansion front) to the late stage of bamboo expansion (year 2021 and bamboo forest), the type of bamboo expansion patches transitioned from boundary expanding patch to inner filling patch and boundary expansion–inner infilling mixed patch. Additionally, the expansion rate of bamboo showed a declining trend. From 2017 to 2021, the bamboo forest (position of 0–20 m) and expansion front (position of 60–80 m) declined by 0.53 m/2a and 0.47 m/2a, respectively. Our research reveals that bamboo expansion exhibits a patchy expanding process, characterized by a sequence of "first spreading outward and then filling inward", whether viewed from the type of expansion pattern or the expansion rate. This process involves continuous plaque addition, expansion, merger, and filling to complete the expansion of a bamboo population. These findings provide valuable insights into the process of bamboo expansion and have important implications for the management and control of bamboo forests.

Keywords: patchy types; expansion pattern; expansion index; expansion rate; shape index; bamboo (*Phyllostachys edulis*)

Citation: Zeng, X.; Luo, H.; Lu, J.; Zhu, X.; He, Y.; Gong, C.; Ren, Z.; Huang, D.; Song, Q.; Yang, Q. The Process of Patchy Expansion for Bamboo (*Phyllostachys edulis*) at the Bamboo–Broadleaf Forest Interface: Spreading and Filling in Order. *Forests* **2024**, *15*, 438. https://doi.org/10.3390/f15030438

Academic Editor: Bruno Foggi

Received: 18 January 2024
Revised: 22 February 2024
Accepted: 22 February 2024
Published: 25 February 2024

1. Introduction

Bamboo (*Phyllostachys edulis*), a giant strong woody grass, has an important ecological, economic, and cultural value [1]; therefore, bamboo has undergone extensive cultivation. However, bamboo, as a typical expansive species [2], possesses a robust rhizome system and grows rapidly [3–5]. These intrinsic strengths enable it to encroach unchecked into adjacent forests [6,7]. The 9th National Forest Inventory in China confirmed the expansion of bamboo-dominant areas, with the total bamboo area increasing from 3.00 Mhm^2 in 1972 to 6.41 Mhm^2 in 2018 [8]. Bamboo spreads uncontrollably to the surrounding forests, which seriously hinders the growth of trees and the regeneration of new saplings, resulting in a simplified community structure [9] and reduced diversity of the plant [7]. Additionally, the expansion of bamboo has increased soil pH [10], changed terrestrial water and nutrient cycles [11,12], affected soil microbial community structures [13], and so on. In recent years, considerable research has been carried out on the process of bamboo expansion [14,15] and the mechanism [14,16,17] and the expansion effects [4,18,19]. However, there is a lack of research on the bamboo expansion processes and patterns, which hinders the understanding of the bamboo expansion process and the research on expansion prevention and control.

Some studies have been carried about the process and pattern of bamboo expansion. For example, Kiyoshi et al. (1996) [20], Isagi and Torii (1997) [21], and Ding et al. (2006) [22] analyzed the expansion distance and patch number of bamboo in Kyoto, Japan and Hangzhou, China respectively. These studies made use of aerial photographs and remote sensing data to conduct the analyses. They indicate that the prevalence of bamboo expansion and the expansion pattern at the landscape scale (10 km^2), but at the community scale, bamboo primarily expands through vegetative reproduction (clonal growth) [23,24]. Specifically, mature (mother) culms provide nutrients to the rhizomes, fostering the formation of new culms (Figure 1), and via culms, the plant moves forward step by step and block by block and gradually occupies the space to realize its expansion. Therefore, to gain a better understanding of the bamboo expansion process, uncover its expansion mechanism, and develop effective control measures, we should understand the pattern and process of bamboo expansion from the community scale on the basis of individuals.

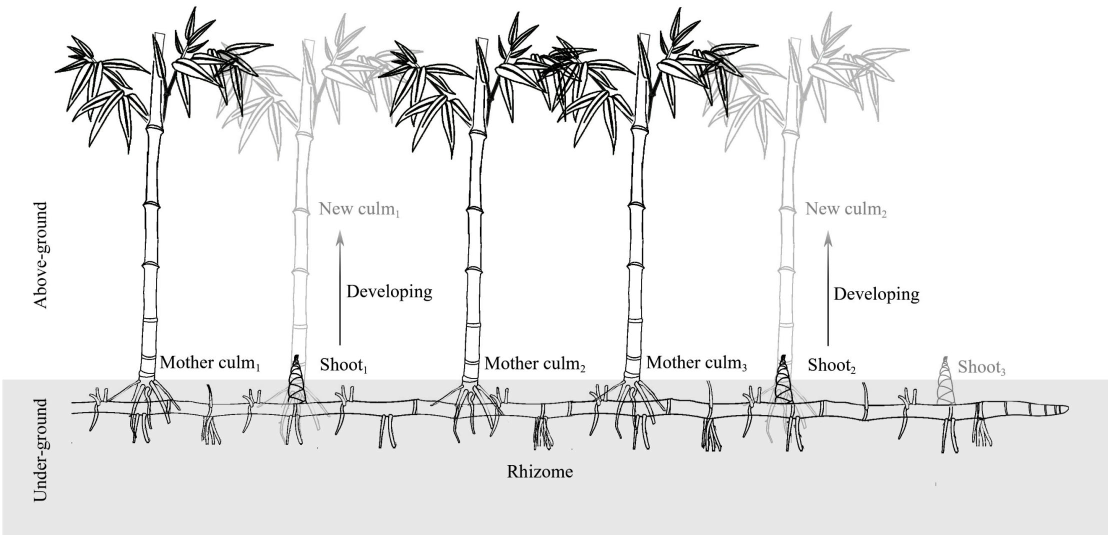

Figure 1. Diagram of vegetative reproduction (clonal growth) of bamboo. Black indicates the current stage of the mother culms and shoots, and gray represents the future formation of new culms and shoots (The distance between the shoot and the mother culm typically ranges from a few decimeters to a few meters).

The bamboo-broadleaf forest transition zone refers to the area where bamboo forests and evergreen broadleaf forests meet. The two ends of this zone are evergreen broadleaf forests or bamboo forests, and the middle is the expansion front. In zones where bamboo expansion is most active, community structure changes most rapidly, and the transition from a broadleaf forest to a bamboo forest is most significant, so it has become an important area for bamboo expansion research [25–27]. In this area, due to increased forest fragmentation caused by factors such as clonal growth of bamboo forests and community disturbance, bamboo demonstrates an epitaxial expansion process [25]. Bamboo expansion involves both spatial expansion and an increase in the number of culms [5,15,22], which includes spatial expansion scales and expansion patterns. The expansion scale is determined by the number and area of new culm patches and mature culm patches, which could be quantitatively described by the expansion index.

The expansion pattern refers to the spatial combination of the mature culm and the new culm, which is of great significance to understanding the bamboo expansion process. Isagi and Torii [21] propose from a landscape-scale perspective that new culms are consistently at the forefront of bamboo forests, expanding from the inside out. However, our perspective suggests that bamboo may first spread outward and then fill inward. Because the growth of new culms requires the mother culms to provide a lot of water and nutrients via underground rhizomes [28], this inevitably brings nutrient and energy losses to the mother bamboo plant. These losses primarily include the consumption of material transfer between new and mature culms, the consumption of new culm growth, and the consumption of rhizome growth [29]. As the distance between the new culms and the mature culms increases, the energy required to transport nutrients and maintain the growth of rhizomes increases. Therefore, when bamboo expands outward and occupies a new plot, it will fill the interior with new culms, thereby reducing the cost of nurturing new culms. Once the new culms are established, they can provide nourishment back to the mother culms and the next generation, enabling further outward expansion to occupy additional plot.

Subtropical natural reserves are mostly suitable habitats for bamboo, and the expansion, through vegetative reproduction (clonal growth), of bamboo in these areas is becoming increasingly severe [22,30–32]. Among them, the Qiyunshan National Nature Reserve (QNNR) located in Chongyi County, Jiangxi Province, China, is known as the hometown of bamboo. The area covered by bamboo forests in this reserve accounts for approximately 17% of the total protected area [33]. It serves as an ideal experimental platform for studying the process and patterns of bamboo expansion at the community scale and for quantifying its expanding rate. Therefore, we selected a representative bamboo–broadleaf transition zone in the QNNR as a research site. Our aim was to test the hypothesis that the pattern of bamboo expansion is first spread outward and then filled inward. Testing this hypothesis illuminates the process and pattern of bamboo expansion into broadleaf forests, offering crucial reference points for controlling bamboo forest expansion.

2. Material and Methods

2.1. Study Species

Bamboo (*Phyllostachys edulis*), a tree-like bamboo species of Poaceae with height of 10–20 m, is naturally distributed in warm temperate and subtropical China [34]. And bamboo has high temperature and humidity requirements for its surrounding environment and is primarily distributed in moist hilly areas between 300 and 800 m above sea level [1]. Bamboo is a type of clonal plant, composed of above-ground bamboo culms and underground rhizomes. The process of bamboo's nutritional reproduction (clonal growth) involves mature (mother) culms absorbing nutrients to support the underground rhizomes. These rhizomes elongate and give rise to shoots. When the shoots develop into new culms, the new generation of culms, in turn, absorb nutrients to supply the underground rhizomes. This process continues in an infinite cycle (Figure 1) [1]. According to the definition of clonal plants [35], the process of bamboo expansion is essentially its clonal growth, involving the increase in the number of culms and the expansion of the population's spatial distribution. Moreover, the process of shoot and rhizome generation is usually not completed within the same year but occurs alternately (in cycles of two years). In one year, there is a large-scale recruitment shoot (referred to as an "on-year"), and in the next year, there is rhizome generation (referred to as a "off-year").

2.2. Study Site

The study was conducted at the Qiyunshan National Nature Reserve (QNNR) in Jiangxi Province, China (113°54′–114°07′ E, 25°41′–25°54′ N, Figure 2), with an elevation of around 2061.3 m. It belongs to the humid subtropical monsoon climate zone, which is characterized by a warm climate and abundant rainfall [36,37]. The mean annual precipitation ranges from 1522 to 1660 mm, and the mean annual temperature is between 18.0 and ~18.4 °C [38]. QNNR's zonal vegetation is evergreen broadleaf forest, but large numbers of bamboo forests remain in some areas.

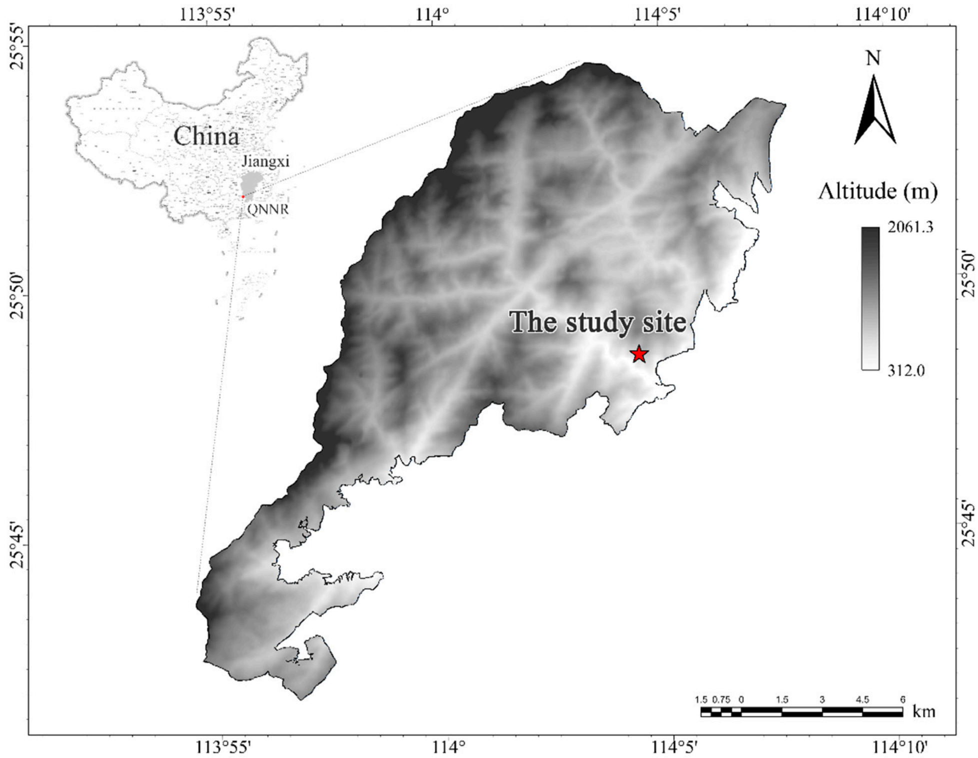

Figure 2. The study location and experimental plot. Locations of Jiangxi province (grey area) and QNNR (red point) are pictured (top left), as well as experimental plot (red star) in the QNNR area.

2.3. Survey Methods and Forest Plot Data

In April 2017, we selected a typical bamboo–broadleaf transition zone plot, which expanded along the slope, according to the CTFS (Centre for Tropical Forest Science) sample plot survey method, at QNNR (Figure 2). The size of plot was 100 m × 50 m, and the coordinate in the lower left corner was NE. Adjacent grid method was used to divide the plot into 200 sub-plots of 5 m × 5 m. We investigated the DBH, total height, and spatial coordinates (x, y) of each plant including trees and bamboo culms with a DBH greater than 1.0 cm in the plot. Following that, in August 2017, 2018, 2019, 2020, and 2021, we investigated the DBH, total height, and spatial coordinates (x and y) of each newly grown culm within the plot. There was a total of 945 culms in this study (Figure 3).

2.4. Data Processing

We selected the population information of bamboo in the major years of 2017, 2019, and 2021. Generally, the bamboo has a biennial bearing cycle, and in QNNR, the singular year is the on-year for it, and the even year is the off-year. In terms of the small number of culms recorded in the off-year, we incorporated them into the previous on-year. We calculated the number of bamboo patches, patch areas, and expansion rates through analyzing the spatial position of all bamboos in the plot. We determined the expansion mode, shape index of patch, and expansion distance based on the spatial relationship between new culms and mother culms to divide the expansion spatial pattern.

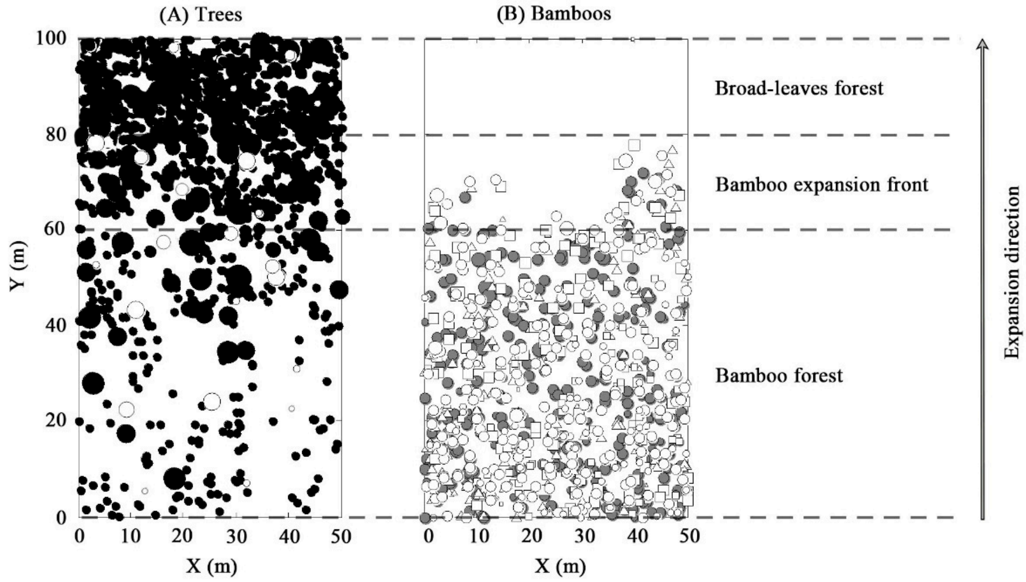

Figure 3. Spatial distribution of trees (**A**) and bamboos (**B**) in bamboo–broadleaf forest transition zone. Tree DBH is indicated by the size of the circle; solid black circles represent alive trees, and hollow circles represent dead trees (**A**). The solid gray circle represents culms established before 2017; the triangle represents culms established in 2017; the square represents culms established in 2019, and the hollow circle represents culms established in 2021 (**B**).

2.4.1. Patch Determination

According to the spatial coordinates of the bamboo culms, the *K*-means clustering analysis method was employed to partition the patches. The *K*-means clustering algorithm divides space into *K* non-overlapping clusters (referred to as patches in this study) and classifies each observation (coordinates of culms in this study) to the nearest centroid [39,40]. Due to the correlation between the number and size of patches and the distance between bamboo culms, this study used the Euclidean distance method to calculate the distance between each pair of culms in the plot. The culms with distances less than or equal to 4 m were merged to form a cluster, based on the crown radius of culms (usually ~2 m) [41].

Afterward, we used the convex hull to obtain the coordinates of the edge vertices of the convex polygon (when the number of culms within the patch is ≥3), determining the shape of the patch. The convex hull operates by taking a set of points *X* and two reference points v_i and v_j. The algorithm starts from point v_i and finds its *K*-nearest neighbors. From each neighbor, we searched the point v_k such that $\overrightarrow{v_i v_k}$ has the smallest angle (θ_{min}) with respect to line $\overrightarrow{v_i v_j}$. This procedure was repeated until $v_k = v_j$ [42].

$$\theta_{min} = \underset{k}{min}\left[cos^{-1}\left(\frac{\overrightarrow{v_i v_k} \cdot \overrightarrow{v_i v_j}}{\| \overrightarrow{v_i v_k} \| \cdot \| \overrightarrow{v_i v_j} \|}\right)\right] \tag{1}$$

2.4.2. Patch Characteristics

We utilized the poly area function to calculate the area of patch, and other indexes about patch including shape index (*SI*), elongation index (*G*), and fractal dimension (*FD*). The calculation formula is as follows:

Shape index of patch (*SI*):

$$SI = \frac{P_i}{2\sqrt{\pi A_i}} \tag{2}$$

Elongation index of patch (*G*):

$$G = \frac{P_i}{\sqrt{A_i}} \tag{3}$$

Fractal dimension of patch (*FD*):

$$FD = \frac{1}{N}\sum_{i=1}^{N} ln(\frac{P_i}{4lnA_i}) \quad (4)$$

where P_i (m) and A_i (m^2) in these three functions are the perimeter and area of *i*-patch, respectively. *N* represents the total number of patches.

2.4.3. Expansion Patch Types

According to the spatial position between new culms and mother culms, the expansion pattern of bamboo can be distributed as following five types: inner filling patch (IF), boundary expanding patch (BE), transboundary leaping patch (TL), expansion–infill mixed patch (BM), and stationary patch (ST, Figure 4).

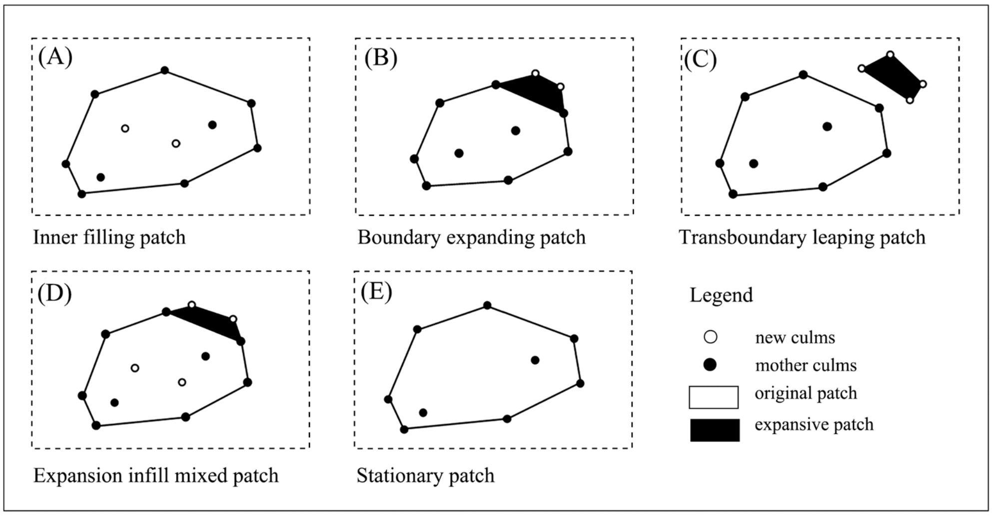

Figure 4. The patch types of bamboo expansion into neighboring forest. (**A**) Inner filling patch (IF), (**B**) Boundary expanding patch (BE), (**C**) Transboundary leaping patch (TL), (**D**) Boundary expansion–inner infilling mixed patch (BM), and (**E**) Stationary patch (ST).

IF: new culms grow inside the patch enclosed by the mother culms, and the patch area remains unchanged and the density of culms increases (Figure 4A). BE: new culms grow at the edge of original patch, resulting in an increase in the area and the density remains unchanged at original patch (Figure 4B). TL: new culms grow outside of the original patch, which form a new patch (or individual plant) separate from original patch (Figure 4C). BM: new culms grow both inside and at the edge of original patch resulting in the patch area and increased culm density (Figure 4D). ST: no new culms appear in or around the original patch (Figure 4E).

2.4.4. Expansion Indexes and Expansion Rate Calculations

We calculated the expansion indexes, expansion distances, and expansion rates of the bamboo area using the functions *EI*, D_{AB}, and *Ea*, respectively. In function (5), *EI* is the expansion index of bamboo patch, with a value range of [−1, 1]. When there were no new culms or no mother culms in the patch, the *EI* equals −1 and 1, respectively. N_n is the number of new culms, and N_m is the number of mother culms. In function (6), D_{AB} is distance between culms A and B of bamboo; x_A and y_A are the *x* and *y* coordinate values of culm A in plot; and x_B and y_B are the *x* and *y* coordinate values of culm B in plot. In function (7), *Ea* is the rate of area expansion; S_0 and S_{0+t} are the sums of bamboo patch areas at the times of *0* and *t*.

Expansion indexes:

$$EI = \frac{N_n - N_m}{N_n + N_m} \tag{5}$$

Expansion distance:

$$D_{AB} = \sqrt{(x_A - x_B)^2 + (y_A - y_B)^2} \tag{6}$$

Expansion rate of area:

$$Ea = \left[\left(\frac{S_{0+t}}{S_0}\right)^{\frac{1}{t}} - 1\right] \times 100\% \tag{7}$$

2.5. Statistical Analysis

We used one-way analysis of variance to examine variations in the distribution patterns, patch characteristics, and expansion indexes of bamboo at different times and different locations. We used Pearson correlation coefficient to analyze the correlation among various parameters of bamboo expansion, including year, x-axis, y-axis, total culm number, number of mother culms, number of new culms, area, density of new culms, total density, expansion index, maximum expansion distance, and mean expansion distance. This statistical analysis was performed using SPSS 22.0 statistical and Matlab 2018a software, and graphs were created using Origin 2022 and Matlab 2018a software.

3. Results

3.1. Spatial Distribution of Trees and Bamboo

In the evergreen broadleaf forest at the bamboo–broadleaf forest transition zone (Figure 3 top), there are numerous live trees and a small number of dead ones. In the middle of the transition zone, the evergreen broadleaf forest gradually transformed into a mixed forest of bamboo and broadleaf trees due to the expansion of bamboo. This transformation resulted in an increase in the number of culms and dead trees (Figure 3 mid). As the evergreen broadleaf forest was transformed into a bamboo forest, consequently, the density of the culms, particularly those aging culms, significantly increased, and fewer live trees persisted there (Figure 3 bottom).

3.2. Expansive Patch Parameters

Bamboo exhibited a patchy expansion pattern at the bamboo-broadleaf forest transition zone 2017 to 2021 (Figure 5). Over the course of five years (three on-years and two off-years), the number of bamboo patches increased from 48 to 52, representing a growth of 8.33%. Additionally, the total and average areas of bamboo patches experienced a growth of 53.78% and 41.95%, respectively. Specifically, the values increased from 1145.28 m^2 to 1761.24 m^2 for the total area and from 23.86 m^2 to 33.87 m^2 for the average area (Table 1). Furthermore, the perimeter of the patch increased from 19.90 m to 22.74 m, and the average number of culms in each patch increased from 10.44 ind./m^2 to 18.17 ind./m^2 (Table 2).

Table 1. The changes in patch parameters for bamboo from 2017 to 2021.

Indexes of Patches	2017	2019	2021
Number of patches (ind.)	48	49	52
Total area of patches (m^2)	1145.28	1600.32	1761.24
Area of maximum patches (m^2)	68.82	66.24	132.81
Mean area of patches (m^2)	$23.86 \pm 11.58\ ^{b}$	$32.71 \pm 17.26\ ^{a}$	$33.87 \pm 20.80\ ^{a}$
Expansion rates (%)	15.89	18.21	4.91
Index of maximum patches (%)	6.01	4.14	7.55

Different letters mean significant differences in mean area of patches among the three years at α = 0.05.

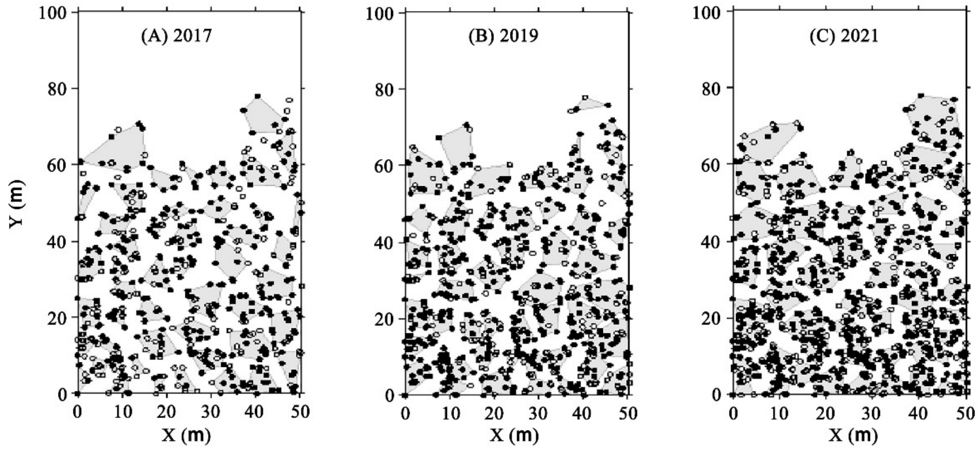

Figure 5. The patterns and processes of bamboo expansion between 2017 and 2021. The solid black dots represent mother culms, while the hollow circles represent newly sprouted culms.

Table 2. The amount, size, and shape for the patches of bamboo in bamboo–broadleaf forest transition zone from 2017 to 2021.

Indexes	2017	2019	2021
Perimeter of patches (m)	19.90 ± 4.50 [b]	22.10 ± 6.05 [ab]	22.74 ± 5.74 [a]
Culm number per patch (ind./patch)	10.44 ± 3.12 [c]	15.76 ± 5.19 [b]	18.17 ± 5.14 [a]
Culm density(ind./m^2)	0.54 ± 0.30 [a]	0.63 ± 0.35 [a]	0.73 ± 0.79 [a]
Mean expansion distance (m)	3.89 ± 0.86 [a]	3.92 ± 1.02 [a]	3.97 ± 0.98 [a]
Shape index (*SI*)	1.21 ± 0.14 [a]	1.14 ± 0.06 [a]	1.21 ± 0.55 [a]
Elongation index (*G*)	4.28 ± 0.51 [a]	4.05 ± 0.22 [a]	4.29 ± 1.96 [a]
Fractal dimension (*FD*)	1.05 ± 0.07 [a]	1.01 ± 0.05 [b]	1.01 ± 0.05 [b]

Different letters indicate significant differences in culm number per patch, culm density, mean expansion distance, shape index, elongation index, and fractal dimension among the three years at α = 0.05.

3.3. Changes in Expansion Patch Types

The type of bamboo expansion patches shifted from the boundary expanding patch (BE) to the inner filling patch (IF) and the boundary expansion–inner infilling mixed patch (BM) from 2017 to 2021 (Figures 4 and 5). The percent of IF and BM to the total patch increased from 10% and 39% to 21.15% and 60.03%, respectively; however, the percentage of BE to the total patch decreased from 38.75% to 9.62% (Figure 6A).

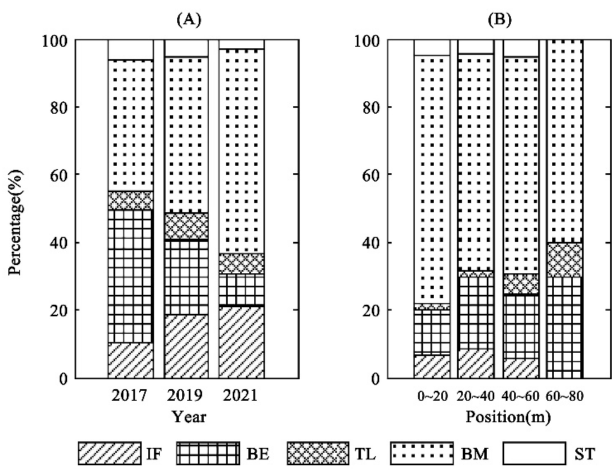

Figure 6. The fraction of bamboo patches according to year (**A**) and transition zone position (**B**) in bamboo–broadleaf forest transition zone. IF—Inner filling patch, BE—Boundary expanding patch, TL—Transboundary leaping patch, BM—Boundary expanding and inner filling mixed patch, and ST—stationary patch.

In terms of the position of the bamboo and broadleaf forest transition zone, within the bamboo forest position (0~20 m), BM emerged as the dominant type of bamboo patch (Figure 6B), comprising 72.95% of the patches, followed by the BE (13.51%), IF (7.12%), ST (4.47%), and TL (1.95%). However, in the bamboo expansion front position (60~80 m), BM decreased to 60.05%, the IF and ST disappeared, and the BE and TL increased to 30.36% and 9.59% (Figure 6B).

3.4. Expansion Indexes and Expansion Rates

The expansion indexes and the expansion rates of bamboo demonstrated a declining trend from 2017 to 2021 (Table 3). In 2017, the expansion indexes for the 0~20 m and 60–80 m ranges of the bamboo–broadleaf forest transition zone were recorded as −0.18 ± 0.36 and 0.17 ± 0.23, respectively. However, by 2021, these indexes had decreased to −0.39 ± 0.20 and −0.28 ± 0.24. The average expansion indexes decreased from −0.25 ± 0.35 to −0.40 ± 0.17, while the average expansion rates increased from 1.55 ± 0.83 m/2a to 1.01 ± 0.36 m/2a.

Table 3. The expansion indexes and rates of bamboo in bamboo–broadleaf forest transition zone from 2017 to 2021.

Type	Position (m)	2017	2019	2021	Average
Expansion index	0~20	-0.18 ± 0.36^{Ba}	-0.37 ± 0.30^{Bb}	-0.39 ± 0.20^{Bb}	-0.32 ± 0.30^{B}
	20~40	-0.35 ± 0.27^{Cb}	-0.09 ± 0.31^{Aa}	-0.43 ± 0.15^{Bc}	-0.27 ± 0.30^{B}
	40~60	-0.35 ± 0.37^{Cb}	-0.12 ± 0.24^{Aa}	-0.44 ± 0.12^{Bc}	-0.30 ± 0.29^{B}
	60~80	0.17 ± 0.23^{Aa}	-0.12 ± 0.01^{Ab}	-0.28 ± 0.24^{Ac}	-0.10 ± 0.26^{A}
	Average	-0.25 ± 0.35^{a}	-0.21 ± 0.31^{a}	-0.40 ± 0.17^{b}	-0.29 ± 0.29
Expansion rate (m/2a)	0~20	1.44 ± 0.43^{Ba}	1.16 ± 0.50^{Bab}	0.91 ± 0.33^{Bb}	1.15 ± 0.47^{B}
	20~40	1.47 ± 0.97^{Ba}	1.64 ± 0.47^{ABa}	0.92 ± 0.28^{Bb}	1.37 ± 0.70^{AB}
	40~60	1.74 ± 0.80^{ABa}	1.55 ± 0.56^{ABb}	1.13 ± 0.34^{ABc}	1.46 ± 0.63^{AB}
	60~80	2.11 ± 2.98^{Aa}	2.04 ± 0.47^{Aa}	1.64 ± 0.34^{Ab}	1.89 ± 1.27^{A}
	Average	1.55 ± 0.83^{a}	1.44 ± 0.55^{a}	1.01 ± 0.36^{b}	1.32 ± 0.64

Different capital letters indicate significant differences in expansion indexes and expansion rates between different positions, and different small letters indicate significant differences in expansion indexes and expansion rates between different years at $\alpha = 0.05$.

The expansion indexes of bamboo showed an increasing trend along the direction of bamboo expansion (from bamboo forest to bamboo expansion front), between 2017 and 2021 (Table 3). At a 0~20 m range of the bamboo–broadleaf forest transition zone (bamboo forest), the expansion indexes in 2017, 2019, and 2021 were observed to be −0.18 ± 0.36, −0.37 ± 0.30, and −0.39 ± 0.20, but at a 60~80 m range of the transition zone (bamboo expansion front), these indexes increased to be 0.17 ± 0.23, −0.12 ± 0.01, and −0.28 ± 0.24, respectively. The average expansion indexes increased from −0.32 ± 0.32 to −0.1 ± 0.26, and the average expansion rates increased from 1.15 ± 0.47 m/2a to 1.89 ± 1.27 m/2a as the bamboo expanded from a 0 to 20 m to 60~80 m position.

3.5. The Relationship among the Variables for Bamboo Expansion Parameters

The x-axis is not related to all parameters of bamboo expansion, and the y-axis (from bamboo forest to broadleaf forest) is highly and significantly positively correlated with patch area, maximum expansion distance, and average expansion distance, while it is highly and significantly negatively correlated with the density of new culms and total culms (Table 4). This indicates that bamboo primarily expands along the y-axis direction, and the expansion distance gradually increases as the y-axis values increase, while the number of culms decrease with the increase in the y-axis.

Table 4. The relationship among the variables for bamboo expansion in the bamboo–broadleaf forest transition zone.

Variables	YE	X	Y	TCN	NMCs	NNCs	A	DNCs	TD	EI	MXED
X	0.07										
Y	−0.01	0.04									
TCN	0.58 **	−0.06	0.00								
NMC	0.56 **	−0.07	−0.04	0.92 **							
NNC	0.27 **	0.00	0.07	0.59 **	0.23 **						
A	0.20 *	0.07	0.59 **	0.43 **	0.36 **	0.34 **					
DNC	−0.06	−0.14	−0.43 **	−0.19	−0.36 **	0.28 **	−0.56 **				
TD	0.27 **	−0.09	−0.58 **	0.06	0.25 **	−0.36 **	−0.56 **	0.25 **			
EI	−0.21 **	0.00	0.11	−0.25 **	−0.58 **	0.59 **	−0.02	0.57 **	−0.51 **		
MXED	−0.25 **	0.07	0.31 **	−0.20	−0.40 **	0.32 **	0.19 *	0.13	−0.55 **	0.64 **	
MED	−0.35 **	0.02	0.28 **	−0.39 **	−0.49 **	0.03	0.09	0.03	−0.49 **	0.49 **	0.81 **

YE: year; X: x-axis; Y: y-axis; TCN: total culm number; NMCs: number of mother culms; NNCs: number of new culms; A: area; DNCs: density of new culms; TD: total density; EI: expansion index; MXED: maximum expansion distance; MED: mean expansion distance. "*" or "**" indicate significant or highly significant correlation at $\alpha = 0.05$.

4. Discussion

Bamboo plays an important role in the construction of the forestry economy [43,44]. However, the expansion of bamboo also gives rise to a range of ecological challenges [12,25,45], such as simplified community structure [9], reduced plant diversity [7], and changed terrestrial water and nutrient cycles [11]. Therefore, it is essential for us to comprehend the processes and mechanisms of bamboo expansion in order to provide guidance for the management and control of bamboo expansion. Our results show that the expansion process of bamboo into the surrounding broadleaf forest follows a patch-based expansion process. From 2017 to 2021, in the 5000 m^2 bamboo–broadleaf forest transition zone plots, the number of bamboo patches increased from 48 to 52, and the patch area increased from 1145.28 m^2 to 1761.24 m^2, which aligns with the findings from the macro-scale results (Table 1). For instance, Isagi and Torii (1997) conducted a comparison of aerial photographs and land-use maps of Tanabe Town, Kyoto, Japan, from 1953, 1975, and 1985 [21]. They observed that the number of bamboo patches in the area increased from 24 to 112 and then to 174, with an average area of 0.67 hm^2, 1.56 hm^2, and 1.75 hm^2, respectively. Furthermore, Ding et al. (2006) applied remote sensing and geographic information system technology to study the bamboo forest patches in a 4284 hm^2 area of Tianmushan in Zhejiang, China [22]. Their findings revealed an increase in the number of bamboo forest patches from 3 to 6, with the largest patch area expanding by nearly 54 times. This shows that the expansion of bamboo into the surrounding areas is characterized by patch expansion at both the macroscopic remote sensing scale and the ground community scale.

It is worth mentioning that this research primarily focuses on revealing the patchy expansion pattern at the community scale. According to the spatial relationship between new and mother culms, the expansion patches of bamboo can be divided into five types (Figure 3): inner filling patch (IF), boundary expanding patch (BE), transboundary leaping patch (TL), boundary expansion–inner infilling mixed patch (BM), and stationary patch (ST). Our findings indicate that the type of bamboo expansion patches shifted from BE in the early stage of bamboo expansion (bamboo expansion front and year 2017) to BM and IF in late stage of bamboo expansion (bamboo forest and year 2021), a shift which fully reflects the expansion process and pattern of bamboo, where it first spreads outward and then fills inward (Figure 5). The expansion distance and the correlation between the expansion index provide additional perspectives that support this rule. Specifically, the expansion distance at the expansion front is greater compared to that within the bamboo forest (Table 3). Moreover, there is a significant positive correlation between the expansion distance and the y-axis (representing the transition from bamboo forest to broadleaf forest) (Table 4; Figure 3).

This shift in patch type may be attributed to the expansion costs involved. On the one hand, bamboo is a clonal plant with physiological integration characteristics, and the mature culm provides nutrients and energy (investment cost of mature bamboo) for the new culms through underground rhizomes [28]. However, this process inevitably leads to nutrient and energy losses for the mature culms [29]. Therefore, as bamboo expands outward and occupies a new plot, it fills the interior with new culms, thereby enhancing the absorption capacity of the bamboo patches or cloned fragments for water, nutrients, and other nutrients. The expansion outward occurs only when the accumulated resources within the patches can adequately support the growth and development of the next generation.

On the other hand, when the number of culms reaches a certain threshold (where the available resources within a patch are insufficient to support the growth of all the culms), it triggers intensified intraspecific competition among them [46]. This heightened competition leads to stunted growth or even the death of some culms, resulting in the cloning fragment directly losing all nutrients in the dead culm (incurring cost losses). However, when the bamboo population reaches a critical mass, expanding outward to establish new culms serve multiple purposes. Firstly, it alleviates intraspecific competition [47]. Secondly, the newly established culms absorb resources from their surroundings (new plots), which are then transferred back to the mother culms as nourishment once the new culms mature [48]. This compensates for the resources consumed by the mother bamboos during the establishment of new culms and the growth of bamboo rhizomes. Therefore, when culm numbers accumulate to a certain extent, expanding outward not only avoids cost losses, but also yields benefits for the cloned fragments or bamboo patches. In essence, bamboo expansion does not occur in a strictly sequential manner based on age. Rather, it follows a strategic process of step-by-step expansion, filling, and subsequent expansion and filling again. Some scholars, in their studies on other clonal plants, also believe that the reproduction of cloned plants has a certain strategic control. This strategy manages the position, size and other characteristics of new (daughter) ramets, enabling them to more effective utilization of space, nutrients, and other resources [49–51].

In addition, our findings demonstrate that along the bamboo–broadleaf transition zone, from bamboo forest to broadleaf forest, the average expansion index of bamboo increased from -0.32 to -0.10, and the average expansion rate increased from 1.15 to 1.89 m/2a (Table 4). This rate is lower compared to the expansion rates reported by Okutomi et al. (1996) for bamboo forests in the suburbs of Kyoto, Japan, which found that the expansion rates of bamboo into shrublands, wasteland, and deciduous broadleaf forests from 1961 to 1987 were 3.0 m/a, 2.5 m/a, and 1.8 m/a, respectively [20]. The discrepancy in expansion rates can be attributed to the differences in stand types. The study conducted by Okutomi focused on shrublands, wasteland and deciduous broadleaf forests, and our study area was located in a protected area, with secondary evergreen broadleaf forests. Shrublands and wasteland have a low canopy density and more niche space, which creates conditions for the encroachment of bamboos. On the other hand, evergreen broadleaf trees tend to be more competitive compared to deciduous broadleaf trees due to their lower resource demand and higher utilization efficiency, such as of light and water [52,53]. Consequently, the rate at which bamboo invades shrublands, wastelands, and deciduous broadleaf forests is higher compared to its expansion rate into evergreen broadleaf forests. Zheng et al. (2023) found that the process of bamboo expansion into evergreen broadleaf forests is hindered by competition from broadleaf trees in the Tianmu Mountain Nature Reserve [54].

5. Conclusions

Bamboo expansion is a process in which bamboo proliferates and expands based on the existing spatial pattern. Our research results indicate that this process occurs in the form of patches, and the types of patches change with the expansion time, showing a "first spreading and then filling" pattern. Our study reveals, for the first time, the specific process and pattern of bamboo expansion, providing a reference for the prevention and control of bamboo plant expansion. However, the reasons why bamboo adopts this expansion pattern are speculative based on previous research findings. Further exploration is needed to understand the mechanisms behind bamboo's adoption of the "first spreading and then filling" expansion strategy. Additionally, building upon this study, it is crucial to include research on the growth patterns of other clonal plants, especially rhizomatous clonal plants, which often exhibit expansive or invasive behaviors. This will contribute to a better understanding of the control of expansive plants (invasive plants).

Author Contributions: Conceptualization, Q.Y.; Software, X.Z. (Xiaoxia Zeng), C.G. and Q.Y.; Formal analysis, H.L.; Investigation, X.Z. (Xiaoxia Zeng), H.L., Jian Lu, X.Z. (Xianglong Zhu), Y.H., C.G., Z.R., D.H. and Q.S.; Resources, H.L. and J.L.; Data curation, X.Z. (Xiaoxia Zeng), J.L., X.Z. (Xianglong Zhu) and Y.H.; Writing—original draft, X.Z. (Xiaoxia Zeng); Writing—review & editing, Q.Y.; Funding acquisition, Q.S. and Q.Y. All authors have read and agreed to the published version of the manuscript.

Funding: This research was supported by the National Natural Science Foundation of China (32060319, 32260335, 32360801, and 41807028).

Data Availability Statement: All data generated or analyzed during this study are included in this published article.

Acknowledgments: We are grateful to the Administration of the Qiyunshan Nature Reserve for providing an experimental platform. We also thank other members of our team for their assistance with the field experiments.

Conflicts of Interest: The authors declare no conflicts of interest.

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