

Article

# Spatial Pattern and Competitive Relationships of Moso Bamboo in a Native Subtropical Rainforest Community

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**Abstract:** Bamboo has invaded native forests worldwide, and its aggressive spread by rhizomes facilitates patch expansion and the eventual replacement of adjacent forests. However, fine-scale studies of the spatial pattern and competitive relationships of bamboo in native forests are still lacking. We obtained data from nine plots in a native south subtropical rainforest in Guizhou Province, northwest China. Pair-correlation functions indicated that competition caused by bamboo expansion has not led to large-scale regular spatial distributions in bamboo forest and negative density-related dependence mechanisms regulating the spatial pattern of the native forest community. Marked correlation functions indicated small bamboo in clusters form colony patches that grow around the larger mature trees, resulting in patch expansion in the native forest community. Mark variogram functions identified significant positive spatial autocorrelation of moso bamboo caused by interactions with similar-sized trees within colony patches. This study showed that moso bamboo has colonized and expanded within the native forest community. Compared to the native forest species, the strategy of patch expansion and equal tree sizes in colony patches of moso bamboo could prevent regular distribution trend and size-asymmetric competition between nearby bamboo for the asymmetric and limited sources (i.e., light) in the forest, enhancing the persistence of moso bamboo in the native forest in our study stand located in a south subtropical rainforest in a river valley.

**Keywords:** bamboo expansion; spatial distribution; size autocorrelation; size equality

## 1. Introduction

Over the past several decades, planetary-scale global changes have intensified, and human activities such as the transformation of natural habitats for agricultural land use is one of the most important factors causing global climate change. Climate change causes fragmentation of natural vegetation, thereby altering ecological communities. The result is consistent losses or changes in species richness and abundance [1,2], especially in tropical and sub-tropical forests [2–4]. For example, monoculture oil palm rubber plantations in continental South East Asia have turned some high-biodiversity land into economically unsustainable plantations [5,6]. In this vein, the proliferation of bamboo plantations has attracted increasing attention [7–11]. Bamboo is famous for its versatility; it not only plays an important role in traditional human economic activities such as culms harvesting or the modern chemical industry but also is a unique part of Asian culture [10,12,13]. The multipurpose nature of bamboo has led to extensive planting worldwide [10]. Approximately 36.8 million hectares of bamboo forest are distributed in tropical, subtropical, and temperate regions [10]. Relevant examples

are the expansion of bamboo forests in Japan and South Africa [7–9]. China's bamboo forest resources are the largest in the world [14]. Bamboo invasion of natural forest communities has been extensively reported, especially in species-rich areas [15–17] and nature reserves [18,19].

Bamboo forests, with their clonal reproduction, are well suited to patch expansion in native forests; for example, *Phyllostachys* spp. are characterized by their aggressive habits and physiological integration [7,9]. This bamboo is spread by its underground rhizomes [7,20] in China and Japan. Bamboo's invasive nature has been described using various terms such as expansion [7,21] and invasion [22–24]. Recent literature has focused on the relative biomass of bamboo plants compared to that of native forest species [8,9], the effects of bamboo on forest species diversity [8,22,25], and the effects on soil biodiversity [11,17,26]. Similar to other invading plant species, bamboo patch expansion in a native forest has resulted in the destruction of the natural forest community structure, loss of species diversity, difficulties in natural regeneration, and stagnation of community succession [25,27,28].

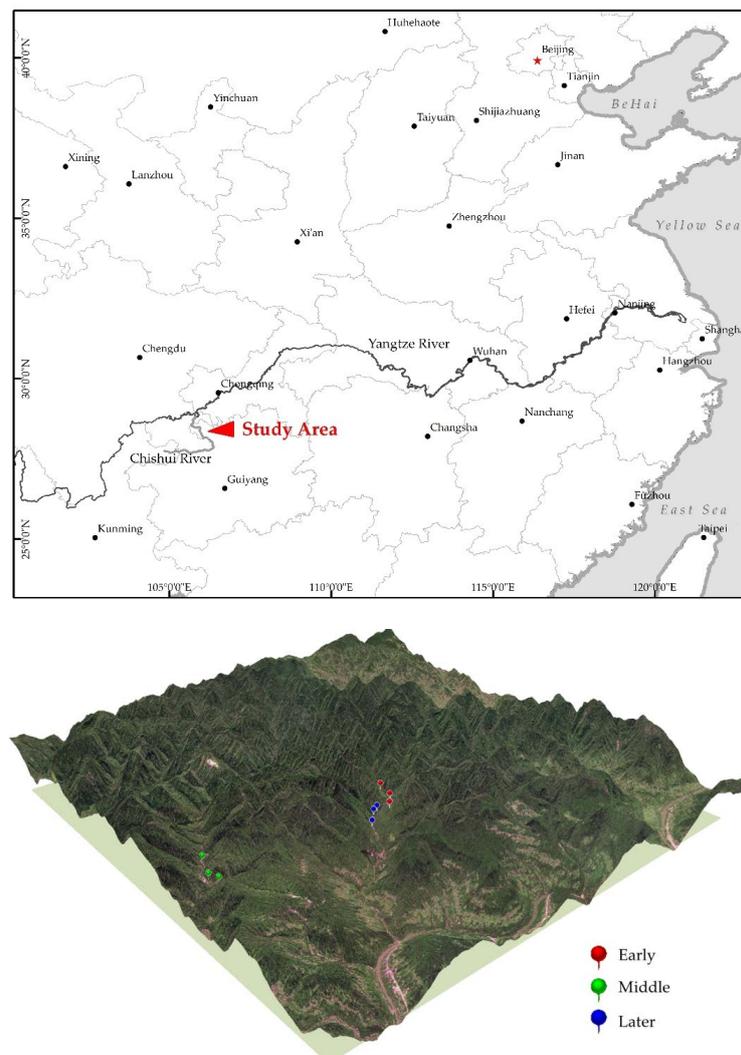
Nevertheless, we consider the study of the spatial distribution during expansion and competitive relationships of bamboo trees in the native forest community to be insufficient, especially at fine spatial scales. Spatial patterning of individuals within a population is closely linked to the ecological processes shaping the population [29]. Thus, tree spatial pattern analysis may not only characterize the spatial distribution of individual trees within a stand but also help to understand the underlying ecological processes producing the pattern [30–32]. Fine-scale spatial analysis using second-order statistics of tree distribution patterns, such as the pair correlation function [29,33,34], can be used to identify competition during succession by comparing the spatial patterns of a given species at subsequent stages of a chronosequence. Strong competition may cause individuals close to each other to die, especially in more crowded environments. In this situation, random thinning could result in a more regular spatial pattern than normally observed during early succession [29,33,35,36]. Competition may at times not be strong enough to cause high mortality but rather lead to a reduction in tree size (e.g., height or diameter at breast height (DBH)). In such situations, the study of size correlation and size autocorrelation in trees spatial distribution patterns can identify the underlying competition relationship of nearby trees [31,33,34,37–41]. Strong competition interactions between neighbouring trees that cause size hierarchies (unequal-sized neighbouring) often leads to asymmetric competition, which was defined as larger-sized trees obtaining a disproportionate share of resources (for their relative size) and suppressing the growth of smaller ones [42,43]. If asymmetric competition occurs between a pair of trees at close proximity during forest development, the bigger-sized individual receives more resources for growth. As a result, there would be a high frequency of pairs of dominant and suppressed trees nearby in later succession, which would cause a negative autocorrelation in plant size [37,42,44].

In this study, we analysed the stand structure, composition, and spatial pattern of bamboo and native species in a river valley harbouring a subtropical evergreen broad-leaved forest in western China. More specifically, we used spatial pattern analysis to infer, from the fine-scale spatial distributions of trees, how bamboo in a native forest compete for and partition space (i.e., the spatial expansion strategy). We considered the following hypotheses. (1) The expansion of bamboo transforms the native forest species composition and diversity. (2) Substantive individuals are increased during the expansion of bamboo into areas previously primarily occupied by native trees, thus resulting in increasingly crowded conditions; competition makes the spatial distribution of the bamboo and the native species gradually more regular in the native forest community. (3) The growth and competition of individuals result in the sizes of neighbouring individual trees (tree height) being smaller than the community average. (4) Competition will result in differences in the sizes (tree height) of neighbouring individual trees in the community, and the tree heights will display negative spatial autocorrelation.

## 2. Materials and Methods

### 2.1. Study Site and Data Collection

The study site was located in the area surrounding the Chishui River, a tributary of the Yangtze River (Figure 1). The tectonic activity in this region during its geological history led to strong river undercutting and traceable erosion; “V”-type river valleys are common in this area, and the altitude ranges from 331 to 1455 m [16,45]. Below 700 m above sea level, the region is characterized by a subtropical humid monsoon climate, with an annual mean temperature of 17.7 °C and an annual mean precipitation of 1200–1300 mm. The type of soil is mainly non-zonal purple, which is neutral to slightly acidic [16,45]. Most of the forests in the river valleys of this region are dominated by south subtropical rainforest species, including *Musa balbisiana* Colla, *Mallotus philippensis* (Lam.) Muell.Arg., *Brassaiopsis glomerulata* (Blume) Regel, *Alsophila spinulosa* (Wall. ex Hook.) R. M. Tryon, *Lasianthus chinensis* (champ.) Benth. and so on [16,45]. However, during the 1980s, local governments encouraged native farmers to increase cultivation of moso bamboo (*Phyllostachys pubescens* Mazel ex Houzeau de Lehaie) through forestland conversion for economic gain [10,16]. With the successful colonization and expansion in this area, moso bamboo has played an increasingly important role in local communities and has even become the dominant species in some areas, especially in warm-humid river valleys at low altitude [16].



**Figure 1.** Location of study area and 3D sketch map of study plot. These maps were produced by ArcGIS software (ArcMap 10.4 and ArcScene 10.0, ESRI, USA).

Although the local government established a nature reserve to protect this area and banned artificial planting of bamboo after 1990, moso bamboo has naturally regenerated and spread throughout the river valley during the past 40 years [16]. Thus, in our study plots, moso bamboo (MB) has gradually replaced many native trees (NTs) and has become the dominant species (Table 1). Nine fixed observation plots were established in the native forest at the bottom of the river valley in 2015. Each plot was 0.12 ha (60 m × 20 m) and was located in the moderate slopes of the river valley (Figure 1). This study focuses on the degree of bamboo expansion in different forest development phases, according to the relative proportion of individual bamboo stems in each plot. The nine fixed plots reflected different bamboo expansion phases (early, middle, and later): three plots in native forest dominated by south subtropical rainforest vegetation (Early, Figure 2a) and another six plots in native forest invaded by bamboo (Middle, Figure 2b; Later, Figure 2c), with the later plots almost completely dominated by bamboo forest. All plots were selected to show similar vegetation characteristics, with no obvious differences in topography, orientation, or elevation. The maximum distance among the replicated plots in the middle phases of bamboo expansion is over 1000 m, and in the later phases of bamboo expansion, the minimum distance among each of the replicated plots is approximately 500 m. All of the moso bamboo and native tree species with diameter at breast height (DBH) >1 cm were stem-mapped using an autofocus total station. All of the individuals were identified to species and measured for DBH and height. Table 1 provides general information on the plots.

**Table 1.** Stand characteristics of all the plots. Three most dominant species in each of the plots (values presented are means ± standard deviation in replicated plot level). DBH: diameter at breast height.

Plot	Slope (°)	Mean Altitude (m)	Mean Density (Tree/ha)	Mean H (m)	Mean DBH (cm)	Dominant Species (% Stems)
Early	<18	536 ± 6	2478 ± 212	4.79 ± 0.43	7.80 ± 1.53	Moso bamboo <i>P. pubescens</i> Mazel ex Houzeau de Lehaie (0) Native tree species <i>M. balbisiana</i> Colla (26.01) <i>M. philippensis</i> (Lam.) Muell.Arg. (15.36) <i>L. chinensis</i> (champ.) Benth. (10.09)
Middle	<22	545 ± 26	2775 ± 590	6.46 ± 0.64	8.92 ± 1.09	Moso bamboo <i>P. pubescens</i> (47.25) Native tree species <i>A. spinulosa</i> (Wall. ex Hook.) R. M. Tryon (13.68) <i>M. balbisiana</i> (7.96)
Later	<24	562 ± 33	2450 ± 383	9.53 ± 1.56	9.42 ± 0.8	Moso bamboo <i>P. pubescens</i> (79.82) Native tree species <i>A. spinulosa</i> (10.2) <i>B. glomerulata</i> (Blume) Regel (4.04)

## 2.2. Data Analysis

### 2.2.1. Community Structure and Quantitative Characteristics

To investigate whether bamboo expansion had dominated the native forest species composition, (the structure and bio-diversity), we calculated the percentages of relative abundance, relative dominance, and frequency for moso bamboo (MB) and native tree (NT) species. Importance values (IVs) were determined by calculating the mean of the above three measures [46]. We used species richness (the Shannon-Wiener index) as the principal measure of species diversity [46]. The tree density (D) was counted for each MB and NT species in the three plots. We also calculated the mean tree height (H) and diameter at breast height (DBH) for MB and NT species in each of the three plots.

### 2.2.2. Pair-Correlation Functions

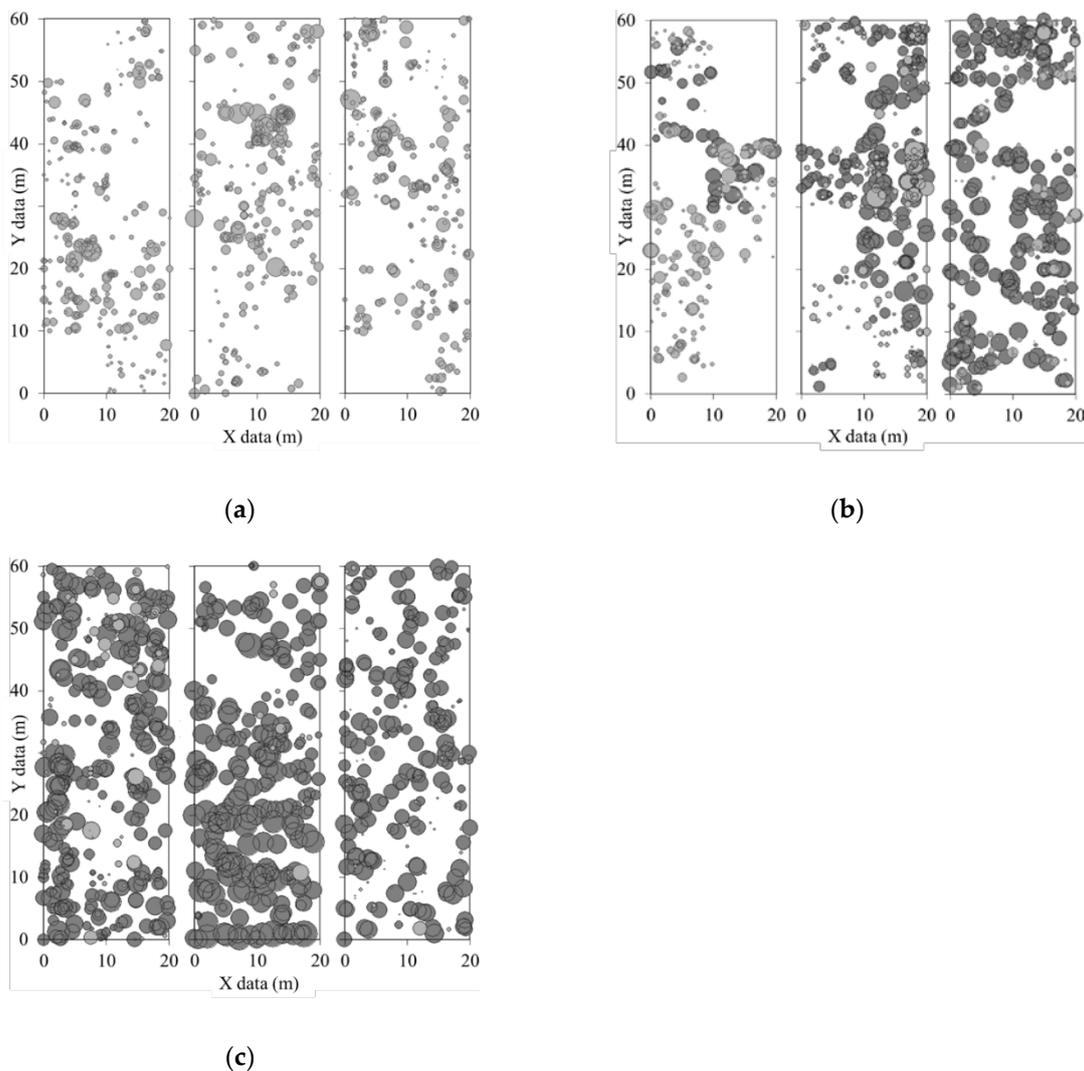
To investigate whether the spatial pattern of MB and NTs would become more regularly distributed during bamboo expansion (hypothesis 2), we used the univariate distance pair correlation function  $g(r)$ , which is based on the expected number of tree individuals (i.e., MB or NT) found at a

distance  $r$  from an arbitrary point divided by the intensity  $\lambda$  of the pattern [31,33,34]; the function can be calculated as follows [34,36]:

$$g(r) = \rho(r) \cdot \lambda^{-2} \quad (1)$$

where  $\rho(r)$  is the second-order characteristic density and  $\lambda$  is the intensity of the process. When  $g(r) = 1$ , the basic spatial pattern of MB and NTs was complete spatial randomness (CSR), whereas  $g(r) > 1$  indicates aggregation, and  $g(r) < 1$  indicates regularity [35,36].

Due to the rapid expansion of moso bamboo and the slightly heterogeneous environment in our plots, the tree intensity of MB and NTs in the three research plots was not approximately constant; our plots were partly affected by first-order heterogeneity (Figure 1). In such a situation, we implemented a null model based on a heterogeneous Poisson process [30,31,35,36]; thus, the intensity  $\lambda$  was not approximately constant, but varied with the spatial location coordinates  $(x,y)$ . We used a moving window with a fixed bandwidth  $R = 5$  to estimate  $\lambda(x,y)$  [31,35]. A heterogeneous Poisson null model also makes it possible to explore only the interaction between trees, avoiding the test results that may have been confounded by the effect of exogenous environment factors (e.g., soil and topography variation, rocks, seed dispersal) [30,36].



**Figure 2.** The stem maps of individual tree species in nine plots in bamboo expansory phases: (a) early, (b) middle, and (c) later. Circles represent the locations of individual plants. Sizes are proportional to tree height; dark grey circles represent moso bamboo, light grey circles represent native forest species.

### 2.2.3. Marked Correlation Functions and Marked Variograms

Marked correlation functions [33,34] and mark variogram functions [34,37–39], which have been widely applied in ecology, can identify the underlying pattern present and detect the relevant spatial scale of size correlation and size autocorrelation at which the ecological process is operating.

In order to explore spatial correlation structure in terms of quantitative tree mark of tree, tree size (height) was used as a “mark” in a mark correlation function (MCF) and mark variograms function (MVF) [37–42]. The MCF analysis is similar to the pair-correlation function  $g(r)$ , but it allowed us to detect density-dependent size correlation caused by competition in nearby tree individuals [40,41]. An estimator of the mark correlation function is given by:

$$K_t(r) = \frac{1}{c_t} \frac{\sum_{i=1, j=1}^n [t(m_i, m_j)] k(|x_i - x_j| - r)}{\sum_{i=1, j=1}^n k(|x_i - x_j| - r)} \quad (2)$$

We used the test function  $t(m_i, m_j)$ , which is especially designed to explore questions regarding competition. In MCF analysis, this test statistic is the product of the two marks (tree height)  $m_i$  and  $m_j$  of trees (i.e., MB or NT) at a distance  $r$ . The non-spatial average of this test function yields  $c_{t1} = \mu^2$ , where  $\mu$  is the average tree height taken over all individuals of the pattern and yields the marked correlation function:

$$k_{mm}(r) : t_k(m_i m_j) = m_i m_j \quad (3)$$

When  $k_{mm}(r) = 1$ , marks are independent at distance  $r$ ; if  $k_{mm}(r) < 1$ , there is a negative correlation between the marks at distance  $r$ , so we would expect that plants located close to each other should be smaller than the population average [40,41] (hypothesis 2).

The MVF analysis measures the frequency of pairs of dominant and suppressed trees in close proximity.  $\gamma_{mm}(r)$  has smaller values if the sizes of the trees in a pair with interpoint distance  $r$  are similar, and larger values if the measurements differ strongly [37–39]. We also used the test function  $t(m_i, m_j)$  which yields the mark variogram function:

$$\gamma_{mm}(r) : t_\gamma(m_i m_j) = \frac{(m_i - m_j)^2}{2} \quad (4)$$

When  $\gamma_{mm}(r) < 1$ , the size of neighbouring trees was a negative autocorrelation at distance  $r$ ; whereas if  $\gamma_{mm}(r) > 1$ , the size of trees was a positive autocorrelation at distance  $r$  (i.e., nearby trees tended to have a different height). In such situation, we expected that competition would result in pairs of MB individuals located close to each other having different heights (hypothesis 4).

For the MCF and MVF analyses, we randomized the marks over all trees, i.e., we repeatedly shuffled the tree height values between pairs of nearby trees until the potential spatial structure in the marks was revealed; thus, we implemented the null model based on an independent marking null model [39,41].

All of the spatial analysis functions were computed in Programita software (Programita 2014, Germany) using a non-grid approach and a ring width of 1 m for all of the functions. Details on the functions used, null models, and edge correction are given in Wiegand and Moloney (2004) [30]. Monte Carlo simulations were simulated to investigate whether the significant departure from a null model process, the 5th lowest and 5th highest of 999 Monte Carlo simulations of appropriate null models were used to construct simulation envelopes for  $g(r)$ ,  $k_{mm}(r)$ , and  $\gamma_{mm}(r)$  functions [40]. We also used a goodness-of-fit (GoF) to summarize the overall fit of null models for a given test statistic; higher values of GoF mean a stronger spatial pattern than lower values. If the rank of the test was larger than 950 (990), the data showed a significant or extremely significant departure from the null model with an error rate  $\alpha = 0.05$  (extremely significant departure,  $\alpha = 0.01$ ). We combined the test statistics of the three replicate plots (for early, middle, and later plots) into a single test statistic [39]. Other analyses and

graphics were performed using R–software (R 3.3.2, package Spatstat 1.48; <http://www.R-project.org/>) and Excel software (Excel 2016, USA).

### 3. Results

#### 3.1. Stand Structure and Composition

All stands were composed of moso bamboo (MB) and native trees (NTs) except the early plots (the native forest in early plot had not been invaded by moso bamboo), but the stand community structure and composition were quite different (Table 2). The importance value (IV) and density of MB was lower in middle plots ( $IV_{\text{early}} = 0.38 \pm 0.14$ ,  $D_{\text{early}} = 1311 \pm 706$ ) and much higher in later plots ( $IV_{\text{middle}} = 0.71 \pm 0.08$ ,  $D_{\text{middle}} = 1956 \pm 286$ ). In contrast to MB, the IV and density of NTs were highest in early plots ( $IV_{\text{early}} = 1$ ,  $D_{\text{early}} = 2478 \pm 212$ ) and lowest in later plots ( $IV_{\text{later}} = 0.29 \pm 0.08$ ,  $N_{\text{later}} = 494 \pm 224$ ). Regarding the sizes of individuals in the community, the average tree height of MB was increased from  $9.25 \pm 0.26$  m to  $11 \pm 1.04$  m, while that of the native trees declined from  $4.79 \pm 0.43$  m to  $3.4 \pm 0.88$  m. The average DBH of MB individuals were lower in the later plots than in the middle plots, being  $10.29 \pm 1.02$  cm and  $10.17 \pm 0.25$  cm, respectively. The average DBH of NT individuals decreased from  $7.8 \pm 1.53$  m to  $6.77 \pm 1.73$  m during the expansion of bamboo.

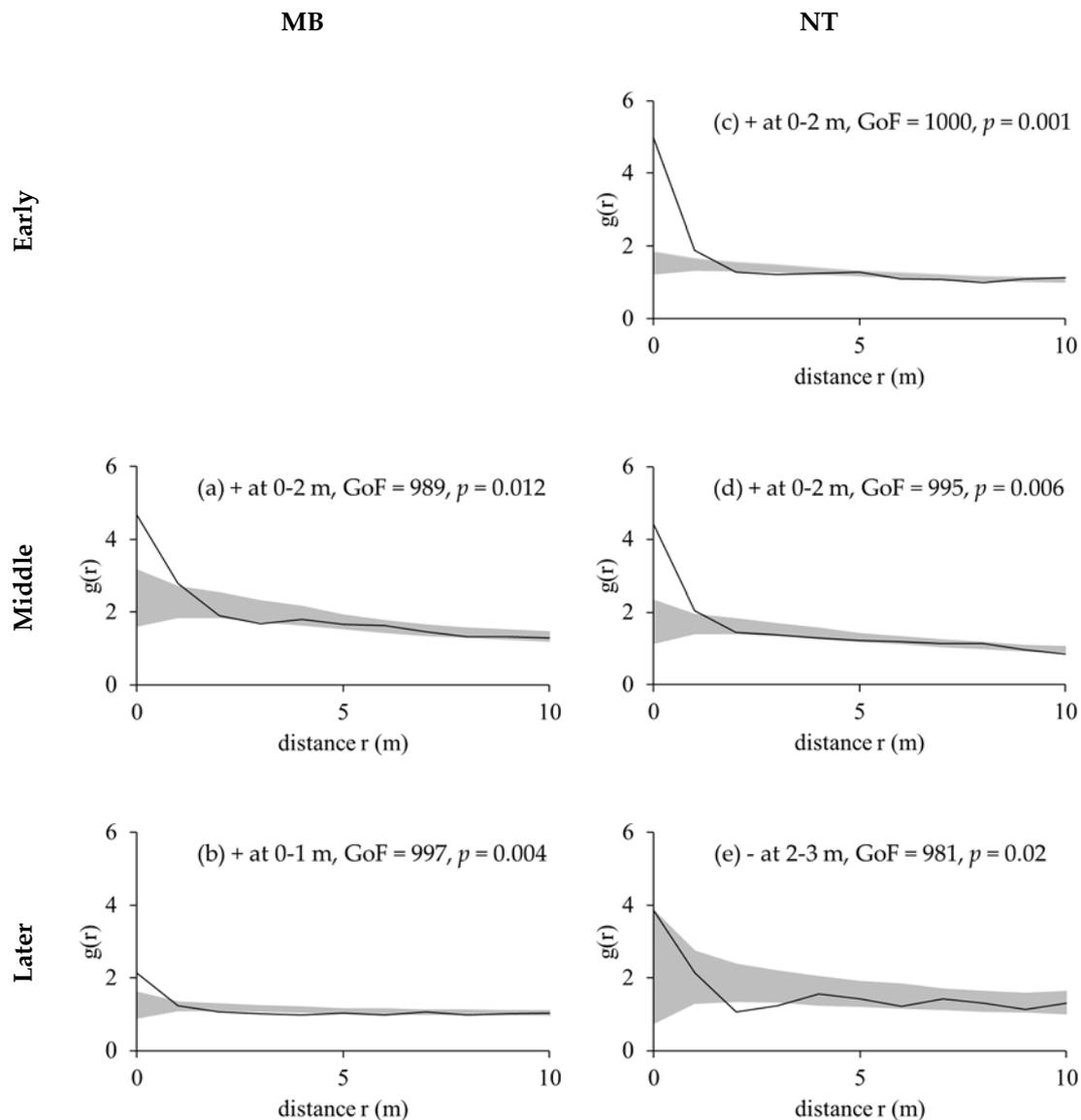
**Table 2.** Stand structure and composition in three expansionary phases of bamboo (values presented are means  $\pm$  standard deviation in replicated plot level). MB: moso bamboo; NTs: native trees.

Traits	Phases of Bamboo Expansionary					
	Early		Middle		Later	
	MB	NTs	MB	NTs	MB	NTs
Tree Density (D)/(ha <sup>-1</sup> )	-	2478 $\pm$ 212	1311 $\pm$ 706	1464 $\pm$ 143	1956 $\pm$ 286	494 $\pm$ 224
Height/(m)	-	4.79 $\pm$ 0.43	9.25 $\pm$ 0.26	4.16 $\pm$ 0.56	11 $\pm$ 1.04	3.4 $\pm$ 0.88
DBH/(cm)	-	7.8 $\pm$ 1.53	10.29 $\pm$ 1.02	7.66 $\pm$ 1.66	10.17 $\pm$ 0.25	6.77 $\pm$ 1.73
Importance Value (IV)	-	1	0.38 $\pm$ 0.14	0.62 $\pm$ 0.14	0.71 $\pm$ 0.08	0.29 $\pm$ 0.08
Shannon-Weiner in plot		2.46 $\pm$ 0.12		1.9 $\pm$ 0.24		0.89 $\pm$ 0.23

Tables 1 and 2 show that the community in early plots were dominated by south subtropical rainforest native trees ( $IV_{\text{early}} = 1$ ), but moso bamboo (MB) has gradually replaced many NTs and has become the dominant species in the middle and later plots ( $IV_{\text{later}} = 0.29 \pm 1.66$ ,  $IV_{\text{later}} = 0.29 \pm 0.08$ ). Compared with early plots dominated by NTs, the IV of NTs and species richness (the Shannon-Weiner index) in middle and later plots declined from  $2.46 \pm 0.12$  to  $0.89 \pm 0.23$ . This above result indicates that the bamboo had been permanently planted in the native forest community, which impacted the community composition and species diversity, thereby verifying hypothesis 1.

#### 3.2. Competition Regular Spatial Distribution Patterns of Tree Species

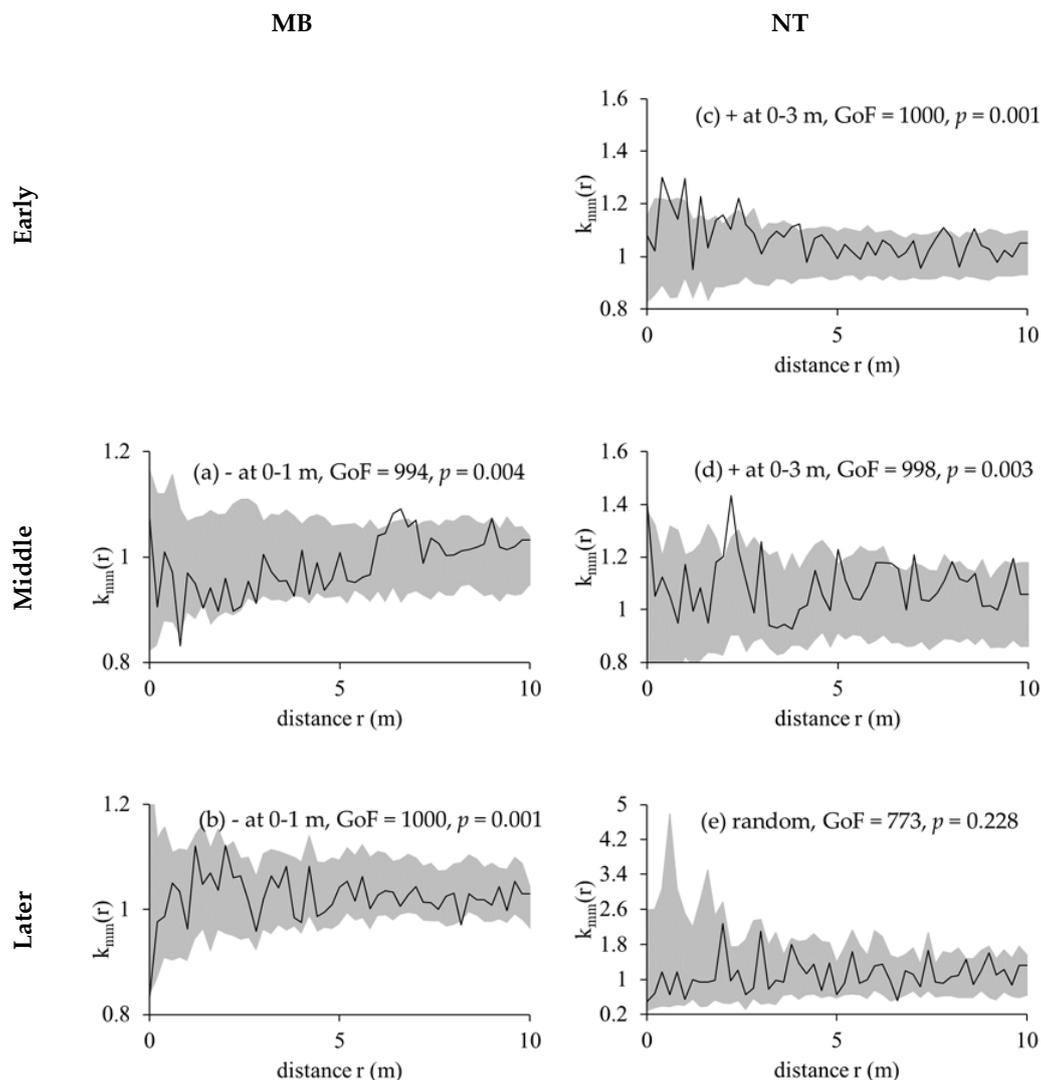
The distance-based univariate spatial point pattern analysis showed that the moso bamboo (MB) forest displayed a significant aggregated distribution pattern at scales of 0–2 m and 0–1 m (Figure 3a,b) in the middle and later plots. The mixed spatial pattern of residual native tree (NT) individuals in the community displayed a significantly aggregated distribution pattern at the 0–2 m scale (Figure 3c) in early plots dominated by NT species. With the bamboo expansion, in terms of the spatial pattern, the aggregation scale of NT forest decreased and finally displayed a significantly regular distribution pattern in the later plots at the 2–3 m scale (Figure 3e). This indicates that the spatial distribution pattern of native forests changed to a more regular distribution at a smaller spatial scale, also in agreement with hypothesis 2. All pair-correlation function tests were significant or extreme significant departures from the null model (Figure 3).



**Figure 3.** Pair-correlation functions of MB (moso bamboo, **a,b**) and NT (native forest, **c,d,e**) in different bamboo expansionary phases for all of nine plots (with the early, middle, and later phases each represented by three plots). Black solid lines denote the observed pair-correlation function. The envelopes (grey areas) denote the range of the pair-correlation function of a random spatial distribution pattern and were constructed using 99% quantiles of 999 Monte Carlo simulations based on the heterogeneous Poisson process null model. If the rank of the test was larger than 950 (990), the data showed a significant or extremely significant departure from the null model with an error rate  $\alpha = 0.05$  (extremely significant departure,  $\alpha = 0.01$ ). An aggregated or regular distribution pattern of points is implied if the observed curve lies above or below the simulation envelopes, respectively.

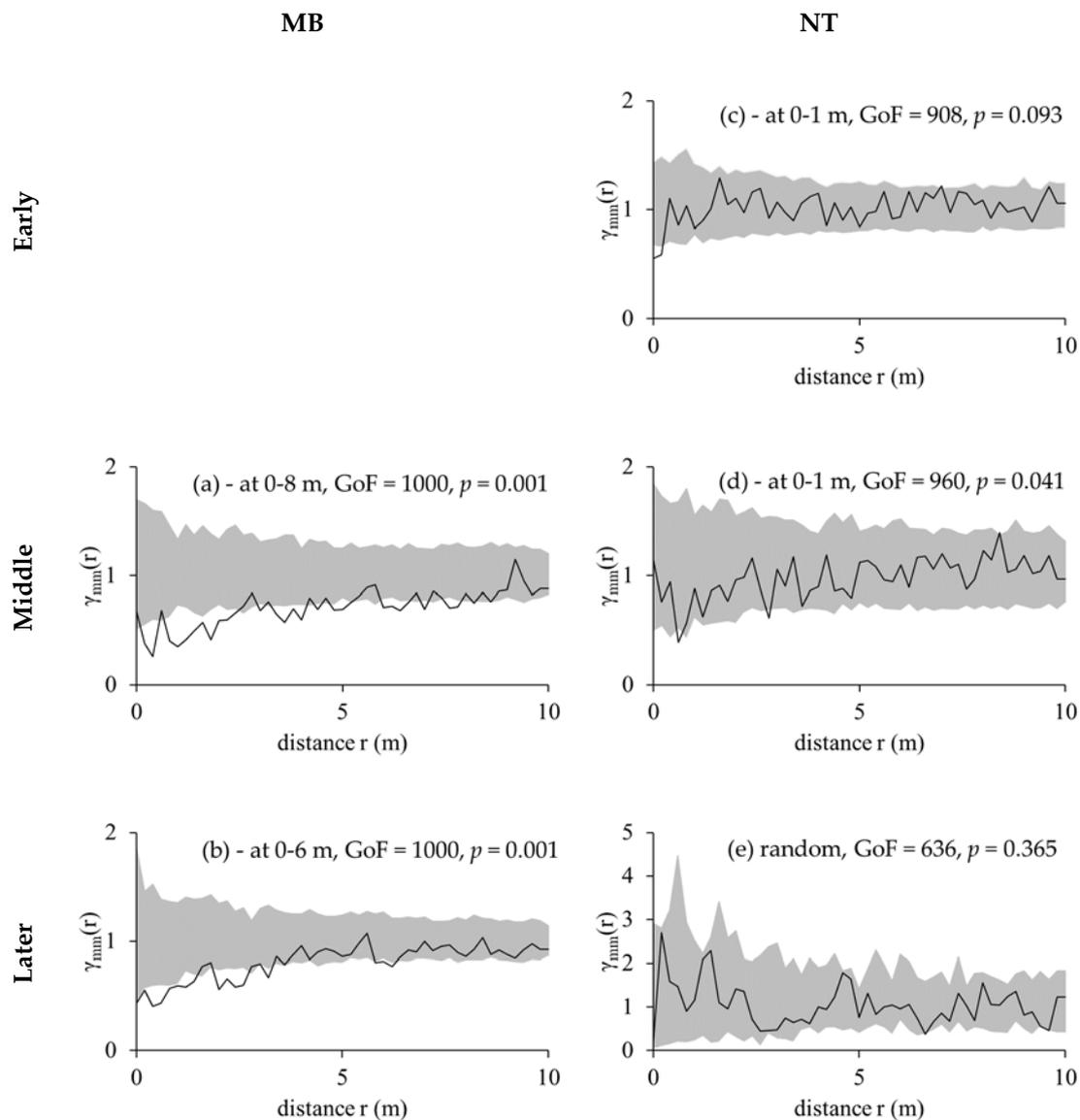
### 3.3. Competition Cause Size Correlation and Autocorrelation

The marked correlation analysis explored the spatial correlation in the marks of tree height; the result found that the tree heights of MB close to each other (at 0–1 m) were significantly smaller than the population average (Figure 4a,b) in middle and later plots, which is in agreement with hypothesis 3. In contrast, the tree height marked correlation analysis of the NT community in early and middle plots showed that larger trees in the native forest had a mostly aggregated distribution (Figure 4c,d) at the smaller spatial scale of 0–3 m, while there was no significant correlation at any scale in later plots (Figure 4e).



**Figure 4.** Mark correlation functions of MB (moso bamboo, **a,b**) and NT (native forest, **c,d,e**) in different bamboo expansionary phases for early, middle, and later plots. Black solid lines denote the observed mark correlation function. The envelopes (grey areas) denote the range of the mark differentiation function of a random assignment of tree size marks and were constructed using 99% quantiles of 999 Monte Carlo simulations based on the independent marking null model. Observed lines that fall above the simulation envelopes indicate that the sizes of neighbouring trees were significantly larger than the population average. Observed lines that fall below the simulation envelopes indicate trees heights of individuals close to each other that were smaller than the population average. If the rank of the test was larger than 950 (990), the data showed a significant or extremely significant departure from the null model with an error rate  $\alpha = 0.05$  (extremely significant departure,  $\alpha = 0.01$ ).

The marked variogram function analysis describes the spatial autocorrelation in the marks of tree heights. The result found that the tree heights of neighbouring individual bamboos displayed an extremely significant positive correlation (Figure 5a,b) at the scales of 0–8 m and 0–6 m in the middle and later plots, respectively, which is in agreement with hypothesis 4. This indicates that the individual bamboos with nearer mutual distances had similar heights, and that competition did not influence the growth of other trees. The analysis using marked variograms of tree heights of native forest species found a very weak, not extremely significant positive correlations ( $p_{\text{early}} = 0.093$ ,  $p_{\text{middle}} = 0.041$ ) at the scale of 0–1 m in the early and middle plots (Figure 5c,d). In later plots, after the bamboo expansion had occurred, no significant correlation was observed at any scale ( $p_{\text{later}} = 0.365$ ) (Figure 5e).



**Figure 5.** Marked variogram functions of MB (moso bamboo, **a,b**) and NT (native forest, **c,d,e**) in different bamboo expansionary phases for all of nine plots (the early, middle, and later phases were each represented by three plots). Black solid lines denote the observed pair-correlation function. The envelopes (grey areas) denote the ranges of the mark differentiation function of a random assignment of tree size marks and were constructed using 99% quantiles of 999 Monte Carlo simulations based on the independent marking null model. Observed lines that fall above the simulation envelopes indicate an aggregation of different tree sizes. If the rank of the test was larger than 950 (990), the data showed a significant or extremely significant departure from the null model with an error rate  $\alpha = 0.05$  (extremely significant departure,  $\alpha = 0.01$ ).

The positive correlation of the mark correlation and negative autocorrelation of variogram at small distances in middle and later plots (Figure 4a,b and Figure 5a,b) indicate that the number of small moso bamboos with similar size that were close to one another increased after bamboo expansion and eventually dominated the native forest. In this case, small bamboo individuals had small neighbours with similar size and large ones had large neighbours, which could diminish the size hierarchy of the forest community.

## 4. Discussion

Bamboo invasion and expansion within natural forest communities in China has had a strong impact on the community structure and composition as well as the species diversity of the native forests [9,17,25]. The moso bamboo colonized and expanded as an invasive species in the native forest community approximately 40 years ago in our stands and had eventually replaced adjacent native forests and became the dominant species in the middle and later plots (Tables 1 and 2). With the differences in the density and importance value of individual trees (MB and NT), the spatial distribution pattern in the community changes as well. Based on spatial point patterns analyses, we analysed the different stand structures and spatial distribution patterns of all nine plots in order to try to illustrate how the ecological processes of tree–tree competition have shaped the community spatial patterns and to examine the spatial competitive strategy of individual bamboo trees as they grow and occupy space in the native forest community.

### 4.1. Different Space Regulation Mechanisms in Moso Bamboo and Native Forest

The importance of density-dependent mortality effects in making the tree spatial distribution more regular has often been noted, especially in survivor trees in late-successional stages [29,33,35,47–49], because strong competition may eliminate suppressed neighbour trees in more crowded environments due to increasing demand on scarce resources. However, previous studies have mainly focused on tree propagation through seeds and seedlings [29,33,35,36]; analyses of density-related regulation mechanisms in vegetative regeneration are still lacking [32]. In our study, we found density-dependent mortality effects also exert a weak impact on vegetative regeneration of bamboo expansion. The results showed that the spatial pattern of MB forest only displayed a significant aggregated distribution pattern at fine scales in later plots, but otherwise had a very weak, non-significant tendency towards regular distribution. However, we found that the mixed spatial pattern of the residual survival native tree species in later plots (which had the lowest NT density) displayed a significant regular distribution trend (Figure 3e, Table 2), indicating that the conspecific density-dependent mortality mechanism obviously regulated the spatial pattern of the native forest community after invasion by the bamboo.

Here, we suggest that regulation mechanisms of density-dependent mortality effects in moso bamboo and the native forest tree species are different; the change in spatial pattern of moso bamboo did not strictly follow a negative density-related mechanism during the processes of colonization and expansion in the native forest community. Our explanation for the difference is that all plots were in different stages of succession; although there was a significant increase in the tree density of bamboo in the middle and later plots, the competitive effects in the MB population were not sufficient to cause substantial death of MB individuals. Previous research has shown that mature trees in bamboo forests can be maintained at a high density without substantial self-thinning [8,9,15,16]. Meanwhile, strong competition may cause native trees that are close to each other to die, especially in more crowded environments, such as in the middle and later plots. In this situation, random thinning could result in a more regular spatial pattern than normally observed during early succession. We suggest that such a phenomenon in moso bamboo is reflected in its spatial strategy of expansion and was related to the vegetative regeneration and physiological characteristics of bamboo forests. This point will be further discussed below.

### 4.2. Bamboo Expands through Small Clonal Patches

The moso bamboo in our study stand is characterized by its aggressive expansionary underground rhizomes [20]. The bamboo forms clonal patches composed of essentially clonal individuals in the form of shoots via the rapidly reproducing underground bamboo root [7–10]. Previous research on the expansion of bamboo plants mainly focused on larger spatial scales, with the size of clonal patches being over 150 m in length [7,8]. However, spatial distribution pattern analysis of plant species at smaller scales can detect the corresponding ecological processes [32,40,41]. Thus, we focused on the

bamboo expanding in the native forest community at a smaller scale. In the pair-correlation analysis, we did not observe that expansion of bamboo and an increase in density result in spatial regulation in MB forest. In such a situation, the distance-based point pattern analysis results may be ambiguous concerning the competitive relationship [35,41]. Thus, we adopted marked variogram and marked correlation analysis to detect the density-dependent sizes reduction and autocorrelation caused by competition in neighbouring individual growth (tree height), and found that smaller-sized (tree height) MB individuals displayed a significantly aggregated distribution at the fine scale (0–1 m) in the middle and later plots (Figure 4a,b). This indicates that after the moso bamboo had expanded and become dominant in the native forest, large mature bamboo were more or less randomly distributed, and small bamboo trees in clusters formed patches that grew around the larger mature trees as the mode of patch expansion in the native forest community.

This mechanism is similar to that in which rhizomes of perennial plants lead to a spreading genet architecture and populations consisting of clonal patches [50]. Underground rhizomes formed by the mature bamboos disperse in the native forest and sprout small clonal ramets of bamboo [7,8,15–19]. We infer that the clonal ramets of moso bamboo in our research areas are distributed in clusters for patch expansion, and that such clonal patches rapidly occupied the native forest community space.

#### 4.3. The Size Equality and Competition in Nearby Bamboo

During the last two decades, the mark variogram has been used as a powerful statistical analysis tool in ecology and forestry; negative or positive autocorrelations from variograms appearing during periods of forest succession and development have been well documented [37–39,44,51,52]. In our research, the variogram of tree height marks in the individual bamboos displayed a significant positive autocorrelation in all of the plots with different densities of moso bamboo (Figure 5a–c). Some authors have concluded that high mortality in clusters of small trees would reduce the probability (frequency) of pairs of superior trees and suppress trees at close proximity, thus yielding a positive autocorrelation in tree size [44,52]. In contrast, bamboo expansion and forest development have not resulted in spatial regulation and substantial self-thinning in our study stands, meaning that there has been no substantial death of small clonal bamboos. To explain the difference, we suggest that the positive spatial autocorrelation of moso bamboo sizes observed is caused by similar-sized trees existing as colony patches [37,42,44]. Moreover, although the increase in bamboo patch expansion and tree density will result in plant communities being more crowded, the competitive relationships in our plots did not result in a high frequency of neighbour dominance or suppression of trees.

We conclude that the competitive relationships in these small tree clusters in bamboo patches may reflect size-symmetric competition. The characteristics of the clonal plants themselves may determine or modify the competitive relationships in plants [53,54]. For example, *Phyllostachys pubescens* has the ability to translocate resources between interconnected ramets [55]. Furthermore, regarding the asymmetric sources of light in the forest, physiological integration in dwarf bamboo plants could support the growth of shaded shoots via the importing of assimilates from unshaded shoots [56]. Such support may result in symmetric (two-sided) individual competition [43,57]. We suggest that the equal tree sizes observed in bamboo patches may prevent size-asymmetric competition for the asymmetric and limited sources in the forest, resulting instead in size-symmetric competition characterized by low levels of density-dependent mortality compared to asymmetric competition [43,56]. This would prevent substantial self-thinning, thus enhancing the persistence of the moso bamboo in native forest.

#### 4.4. Management of Moso Bamboo in Forests

Although the expansion of bamboo has caused negative effects on natural forest and species diversity [25,27,28], different from the common invasive species, moso bamboo has had high economic value and plays an important role in traditional human economic activities [10,12,13]. Some strategies for controlling bamboo invasions have been previously proposed. Suzuki and Nakagoshi (2008) claimed that management factors (e.g., bamboo-shoot harvest) strongly affected bamboo expansion in

typical bamboo production regions in eastern and western Japan [7]. Cai et al. (2003) proposed the method of digging ditches and filling them with water in order to inhibit of expansion of underground rhizomes [58]. Although these forces can restrict the speed and range of a bamboo invasion, they can be difficult to implement for a long time in situations of continuously rising labour costs. On the other hand, we suggest that decision makers should balance the importance of economic development and ecological protection. Indeed, economic development must be fully integrated with strategies for maintaining biodiversity and resource conservation, especially in impoverished areas. Specific opinions are as follows. Firstly, publicity and education need to be promoted in order to enhance the concept and awareness to ecological protection. Secondly, to be successful in the long run, when formulating and implementing conservation policies restricting bamboo forest cultivation and management there is a need for greater consideration of the potential impacts and benefits to indigenous people. Thirdly, bamboo forest cultivation should avoid areas near ecologically sensitive areas in order to reduce the risk of biological loss.

## 5. Conclusions

In summary, our study illustrated how fine-scale spatial analyses can help to establish a better understanding of the ecological processes involved in bamboo expansion in native forests. The research showed that the moso bamboo has colonized and expanded within the native forest, leading to many native trees (NTs) gradually being replaced, thereby reducing species diversity. Pair-correlation analysis demonstrated that moso bamboo was not regulated by negative density-related mechanisms, so that mature individuals could be maintained at a high density. Marked correlation functions demonstrated that plants located close to each other were on average smaller than the population mean, indicating that small bamboo in clusters form colony patches that grow around the larger mature trees, resulting in patch expansion in the native forest community. Mark variogram functions indicated significant positive spatial autocorrelation of moso bamboo caused by similar-sized trees existing in colony patches, indicating that competitive relationships did not result in a high frequency of neighbouring superior trees and suppressed trees in bamboo forest. We conclude that moso bamboo has dominated the native forest community in part of our research stand. Compared to the native forest species, the clonal patch expansion and equal tree size in colony patches of moso bamboo may reduce the regular distribution trend, preventing substantial self-thinning and size-asymmetric competition. This spatial expansion strategy enhances the persistence of moso bamboo in native forests in our study area in a south subtropical rainforest in a river valley.

In this paper, our study mainly revealed how bamboo in native forest competes and partitions space at a fine scale (tree to tree competition processes mainly occur at such scale [32–37]). Combined with previous relevant studies [8,9,11,17,22,25–28], we believe that the potential negative impacts of bamboo expansion should be considered by farmers and policy makers. Furthermore, in order to build upon the findings of this study, related research with more independent replicated plots and larger areas of plots should be carried out in the future. Knowledge gained from such research will help to restrain the arbitrary expansion of bamboo plants, which may be especially for the protection of rare and endangered species.

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