Postprint of Species Composition Changes and Community Structure Dynamics of Secondary Savanna Shrubland in Dry-Hot Valleys

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Abstract

To reveal the successional dynamics of secondary savanna shrubland communities in the dry-hot valleys of the Sichuan Panzhihua Cycas National Nature Reserve, this study investigated a 1 hm^2 permanent plot established within the community in 2015. Through the first re-survey in 2020, we examined species composition, community diversity, importance values, mortality rates, recruitment rates, and diameter at breast height (DBH) to analyze the dynamics of community species composition and structure over the 5-year period. The results showed that: (1) In 2020, the community contained 18 woody species belonging to 15 families and 18 genera, representing an increase of 1 genus and 1 species compared to 2015. While the composition of dominant species remained unchanged, their dominance exhibited significant changes. Among the six populations with importance value (IV) > 1, five tree species showed increased IV, while only the Cycas panzhihuaensis population exhibited decreased IV, though it remained the dominant constructive species in the community. The dominance of tree populations such as Quercus cocciferoides and Terminalia franchetii increased significantly. (2) In 2020, the number of woody individuals with DBH ≥ 1 cm in the community increased to 1,710, and the mean DBH increased from 11.10 cm to 11.17 cm. The annual mortality rate of the community was 0.29%, with a mean DBH of 11.84 cm for dead individuals. The annual recruitment rate was 2.75%, with a mean DBH of 4.96 cm for recruited individuals. Individual mortality occurred in seven populations, while recruitment occurred in nine populations. (3) Although the population size of Osyris wightiana decreased, nine populations expanded and four populations remained stable. The mean DBH of Cycas panzhihuaensis and Osyris wightiana populations decreased, while the mean DBH of all other populations increased to varying degrees. As forest succession proceeds, the importance of interspecific competition within the community will gradually increase. Tree species such as Quercus cocciferoides and Terminalia franchetii will occupy dominant positions in future successional processes, but they will not threaten the dominant status of the Cycas panzhihuaensis population in the short term. The death of large-diameter individuals was the main reason for its significantly reduced dominance. In future community succession, Cycas panzhihuaensis will form a transitional secondary forest community with tree species such as Quercus cocciferoides and Terminalia franchetii, representing a dry-hot valley secondary savanna shrubland where tree species gradually gain dominance during succession toward a climatic climax community.

Full Text

Dynamics of Community Composition and Structure in Secondary Savanna Shrub Forest of Arid-Hot Valley in National Nature Reserve of Cycas panzhihuaensis

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Abstract: To reveal the successional dynamics of secondary savanna shrub forest communities in the arid-hot valley of the National Nature Reserve of Cycas panzhihuaensis, this study examined a 1 hm^2 permanent plot established in 2015 and re-censused in 2020. Community dynamics over the past five years were analyzed through investigations of species composition, community diversity, importance values, mortality rates, recruitment rates, and diameter at breast height (DBH). The results showed: (1) In 2020, the community contained 18 woody species belonging to 15 families and 18 genera, representing an increase of one genus and one species compared to 2015. While the dominant species composition remained unchanged, their dominance shifted significantly. Among the six populations with importance values (IV) > 1, five species showed increased IV, while only the Cycas panzhihuaensis population decreased, though it remained the dominant constructive species. Arbor species such as Quercus cocciferoides and Terminalia franchetii exhibited significantly increased dominance. (2) By 2020, the number of woody individuals with DBH ≥ 1 cm increased to 1,710, with mean DBH rising from 11.10 cm to 11.17 cm. The annual mortality rate was 0.29% (mean DBH of dead individuals: 11.84 cm), while the annual recruitment rate was 2.75% (mean DBH of recruits: 4.96 cm). Seven populations experienced individual mortality, and nine populations showed recruitment. (3) Although the Osyris quadripartita population decreased in size, nine populations expanded and four remained stable. Mean DBH decreased only in Cycas panzhihuaensis and O. quadripartita, while all other populations showed varying degrees of increase. As forest succession progresses, the importance of interspecific competition will gradually increase. Arbor species such as Q. cocciferoides and T. franchetii will occupy dominant positions in future successional processes, though they will not threaten the dominant status of C. panzhihuaensis in the short term. The death of large-diameter individuals is the primary reason for the significant decline in its dominance. In future community succession, C. panzhihuaensis will form a transitional secondary forest community with Q. cocciferoides, T. franchetii, and other arbor species, gradually shifting from a secondary savanna shrub forest toward a climatic climax community where arbor species become increasingly dominant.

Keywords: species composition, community diversity, community succession, secondary savanna shrub forest of arid-hot valley, National Nature Reserve of Cycas panzhihuaensis

Introduction

The formation and maintenance mechanisms of forest biodiversity can be studied at different scales. At the community scale, the mechanisms underlying species diversity formation and maintenance are inseparable from the structural characteristics of forest communities (Zang et al., 2001). Forest community structure and species composition dynamics not only form the basis of ecosystem processes and functions but also represent the long-term outcome of interactions between organisms and their environment. These dynamics influence carbon sequestration and material turnover rates in forest ecosystems (Xiao et al., 2014), reflect community productivity levels (Zhang & Chen, 2015), and determine community resilience to disturbances (Jayakaran et al., 2014). Furthermore, they provide crucial information for understanding forest community successional patterns (Tilman et al., 2006) and revealing mechanisms of species coexistence and biodiversity maintenance (Loreau et al., 2001).

Regarding forest community structure and characteristics, international scholars have conducted relevant studies across various forest types, including the Himalayan region (Shaheen et al., 2012), clear-cut areas in Panama (Hooper et al., 2004), tropical forests in Malaysia (Khairil et al., 2014), and tropical montane cloud forests (Shi & Zhu, 2009). These studies have found that forest community structure is closely related to factors such as elevation, slope, human activities, fire disturbance, and soil properties. Some researchers have compared the effects of moisture gradients on plant species richness, diversity, and community composition under grazed versus ungrazed conditions (Meyers et al., 2014), revealing spatial autocorrelation patterns where human disturbance and moisture gradients influence community structure and species diversity in opposite directions, and demonstrating how different community management practices and invasive species spread drive community changes. Correspondingly, numerous domestic studies have also emerged (Fang et al., 2004; Long et al., 2011; Sheng et al., 2012; Xu et al., 2013), most of which are based on large permanent forest plots (Ye et al., 2008; Zhu et al., 2008; Hu et al., 2010; Liu et al., 2011; Xu & Jin, 2012; Kuang et al., 2014). This indicates that establishing permanent plots for forest community research is widely recognized and has become a key direction in forest biodiversity research (He et al., 1998).

In recent years, forest community succession studies based on permanent plots have emerged from different perspectives, covering species composition (Chen, 2009), population dynamics (Ji, 2016), community structure (You et al., 2016), seedling regeneration (Liu et al., 2017), growth forms (Wang et al., 2011), and community diversity (Ni, 2014). Some scholars have attempted to explore community successional mechanisms from the perspective of forest community dynamics (Pickett & McDonnell, 1989), involving different regions and forest types (Gao et al., 2013). These studies have not only elucidated habitat fluctuation constraints and density-dependent mechanisms affecting forest community population dynamics and regeneration (Wang et al., 2011) but also summarized artificial afforestation patterns similar to natural forest regeneration (Chen et al., 2021) and proposed integrated research concepts for forest community succession and assembly mechanisms (Chang & HilleRisLambers, 2016).

Arid-hot valleys represent ecologically fragile regions with severe soil erosion (Yang et al., 2002; Ming & Shi, 2007; Peng et al., 2013). Characterized by a "three-dimensional climate based on the south subtropical zone," these areas experience high temperatures, drought, and high evaporation rates. Although plant species are relatively scarce, China-endemic and endangered species are distributed here (Yang et al., 2015), developing special valley-type semi-savanna and savanna plant communities dominated by grasses and succulent, thorny shrubs (Jin & Ou, 2000; Jin, 2002; Ma & McConchie, 2001). Domestic arid-hot valley forest communities are mainly distributed in Yunnan and Sichuan provinces (Ma & McConchie, 2001). Current research on arid-hot valley forest communities has primarily focused on community structure (He et al., 2020), plant biomass (Yuan et al., 2020), biodiversity (Liu et al., 2020; Zhang et al., 2020), and plant utilization of soil nutrients and water (Lin et al., 2019) in Yunnan' s arid-hot valleys.

The secondary savanna shrub forest of the arid-hot valley within the National Nature Reserve of Cycas panzhihuaensis is located in the experimental zone of the reserve at elevations between 1,500 m and 2,300 m. This community represents a secondary savanna shrub forest formed on mountain leeward slopes after degradation due to human disturbance (grazing) and year-round seasonal foehn effects, with low shrubs and herbaceous plants as constructive species. It is in the initial stage of secondary succession toward the climatic climax (evergreen coniferous-broadleaved mixed forest of arid-hot valley) (Ma & McConchie, 2001). Currently, studies on plant community dynamics and succession in arid-hot valleys based on permanent plots are still rare, and research on secondary savanna shrub forests in the National Nature Reserve of Cycas panzhihuaensis has not yet begun. Based on a 1 hm^2 permanent plot in the secondary savanna shrub forest of the arid-hot valley within the National Nature Reserve of Cycas panzhihuaensis, this study compared and analyzed tree census data from 2015 and 2020 to address the following scientific questions: (1) How does 5-year secondary succession affect community species composition, diversity, and dominance? (2) Do population dynamic characteristics of various species change according to forest successional patterns? (3) Can community secondary succession promote changes in dominant species?

1.1 Study Area Overview

The study site is located in the National Nature Reserve of Cycas panzhihuaensis (101°32 15 -101°35 46 E, 26°36 31 -26°38 24 N) at the southeastern front edge of the Hengduan Mountains where it transitions to the Yunnan-Guizhou Plateau, at the border of Sichuan and Yunnan provinces. This area represents a typical section of the Jinsha River valley, characterized by steep terrain, deep valley incision, large relative mountain height, and enclosed topography. The reserve protects the arid-hot valley evergreen coniferous-broadleaved mixed forest ecosystem and its associated wildlife, plants, and landforms (valley landscapes). The total area of the reserve is 13.58 km^2. Influenced by the arid-hot valley climate effect, the study area belongs to the south subtropical semi-arid valley climate type, with mild winters, abundant sunshine, and rich heat resources. The annual mean temperature is 19.7-20.5°C, the highest in Sichuan Province. May is the hottest month, while December or January is the coldest. The rainy season extends from early June to October, and the dry season from November to May of the following year, with over 300 frost-free days annually.

The terrain slopes from northwest to southeast, with the Fengjia Ridge traversing the north and numerous “chicken-claw ridges” running longitudinally. The highest elevation is 2,259.6 m (Tuanshanbao), and the lowest is 1,120 m (the intersection of Houzigou and the reserve boundary), with a relative elevation difference of 1,139.6 m. Most rocks in the area are Sinian Dengying Formation limestone and Ordovician dolomitic limestone. Soil development shows obvious vertical distribution characteristics: red limestone soil below 1,500 m elevation, and brownish-yellow limestone soil above 1,500 m. The zonal climax vegetation is arid-hot valley evergreen coniferous-broadleaved mixed forest. The main dominant species in the study plot include Cycas panzhihuaensis, Quercus cocciferoides, Terminalia franchetii, and Morus mongolica (Yang et al., 2015).

1.2 Data Collection

From July to October 2015, following the monitoring plot establishment methods of the Smithsonian Tropical Research Institute’ s Center for Tropical Forest Science (CTFS), a 1 hm^2 (100 m × 100 m) permanent plot was established in the secondary savanna shrub forest of the arid-hot valley within the National Nature Reserve of Cycas panzhihuaensis using a total station electronic tachometer (GTS-102N, Topcon Corporation, Tokyo, Japan). The plot was divided into 400 subplots of 5 m × 5 m. All woody plants with diameter at breast height (DBH) $\geq$ 1 cm were tagged and surveyed, recording scientific names, DBH, height, and coordinates for each plant. Specimens were collected for laboratory identification when field identification was not possible. A re-census was conducted in October 2020. For newly emerged woody individuals with DBH $\geq$ 1 cm (recruits), the same survey method as in 2015 was applied. For existing individuals with DBH $\geq$ 1 cm, only DBH, height, and growth status were recorded.

The initial survey identified 1,512 woody plant individuals (including branches and sprouts) with DBH $\geq$ 1 cm, belonging to 17 species, 17 genera, and 15 families. The community was dominated by Cycadaceae, Fagaceae, and Combretaceae, with C. panzhihuaensis as the constructive species. Other dominant populations included Q. cocciferoides, T. franchetii, M. mongolica, Diospyros dumetorum, and Albizia kalkora.

1.3 Data Analysis Methods

The Flora of China (FOC) (http://www.iplant.cn/foc/) and Flora Reipublicae Popularis Sinicae (FRPS) (http://www.iplant.cn/frps) online databases were consulted to verify scientific names and growth forms of woody plant species in the plot. Importance value was used to characterize species dominance in the community (Ye et al., 2008), calculated following methods in *Plant Community Ecology* (Wang, 1987) and *Experimental Manual of Plant Community* (Wang et al., 1996). Importance value (IV) = [Relative Density (RD) + Relative Frequency (RF) + Relative Prominence (RP)]/3. Relative Density (RD) = (Density of a single population (D) / Sum of densities of all populations) × 100, where single population density (D) = Number of individuals in the population / Sample area. Relative Frequency (RF) = (Frequency of a population (F) / Sum of frequencies of all populations) × 100, where population frequency (F) = Number of subplots where the population occurs / Total number of subplots. Relative Prominence (RP) = (Prominence of a population (P) / Sum of prominence of all populations) × 100, where population prominence (P) = Sum of cross-sectional areas at breast height of all individuals in the population.

Three widely used diversity indices were selected to measure community species diversity (Zhang, 2011). The formulas are as follows:

Shannon-Wiener diversity index (H):

Pielou evenness index (E):

Margalef richness index (RM):

In formulas (1), (2), and (3), S represents the total number of species in the plot; NN represents the total number of individuals of all species in the plot; Pi represents the proportion of species i individuals among all individuals, where Pi = ni/NN; and ni represents the number of individuals of species i.

Population and community changes were analyzed using mortality rate (m), recruitment rate (r), and population size change rate (λ) (Condit et al., 1999). The calculation formulas are:

In formulas (4), (5), and (6), t is the survey interval time; n_0 and n represent population sizes at the first survey and after time t, respectively; and S represents the number of surviving individuals after time t.

Data analysis was performed using Excel, and figures were created using OriginPro 8.0.

2.1 Changes in Community Species Diversity

From 2015 to 2020, the community' s woody plant species increased from 15 families, 17 genera, and 17 species to 15 families, 18 genera, and 18 species. Three species recorded in 2015 disappeared due to mortality in the 2020 survey, while four new species were recorded in 2020. The number of dead individuals and recruited individuals were equal for both disappeared and newly recorded species (Table 1). The Shannon-Wiener diversity index showed the greatest change, increasing by 16.11%, followed by the Margalef richness index, while the Pielou evenness index showed the smallest increase (Table 2).

Table 1 Death and new recorded species in community from 2015 to 2020

Species	No. of individuals	Growth form	Remark
Leucaena leucocephala		Shrub	Disappeared populations due to death in 2020
Trema levigata		Arbor	
Toxicodendron succedaneum		Arbor	
Dalbergia obtusifolia		Arbor	
Solanum erianthum		Arbor	
Fraxinus trifoliolata		Shrub	
Populus yunnanensis		Arbor	
Dalbergia obtusifolia		Arbor	New recorded species in 2020
Solanum erianthum		Arbor	

Species	No. of individuals	Growth form	Remark
Fraxinus trifoliolata		Shrub	
Populus yunnanensis		Arbor	

Table 2 Change of community species diversity from 2015 to 2020

Year	Numbers of individuals	Shannon-Wiener index	Margalef index	Pielou index
2015				
2020				

2.2 Changes in Dominance of Major Populations

Among common populations with importance values greater than 1, only one population showed decreased importance value, while the other five increased to varying degrees. Cycas panzhihuaensis remained the constructive species, but its importance value decreased significantly from 69.70 (2015) to 42.35 (2020). The populations with the largest importance value increases were Q. cocciferoides and T. franchetii, rising from 13.04 (2015) and 6.23 (2015) to 25.46 (2020) and 15.36 (2020), respectively. Additionally, importance values of M. mongolica (3.04–5.65), D. dumetorum (2.42–3.74), and A. kalkora (1.58–3.41) also increased to varying degrees (Figure 1 [Figure 1: see original paper]).

Figure 1 Change of importance values of common tree species in community from 2015 to 2020 (PZHST: *Cycas panzhihuaensis*; TXL: *Quercus cocciferoides*; DLR: *Terminalia franchetii*; MS: *Morus mongolica*; YS: *Diospyros dumetorum*; SH: *Albizia kalkora*)

2.3 Community Regeneration

From 2015 to 2020, the number of woody plant individuals with DBH $\geq$ 1 cm in the community increased from 1,512 to 1,710, a 13.1% increase. Twenty-two individuals died, and 226 individuals were recruited (excluding newly appearing species). The annual mortality rate was 0.29%, the annual recruitment rate was 2.75%, and the population size change rate was 2.46%.

Seven populations experienced individual mortality, accounting for 41.2% of the total number of populations in 2015. These included 8 individuals of C. panzhihuaensis, 8 of Q. cocciferoides, 2 of M. mongolica, 1 of T. franchetii, 1 of *Eriobotrya prinoides*, 1 of *Toxicodendron succedaneum*, and 1 of *Desmodium yunnanense*. Nine populations showed varying degrees of recruitment, accounting for 53.0% of total species, including 10 individuals of C. panzhihuaensis, 85 of Q. cocciferoides, 93 of T. franchetii, 14 of M. mongolica, 6 of D. dumetorum, 11 of A. kalkora, 3 of *E. prinoides*, 1 of *Ficus virens*, 2 of *Firmiana major*, and 1 of *D. yunnanense.* Five populations experienced both mortality and recruitment simultaneously, accounting for 29.4% of total species.

Annual mortality rates across populations ranged from 0% to 13.86%, and annual recruitment rates ranged from 0.18% to 21.97%. Nine populations increased in individual numbers, with population size change rates ranging from 0.04% to 21.97%. The population with the largest increase was *F. major*, while C. panzhihuaensis showed a relatively small increase. Four populations remained stable in individual numbers, and only one population (*Osyris quadripartita*) decreased (Table 3).

Table 3 Change of each population in community from 2015 to 2020

Species	Annual mortality rate (%)	Annual recruitment rate (%)	Rate of population size change (%)
Cycas panzhihuaensis			
Quercus cocciferoides			
Terminalia franchetii			
Morus mongolica			
Diospyros dumetorum			
Albizia kalkora			
Osyris quadripartita			
Vitex negundo			
Eriobotrya prinoides			

Species	Annual mortality rate (%)	Annual recruitment rate (%)	Rate of population size change (%)
Toona ciliata			
Ficus virens			
Sapindus saponaria			
Firmiana major			
Desmodium yunnanense			

Note: Disappeared populations due to death and new recorded species in 2020 were not listed in this table.

2.4 DBH Changes

From 2015 to 2020, mean DBH of the community increased from 11.10 cm to 11.17 cm, a 0.63% increase. Mean DBH decreased only in C. panzhihuaensis and O. quadripartita populations, from 12.59 cm and 6.82 cm to 11.35 cm and 3.65 cm, respectively (decreases of 9.81% and 46.57%). All other populations showed varying degrees of DBH increase, with growth rates ranging from 1.40% to 6.23% (Table 4).

The 22 dead individuals had a mean DBH of 11.84 cm. Among the nine dead individuals with DBH $>$ 10 cm, only one was *M. mongolica*, with the rest being C. panzhihuaensis. Individuals with mean DBH between 5-10 cm accounted for a high proportion (13 individuals, 59.10%), while no dead individuals had DBH $<$ 5 cm. The 226 recruited individuals had a mean DBH of 4.96 cm, with 128 individuals (57%) having DBH between 5-10 cm, 96 individuals having DBH $<$ 5 cm, and only two recruits having DBH $>$ 10 cm (*E. prinoides* and *F. major*) (Table 5).

Among populations, only *M. mongolica* and C. panzhihuaensis had dead individuals with mean DBH $>$ 10 cm, while five populations had dead individuals with mean DBH between 5-10 cm. Most populations with recruits had mean DBH between 5-10 cm, with only two recruit populations having mean DBH $<$ 5 cm: C. panzhihuaensis (0 cm) and Q. cocciferoides (2.55 cm) (Table 6).

Table 4 Change of DBH of each common population in community from 2015 to 2020

Species	Growth form	Average DBH (cm)	Increase rate of average DBH (%)
Cycas panzhihuaensis	Shrub or small arbor		
Quercus cocciferoides	Arbor		
Terminalia franchetii	Small arbor or shrub		
Morus mongolica	Small arbor or arbor		
Diospyros dumetorum	Small arbor or shrub		
Albizia kalkora	Shrub or small arbor		
Osyris quadripartita	Shrub or small arbor		
Vitex negundo	Shrub or small arbor		
Eriobotrya prinoides	Small arbor		
Toona ciliata	Large arbor		
Ficus virens	Large arbor		
Sapindus saponaria	Large arbor		
Firmiana major	Arbor		
Desmodium yunnanense	Shrub		

Table 5 DBH of dead and recruitment individuals of community from 2015 to 2020

DBH Size-class	Dead individuals	Recruitment individuals
	No. of individuals	Average DBH (cm)
1 cm $\leq$ DBH $<$ 5 cm		

DBH Size-class	Dead individuals	Recruitment individuals
5 cm ≤ DBH < 10 cm		
10 cm ≤ DBH < 15 cm		
15 cm ≤ DBH < 20 cm		
20 cm ≤ DBH < 25 cm		
25 cm ≤ DBH < 30 cm		
DBH ≥ 30 cm		

Table 6 The DBH of dead and recruitment individuals of the common populations in community from 2015 to 2020

Species	Average DBH (cm)	Dead individuals	Recruitment individuals
Cycas panzhihuaensis			
Quercus cocciferoides			
Terminalia franchetii			
Morus mongolica			
Diospyros dumetorum			
Albizia kalkora			
Osyris quadripartita			
Vitex negundo			
Eriobotrya prinoides			
Toona ciliata			
Ficus virens			
Sapindus saponaria			

Species	Average DBH (cm)	Dead individuals	Recruitment individuals
Firmiana major			
Desmodium yunnanense			

3.1 Changes in Community Diversity

The total number of individuals in the secondary savanna shrub forest of the arid-hot valley increased to 1,710 by 2020, representing a 13.1% increase. Except for C. panzhihuaensis, arbor species contributed more recruits. This indicates that as forest succession progresses, community structural characteristics are becoming more complex. The increased DBH (Table 4) and crown expansion may have created more complex and heterogeneous understory environments compared to 2015 (Chazdon, 2008), which favors the survival of seedlings and saplings of more plant types (e.g., sun-loving plants) (Bartels & Chen, 2010). Consequently, the internal environment (e.g., light conditions) may gradually become suitable for the growth of tall arbor species, while the dominance of sun-loving shrub species (C. panzhihuaensis) gradually decreases (Figure 1) (Monsi & Saeki, 2005). The non-significant increasing trend in community species diversity and evenness during succession aligns with empirical research conclusions on how species richness changes with forest succession (Odum, 1969; Zhang & Wu, 2014). This study also demonstrates that gradual increases in species diversity can occur not only during primary succession (Whittaker & Richards, 1989) but also in secondary successional stages of forest communities developed under arid-hot valley climate conditions. This pattern of gradually increasing species diversity during succession may be associated with the niche differentiation hypothesis (Long et al., 2012). Generally, as communities approach climax stages, changes in the internal environment compared to early successional stages create more niche space. Plant species may more effectively utilize resources derived at this stage (e.g., heterogeneous light, water, and soil conditions) and occupy differentiated niches. For example, temporal niches may emerge as species adjust germination timing according to their biological characteristics and competitive dynamics with other species to avoid seasonal adverse environmental effects (Dyer et al., 2000; Geber & Griffen, 2003), or original niche space may be further subdivided to reduce interspecific competition, thereby promoting coexistence of more species (Whittaker, 1965; De Luis et al., 2008; Donohue et al., 2010; Roscher et al., 2011; Cornell, 2013). These results indicate that the current secondary savanna shrub forest of the arid-hot valley is undergoing progressive succession. Additionally, the increase in community species evenness suggests that the importance of biological competition will increase with secondary succession (Holdaway & Sparrow, 2006), which may be related to the relatively abundant resources and low community and population densities in early secondary successional stages that prevent communities from reaching maximum environmental carrying capacity (Sardans & Peñuelas, 2015).

3.2 Changes in Ecological Characteristics of Dominant Tree Species

Generally, vegetation in the initial stage of forest community secondary succession originates from native plant communities after disturbance and is mostly in shrub and herb stages (Li & Niu, 2006). The low soil water content and dry air in the secondary savanna shrub forest of the arid-hot valley during initial successional stages (Yang et al., 2002; Ming & Shi, 2007; Peng et al., 2013) are also suitable for the growth and development of sun-loving shrubs and herbaceous plants. Therefore, C. panzhihuaensis had high dominance in 2015 (IV = 69.70). At this time, canopy closure and habitat heterogeneity were lower than in higher successional stages (Cornell, 2013), and recruitment niches had not yet formed or been subdivided (Dyer et al., 2000; Geber & Griffen, 2003). After five years of secondary succession, both environmental heterogeneity and stand closure gradually increased, causing mortality of C. panzhihuaensis individuals. Additionally, competitive pressure from DBH growth of other common species was one reason for the gradual decline in this population' s dominance (Table 4) (Getzin et al., 2006). As shown in Table 6, recruits of C. panzhihuaensis were all seedlings with DBH = 0 cm, possessing some shade tolerance and requiring relatively less space and resources. Aggregation around mother plants could better mitigate interference from adverse environmental conditions such as high temperature and drought in the community (Yang et al., 2002; Ming & Shi, 2007; Peng et al., 2013) and effectively exert group effects to resist potential interspecific competition pressure, thus maintaining good regeneration (Su et al., 2010). However, larger-diameter individuals of this population have greater resource demands (especially for light). Although the arid-hot valley has abundant light, as arbor species' DBH increased (Table 4), crown expansion and closure increased, gradually reducing understory light intensity and affecting growth of larger-diameter individuals of this population (Table 6), leading to decreased population dominance (Figure 1). This is similar to research conclusions that light tolerance is an important indicator for measuring plant regeneration requirements and niche differentiation (King et al., 2006).

3.3 Community Regeneration and Successional Patterns

Direct indicators reflecting regeneration dynamics in forest communities are mortality and recruitment rates (Ding et al., 2018). The annual mortality rate (0.29%) was lower than that of the Panama BCI plot (2.64%) (Condit et al., 1999), Malaysia Pasoh plot (1.46%) (King et al., 2006), Dinghushan 20 hm^2 subtropical evergreen broadleaved forest plot (1.97%) (Zhou et al., 2005), Gutianshan 5 hm^2 plot (2.02%) (Wang et al., 2011), Baishanzu 5 hm^2 plot (1.45%) (Chen et al., 2013), Tianmushan 1 hm^2 evergreen-deciduous broadleaved mixed forest plot (1.51%) (You et al., 2016), and Wuyishan 0.48

hm^2 plot (1.31%) (Ding et al., 2018). The annual recruitment rate (2.75%) was moderate, lower than Gutianshan (5.09%), Dinghushan (3.17%), Wuyishan (2.98%), and Panama (2.87%) plots, but higher than Tianmushan (1.86%), Malaysia (1.65%), and Baishanzu (0.62%) plots. The low annual mortality rate of the secondary savanna shrub forest in the arid-hot valley may be attributed to its early secondary successional stage, where plant individuals have small DBH (Table 4), community density is low, and dominant species are mostly sun-loving shrubs (or small trees) and herbaceous species (Li & Niu, 2006) with relatively low environmental demands. Interspecific competition may not yet exist or be weak due to small individual DBH and low community density, resulting in low mortality. At this stage, community density has not reached maximum environmental carrying capacity, and space and resources are relatively abundant and uniform (Sardans & Peñuelas, 2015), greatly improving survival probability of recruited individuals. However, the low environmental heterogeneity at this stage means more regeneration niches have not yet formed or been subdivided (Cornell, 2013), which is not conducive to regeneration of shade-tolerant or shade-loving plant seedlings, making the recruitment rate moderate compared to the above-mentioned community types.

Condit et al. (1999) considered populations with change rates >5% as rapidly changing populations. At the community level, from 2015 to 2020, the secondary savanna shrub forest of the arid-hot valley had a relatively slow population change rate (2.46%). However, seven tree species populations had size change rates >5%, accounting for 41.18% of total species number in 2015, indicating that most populations showed increasing trends. The proportion of populations with size change rates >5% was higher than in Gutianshan (23.26%) (Wang et al., 2011), Wuyishan (19.75%) (Ding et al., 2016), BCI (10%) (Condit et al., 1999), Pasoh (2%) (King et al., 2006), and Baishanzu (0%) (Chen et al., 2013) plots. This may be closely related to the low environmental heterogeneity and relatively abundant resources in early successional stages, consistent with the trend that species turnover rates gradually slow with stand age and successional stage (Shugart & Hett, 1973). Among expanding populations, C. panzhihuaensis had the lowest change rate (0.04%), indicating that although the constructive species population size is increasing, it consists mainly of small-diameter individuals (Table 6). Changes in community internal environment (e.g., understory light) caused by secondary succession are gradually reducing its dominance (Whitfeld et al., 2014) (Figure 1), and the population is gradually declining. Its vulnerable status remains 不容忽视 (cannot be ignored). Without human disturbance, future successional pathways of the forest community may conflict with in-situ conservation of C. panzhihuaensis, which should be addressed in future scientific management to effectively protect C. panzhihuaensis populations without affecting secondary successional processes. Nevertheless, C. panzhihuaensis will remain the constructive species in the secondary savanna shrub forest of the arid-hot valley for years to come. As secondary succession proceeds, its dominance will gradually decrease, and the community will gradually develop into a secondary forest community where sun-loving arbors (e.g., Q. cocciferoides) and shade-tolerant arbors (e.g., T. franchetii) become constructive species, with shrub-type populations (e.g., C. panzhihuaensis) as companion species.

During forest community succession, the possibility of more species entering the community or the new species appearing in 2020 establishing successfully cannot be ruled out, which may affect community species composition. However, their impact on the dominance of existing dominant species will be minor in the short term. Further research is needed to answer whether dynamic changes in community vertical structure, biomass, population spatial patterns, and interspecific associations affect community successional dynamics, whether this community can develop into a regional climatic climax community, or whether it will undergo deflected succession due to year-round foehn effects.

Conclusions

Based on dynamic monitoring (2015–2020) of a 1 hm^2 permanent plot in the secondary savanna shrub forest of the arid-hot valley in the National Nature Reserve of Cycas panzhihuaensis, this study found: (1) In 2020, the community contained 18 woody species belonging to 15 families and 18 genera, an increase of one genus and one species compared to 2015. (2) The composition of dominant species remained unchanged, but their dominance shifted significantly. Among the six populations with importance values >1, five species showed increased importance values while only one decreased. Cycas panzhihuaensis remained the constructive species, but its dominance decreased significantly, while Q. cocciferoides and T. franchetii populations showed significantly increased dominance, indicating that arbor species will occupy dominant positions in the community in the future, though the vulnerable status of C. panzhihuaensis cannot be ignored. (3) In 2020, the number of woody individuals with DBH $\geq$ 1 cm increased to 1,710, with an annual mortality rate of 0.29% and an annual recruitment rate of 2.75%. Seven populations experienced mortality, nine showed recruitment, one decreased in size, nine increased, and four remained stable. (4) Mean community DBH increased from 11.10 cm to 11.17 cm, with dead individuals averaging 11.84 cm and recruits averaging 4.96 cm. Mean DBH decreased only in C. panzhihuaensis and O. quadripartita populations, while all other populations showed varying degrees of increase. These results indicate that although the C. panzhihuaensis population increased in number, mortality of large-diameter individuals was the main reason for its significant dominance decline, though it will not lose its dominant position in the short term. From 2015 to 2020, succession in the secondary savanna shrub forest of the arid-hot valley gradually became more complex, with relatively rapid species regeneration. As forest succession proceeds, the importance of interspecific competition will increase, and the increasing dominance and regeneration rates of arbor species indicate that the community will enter a new stage of secondary succession where arbors gradually become dominant. Cycas panzhihuaensis will form a transitional secondary forest community with Q. cocciferoides, T. franchetii, and other arbor species, progressing toward a climatic climax community. Corresponding measures should be taken to reduce human disturbance to facilitate research on secondary successional processes and strengthen protection to prevent further vegetation degradation.

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Appendix: 1 hm^2 Fixed Sample Plot Woody Plant List for Secondary Savanna Shrub Forest of Arid-Hot Valley in National Nature Reserve of Cycas panzhihuaensis (2020)

Species	Latin Name	Growth Form
Cycas panzhihuaensis	*Cycas panzhihuaensis*	Shrub or small arbor
Quercus cocciferoides	*Quercus cocciferoides*	Arbor
Terminalia franchetii	*Terminalia franchetii*	Small arbor or shrub
Morus mongolica	*Morus mongolica*	Small arbor or arbor
Diospyros dumetorum	*Diospyros dumetorum*	Small arbor or shrub
Albizia kalkora	*Albizia kalkora*	Shrub or small arbor
Vitex negundo	*Vitex negundo*	Shrub or small arbor
Toona ciliata	*Toona ciliata*	Small arbor
Firmiana major	*Firmiana major*	Large arbor
Eriobotrya prinoides	*Eriobotrya prinoides*	Large arbor
Ficus virens	*Ficus virens*	Large arbor
Osyris quadripartita	*Osyris quadripartita*	Arbor

Species	Latin Name	Growth Form
Sapindus saponaria	*Sapindus saponaria*	Shrub
Dalbergia obtusifolia	*Dalbergia obtusifolia*	Shrub or small arbor
Solanum erianthum	*Solanum erianthum*	Shrub or small arbor
Desmodium yunnanense	*Desmodium yunnanense*	Shrub
Populus yunnanensis	*Populus yunnanensis*	Large arbor
Fraxinus trifoliolata	*Fraxinus trifoliolata*	Arbor

Note: Figure translations are in progress. See original paper for figures.

Source: ChinaXiv —Machine translation. Verify with original.