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Abstract: *Cyclocarya paliurus* (Batal.) Iljinsk. is mainly distributed in the subtropical areas of China. The leaves of this species are rich in beneficial secondary metabolites exhibiting bioactivity against human diseases, including hyperlipemia, diabetes, and hypertension. To explore the adaptability and distribution characteristics along the environmental gradient of this species, investigation of the characteristics of *C. paliurus* communities is necessary. In this study, we established 31 sample plots, each 20 m \times 20 m, and comparatively analyzed the species composition, species importance value, and tree species diversity of different *C. paliurus* communities in 2 years. Canonical correspondence analyses were carried out: the first between tree-species importance value and 12 environmental factors, and the second between *C. paliurus* population-related indices and the 12 environmental factors. On the basis of these analyses, we identified tree species varying markedly in abundance in the studied *C. paliurus* communities. Several tree species showed adaptive characteristics similar to those of *C. paliurus*. We also observed that the *C. paliurus* importance value varied along elevational, longitudinal, and temperature gradients. Our findings should be valuable for prediction of *C. paliurus* adaptive areas and mixed forest afforestation in different distribution areas.

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Keywords: spatial distribution characteristics; importance value; *Cyclocarya paliurus*; canonical correspondence analysis

1. Introduction

Cyclocarya paliurus distributed in the subtropical areas of China, is the only extant species in a genus formerly present in North America and Europe [\[1,](#page-12-0)[2\]](#page-12-1). This species grew at middle elevations in mountainous areas [\[2\]](#page-12-1). The leaves of *C. paliurus* have long been consumed as a tea and contain abundant active compounds, including phenolics, triterpenoids, and polysaccharides, all of which are beneficial to human health [\[3–](#page-12-2)[6\]](#page-12-3). Considerable efforts are currently being focused on the genetic and environmental interaction of *C. paliurus*. Previous studies have analyzed the genetic diversity and structure of *C. paliurus* populations [\[2\]](#page-12-1), the responses of individual secondary metabolites to abiotic factors [\[7](#page-12-4)[–9\]](#page-13-0), and phenotypic variations in secondary metabolite accumulation among populations [\[10,](#page-13-1)[11\]](#page-13-2). Genotyping of *C. paliurus* germplasm at the population level has revealed that different genotypes respond differently to abiotic factors, including shading [\[12\]](#page-13-3), light regime [\[13\]](#page-13-4), and other environmental aspects [\[8,](#page-13-5)[9\]](#page-13-0).

Despite the above research progress, spatial distribution characteristics of *C. paliurus* communities are still lacking. *C. paliurus* is distributed in the valleys of the Dabie, Wuyi, Nanling, Wu, and Xuefeng mountains in the subtropical regions of China [\[2\]](#page-12-1). Trees of this species are always scattered in small populations of five to 20 individuals. A molecular marker analysis of a *C. paliurus* population from Muchuan, Sichuan Province, uncovered high-level genetic diversity in this only extant member of the genus [\[2\]](#page-12-1). This indicates that the center of origin of *C. paliurus* was near present-day Sichuan Province and that

this species is a Quaternary relic. The species is intolerant of flooding [\[2\]](#page-12-1) and thus has adapted to low elevations of mountainous habitats with suitable light conditions. Previous research has revealed that *C. paliurus* is always sporadically distributed, which implies limited adaption and poor regeneration ability in forest communities [\[2,](#page-12-1)[14](#page-13-6)[,15\]](#page-13-7). *C. paliurus* seeds exhibit both exogenous and endogenous dormancy and remain deeply dormant for 2 years in natural environments [\[3\]](#page-12-2). Xiong et al. [\[16\]](#page-13-8) reported that *C. paliurus* recruitment has a strong positive response to forest gaps. Additionally, a resource conservation strategy for this species is urgently needed because of its limited regeneration, narrow water requirements and scattered distribution. Research on the adaptive characteristics of *C. paliurus*, including the responses of *C. paliurus* communities and populations to a wide range of environmental variations, is thus critically needed. In this study, we subjected data from multiple *C. paliurus* communities to canonical correspondence analysis (CCA) to investigate their living patterns. Our objective was to identify the *C. paliurus* communites distribution characteristics along environmental gradient in forests.

2. Materials and Methods

2.1. Data Collection

We investigated *C. paliurus* communities situated at different longitudes, latitudes, and elevations in their main distribution areas. Except for small communities could only set less sample plots, we established four or five 20 m \times 20 m sample plots in each community. In total, 31 sample plots were set up in seven regions from Sichuan Provnice, Jiangxi Province, Hubei province, Guangxi Zhuang Autonomous Region and Anhui Province (Figure [1\)](#page-1-0). In each sample plot, we recorded the species, diameter at breast height (DBH), tree height, and crown diameter of each living tree having a DBH \geq 1 cm and height \geq 1.3 m. Latitude, longitude, and elevation were measured by GPS, and aspect and slope were measured with a hand-held compass (DQL-5, Harbin Optical Instrument Factory, Harbin, China) in 2 years. Aspect was also recorded in terms of numerical grades in segments of 45°, starting from the north: 1 for a north slope (247.5°–292.5°), 2 for a northeast slope (292.5°–337.5°), 3 for a northwest slope (202.5°–247.5°), 4 for an east slope (337.5°–22.5°), 5 for a west slope (157.5°–202.5°), 6 for a southeast slope (22.5°–67.5°), 7 for a southwest slope (112.5°–157.5°), and 8 for a south slope (67.5°–112.5°). In this system, a larger aspect value thus corresponds to a more southward-facing slope receiving more light [\[17\]](#page-13-9).

Figure 1. Sampling plots of *C. paliurus* communities. h1–h5: Hefeng county of Hubei province, j1–j7: Yongfu county of Guangxi Zhuang Autonomous Region, m1–m6: Muchuan county of Sichuan Province, n1–n2: Wuning county of Jiangxi Province, s1–s4: Shucheng county of Anhui Province, t1–t4: Tonggu county of Jiangxi Province, w1–w4: Wufeng county of Hubei province.

Three soil-sampling locations were randomly selected in each 20 m \times 20 m sample plot. After removing surface litter, 300 g of soil was collected from 0–20 cm and 20–40 cm depths with a soil auger, with three replicates. Soil samples from the two layers were combined, air dried, cleaned of debris, and passed twice through a 100-mesh sieve. The pH was then measured with a pH meter. To obtain a soil profile of each plot, soil was sampled with a circular soil cutter and dried at 105 \degree C to a constant weight, and soil bulk density was measured.

Climate data were obtained from the National Meteorological Data Service Center of China to serve as the closest approximate values for annual mean temperature, maximum temperature, minimum temperature, and annual mean rainfall in each region.

2.2. Data Analysis

As a comprehensive quantity index, we calculated the importance value (IV) of each tree species as follows:

IV = (relative frequency + relative abundance + relative cover degree)/3 (1)

We calculated values of various diversity indices, including species richness and Simpson diversity, Shannon–Wiener diversity and Pielou uniformity indices. In these equations, *RO* represents the number of species, and *Pi* is the relative frequency of species *i* in the community.

Species richness: *S* = *RO* Simpson diversity: $D = 1 - \sum P_i^2$ Shannon–Wiener diversity: $H = -\sum P_i \ln P_i$ Pielou uniformity: $E = H / ln S$

Canonical correspondence analysis (CCA) is used to describe the spatial distribution characteristics of communities, including herbaceous plants, forests, animals, and microbes [\[18–](#page-13-10)[23\]](#page-13-11). This method combines species variables with complicated environmental ones to facilitate extraction of correlations to the maximum extent objectively possible. In addition, a CCA plot can be used to visualize how factors influence one another. To analyze the tree species distribution characteristics in *C. paliurus* communities, the first CCA was carried out using species IV as the response variable and 12 environmental factors as the explanatory variables. The following matrices were established: factor matrix 1 (31 sample plots \times 30 major tree species IV) and factor matrix 2 (31 sample plots \times 12 environmental factors). To analyze *C. paliurus* spatial distribution characteristics along with environment variation, the second CCA was carried out using ecological indices of *C. paliurus* communities (*C. paliurus* IV, abundance, relative abundance, and relative cover degree; species richness; Simpson diversity, Shannon–Wiener diversity, and Pielou uniformity indices) as response variables and environmental factors as explanatory variables. We constructed the following matrices: factor matrix 1 (31 sample plots × 8 ecological indices of *C. paliurus* communities) and factor matrix 2 (31 sample plots \times 12 environmental factors). All CCAs were conducted using the vegan $v1.8$ -5 package [\[24\]](#page-13-12) in the R $v3.4.4$ statistical environment (R Development Core Team 2018) with the package vegan v. 1.8–5 [\[25\]](#page-13-13). Scatter plot construction and correlation analyses were conducted using SPSS statistics software (Version 19.0, Chicago, IL, USA)

3. Results

We analyzed *C. paliurus* communities represented by 31 sample plots in the seven major distribution areas shown in Figure [1](#page-1-0) (Muchuan, Sichuan Provnice; Tonggu and Wuning counties, Jiangxi Province; Wufeng and Hefeng counties, Hubei province; Yongfu County, Guangxi Zhuang Autonomous Region; Shucheng County, Anhui Province). The sample plots were located along an environmental gradient suitable for in-depth analysis and were overall a good representation of *C. paliurus* community distribution characteristics (Table [1\)](#page-4-0). The sampling design covered a wide latitudinal and longitudinal range, spanning form 103.79◦ N to 116.54◦ N and from 24.61◦ E to 31.04◦ E and across an altitudinal gradient of approximately 1100 m, between 744 and 1829 m. The climate was also very variable with annual temperature ranging from 12.99 to 24.62 °C, minimum temperature ranging from 3.54 to 8.12 ◦C and maximum temperature ranging from 28.5 to 33.1 ◦C. Besides, precipitation gradient reached nearly 800 mm (from 1326 to 2100 mm). The sample plots distributed in all directions of aspect varying from 10 to 50° slope. The soil pH (3.18 to 5.92 acidic), 0–20 cm soil bulk density (0.55 to 1.62 g/cm^{-3}) and 20–40 cm soil bulk density (0.54 to 1.48 g/cm^{-3}) were recorded and also showed large difference.

As shown in Table [2,](#page-5-0) we identified 190 tree species in the 31 sample plots. We calculated the IV of each species, which summed to a total IV of 22.96. Among the identified species, the IV of *C. paliurus* summed across the 31 sample plots was 7.42, corresponding to 32% of total IV. The sum of the IV of the top 30 tree species, which included *C. paliurus*, was 15.51, which represented 68% of the total IV of the 190 tree species. On the basis of these results, we accordingly used the IVs of the first 30 tree species in subsequent analyses.

In addition to *C. paliurus*, several tree species had a broad distribution range. The most widespread species after *C. paliurus* was *Acer davidii*, which was distributed in five regions: Hefeng County, Hubei Province; Yongfu County, Guangxi Zhuang Autonomous Region; Muchuan County, Sichuan Province; Wuning County, Jiangxi Province; and Shucheng County, Anhui Province. *Acer elegantulum* and *Liquidambar formosana* were each present in four regions. In contrast, several tree species showed limited adaption, being distributed in only one region, including *Cryptomeria fortunei* and *Castanea henryi* (both only in Hefeng County, Hubei Province, China), *Ilex centrochinensis* (Muchuan County, Sichuan Province, China), *Taxus chinensis* (Tonggu County, Jiangxi Province, China), *Dendrobenthamia capitata* (Wufeng County, Hubei Province, China), *Lithocarpus glaber* (Yongfu County, Guangxi Zhuang Autonomous Region, China), and *Tapiscia sinensis* (Shucheng County, Anhui Province, China).

With regard to species presence in plots, *A. davidii* was distributed in 11 sample plots, the most of any species except *C. paliurus*. *Acer elegantulum*, *Cinnamomum wilsonii*, and *Lithocarpus harlandii* each appeared in nine sample plots, while *Dendropanax dentiger* and *Eurya japonica* were both found in eight. *Liquidambar formosana* occupied seven sample plots. Finally, *Cryptomeria fortunei* and *Castanea henryi* were only distributed in two sample plots.

A CCA between the 30 major tree species in the *C. paliurus* communities and 12 environmental factors was conducted (Table [3\)](#page-6-0). The results obtained using the CCA model were significant at the $p = 0.001$ level and effectively revealed that most of the tested environmental factors contribute to species distributions in *C. paliurus* communities. According to the model, the 12 environmental factors were responsible for 61.2% of the variation in tree species total IV, with the first four and two principal components explaining 37.1 and 21.2% of the variation, respectively.

As shown in Figures [2](#page-6-1) and [3,](#page-7-0) the 31 sample plots were distributed along various environmental gradients. The most extreme gradients were those of precipitation (1326 to 2100 mm), annual mean temperature (12.99 to 24.62 °C), annual minimum temperature (3.54 to 8.12 °C), and longitude (31.04° E to 24.61° E), which were the environmental factors with the greatest influence on tree species distribution. We found that tree species distribution markedly varied along the environment gradients. Unlike most species, the distribution of *C. paliurus* was relatively unaffected by the environment of its communities. *Swida macrophylla*, *Clerodendrum japonicum*, and *Castanea henryi* preferentially inhabited areas with higher precipitation (nearly 2000 mm), while *I. ficoidea* Hemsl., *Cinnamomum wilsonii*, *Castanopsis fargesii* Franch., *I. centrochinensis*, and *Diplospora dubia* were more likely to be distributed in areas with higher annual minimum temperatures (nearly 3 ◦C). In addition, *Dendrobenthamia capitata*, *Bothrocaryum controversum*, *A. palmatum* Thunb, and *Carpinus viminea* tended to occupy higher longitudes (nearly 30◦ E). *Cunninghamia lanceolata*, *Liquidambar formosana*, and *Dendropanax dentiger* were adapted to habitats similar to *C. paliurus*, with IVs of 0.45, 0.42, and 0.21, respectively. The IVs of all recorded species, however, were much lower than that of *C. paliurus* (7.42).

Sample Plots	Lat $({}^{\circ}{\rm N})$	Lon $\rm ^{\circ}E)$	Slo \mathbf{C}	Asp	Alt (mm)	Tem $(^{\circ}C)$	LTem $(^{\circ}C)$	HTem $(^{\circ}C)$	Prec (mm)	pH	SW ₁ (g/cm^3)	SW ₂ (g/cm^3)
h1 h2 h3 h4 h5	109.13-109.98	$30.1 - 30.02$	12–48	1–5	1106-1283	12.99	-5.28	28.5	2100	$4.54 - 5.7$	$1.04 - 1.62$	$0.97 - 1.48$
j1 j2 j4 j5 j6 j7	104.95-104.96	$24.61 - 24.63$	$10 - 40$	$2 - 5$	1539–1829	18.91	3.54	33	1326	$3.83 - 4.49$	$0.55 - 0.85$	$0.54 - 0.9$
m ₁ m ₂ m ₃ m ₄ m ₅ m ₆	103.79	28.97	$19 - 32$	1–8	1192–1230	15.85	1.38	29.71	1589	$3.18 - 3.39$	$0.57 - 0.73$	$0.68 - 0.89$
n1 n2	115.26–115.32	29.01–29.09	22		771–780	16.75	-1.83	33.1	1862	$4.59 - 4.64$	$0.92 - 0.97$	$0.96 - 1$
s1 s2 s3 s4	116.54	31.04	$24 - 45$	$3 - 7$	764-831	14.45	-8.12	31.32	1603	$4.88 - 5.28$	$0.99 - 1.11$	$1.07 - 1.18$
t1 t2 t3 t4	114.21–114.22	28.52-28.53	$38 - 50$	$5 - 7$	790-860	16.82	-1.85	32.7	1487	$4.55 - 4.69$	$0.76 - 0.83$	$0.85 - 0.97$
w1 w2 w3 w4	110.43-110.46	29.86-29.97	18–38	$2 - 6$	1340–1536	13.12	-5.49	28.65	1704	$5.29 - 5.92$	$0.85 - 1.04$	$1.06 - 1.19$

Table 1. Environmental factors of *C. paliurus* communinties sample plots.

Lat: latitude, Lon: longitude, Slo: slope, Asp: aspect, Prec: precipitation, Tem: annual temperature, LTem: lowest temperature, HTem: highest temperature, Prec: precipitation, pH: pH, SW1: 0–20 cm soil bulk density, SW2: 20–40 cm soil bulk density. h1–h5: Hefeng county of Hubei province, j1–j7: Yongfu county of Guangxi Zhuang Autonomous Region, m1–m6: Muchuan county of Sichuan Province, n1–n2: Wuning county of Jiangxi Province, s1–s4: Shucheng county of Anhui Province, t1–t4: Tonggu county of Jiangxi Province, w1–w4: Wufeng county of Hubei province.

 \overline{a}

Table 2. Important values of the top 30 trees in the community of *C. paliurus.*

h1–h5: Hefeng county of Hubei province, j1–j7: Yongfu county of Guangxi Zhuang Autonomous Region, m1–m6: Muchuan county of Sichuan Province, n1–n2: Wuning county of Jiangxi Province, s1–s4: Shucheng county of Anhui Province, t1–t4: Tonggu county of Jiangxi Province, w1–w4: Wufeng county of Hubei province. IV: importance value.

***: significant in 0.001 level.

Table 3. Canonical correspondence analysis (CCA) results for tree species of *C. paliurus* communities with environmental factors.

CCA1

Figure 2. CCA ordination diagram of *C. paliurus* communites sample plots and environmental. con1~31: sample plots 1 to 31, Lat: latitude, Lon: longitude, Slo: slope, Asp: aspect, Prec: precipita Table [1.](#page-4-0) 0–20 cm soil bulk density, SW2: 20–40 cm soil bulk density.

Figure 3. CCA ordination diagram of tree species in *C. paliurus* communites and environmental factors. Abbreviations: A1: *C. paliurus*, A2: Cunninghamia lanceolata, A3: Liquidambar formosana Hance, A4: Ilex ficoidea Hemsl. A5: Cinnamomum wilsonii Gamble, A6: Litsea elongate, A7: Taxus chinensis, A8: Ilex centrochinensis, A9: Cryptomeria fortune, A10: Acer davidii Franch. A11: Dendrobenthamia capitata, A12: Lithocarpus glaber, A13: Castanopsis fargesii Franch. A14: Bothrocaryum controversum, A15: Swida macrophylla, A16: Lithocarpus harlandii, A17: Lindera communis Hemsl. A18: Platycarya strobilacea. A19: Clerodendrum japonicum. A20: Diplospora dubia, A21: Castanea henryi, A22: Acer palmatum Thunb. A23: Acer elegantulum, A24: Camellia cuspidate, A25: Pinus massoniana Lamb. A26: Dendropanax dentiger, A27: Tapiscia sinensis, A28: Eurya japonica Thunb. A29: Carpinus viminea, A30: Picrasma quassioides Picrasma quassioides, Lat: latitude, Lon: longitude, Slo: slope, Asp: aspect, Prec: precipitation, Tem: annual temperature, LTem: lowest temperature, HTem: highest temperature, Prec: precipitation, pH: pH, SW1: 0–20 cm soil bulk density, SW2: 20–40 cm soil bulk density.

The tree species distributional characteristics of *C. paliurus* communities were described according to the above CCA model. To further analyze *C. paliurus* population distribution, another CCA model was applied. The following data from the 31 sample plots were used as the response variables (Table [4\)](#page-8-0): species richness; Shannon–Wiener, Pielou, and Simpson indices; and *C. paliurus* IV, abundance, relative abundance, and relative coverage. As explanatory variables, we used the 12 environmental factors described above.

The results of the second CCA are shown in Table [5.](#page-8-1) As indicated by the table, the 12 environmental factors explained 65.2% of the variation in the distributional characteristics of *C. paliurus* populations. The first four principal components were the main contributors, with 62.5% of the variation explained by the first two principal components, namely, 35.6% by CCA1 and 26.9% by CCA2. The CCA plot of the first two principal

Table 4. Sample plots ecology diversity index related to *C. paliurus* population.

Ri: Tree species richness, Shanon: Shannon index, Pielou: Pielou index, Simpson: Simpson index, RAb: *C. paliurus* relative abundance, Rc: *C. paliurus* relative coverage, Rf: *C. paliurus* relative frequency, IV: *C. paliurus* important value.

Table 5. CCA results for ecological index of *C. paliurus* population with environmental factors.

components was therefore able to describe most of the distributional characteristics of

***: significant in 0.001 level.

C. paliurus populations.

As shown in Figure [4,](#page-9-0) the 31 sample plots were distributed along broad environmental gradients. According to the results of the CCA, the environmental factors with the closest relationship with the distributional characteristics of *C. paliurus* populations were annual maximum temperature, elevation, longitude, slope, aspect, and annual mean temperature.

Our analysis indicated that the IV of *C. paliurus* populations was influenced by elevation and temperature (Figure [5\)](#page-9-1). We found that the *C. paliurus* populations with the highest IVs tended to occur in places with lower elevations and higher temperatures. The IV of *C. paliurus* in these sample plots was higher than 0.3, whereas values in other plots ranged from 0.26 to 0.08. The relative abundance and relative coverage of *C. paliurus* had variation patterns similar to that of IV, with relative abundance the most sensitive. Conversely, *C. paliurus* abundance and tree species richness were relatively unaffected by the environment. The three ecological diversity indices (Shannon–Wiener, Pielou, and Simpson) were sensitive to aspect, which indicates that light conditions influenced, albeit weakly, the distribution of *C. paliurus* stands.

On the basis of the second CCA, the most correlated variables were selected (Figure [6\)](#page-10-0). The IV of *C. paliurus* varied along an elevational gradient $(R = -0.54, p < 0.01)$, while *C. paliurus* abundance similarly varied with longitude (*R* = 0.695, *p* < 0.01). Even though the sample plots were broadly distributed, the variation in *C. paliurus* IV and relative abundance still followed environmental gradients. As the elevation increased from 750 to 1900 m, the IV of *C. paliurus* declined from 0.4 to 0.1, at the same time, *C. paliurus* relative abundance increased from 0.05 to 0.4 as longitude increased from $100°$ E to $120°$ E. As shown in Figure [5,](#page-9-1) the IV, relative abundance, and relative coverage of *C. paliurus* exhibited identical patterns of variation. In particular, their values were positively correlated with

increasing longitude, annual maximum temperature, and annual mean temperature and were negatively correlated with elevation.

 \sim

Figure 4. CCA ordination diagram of *C. paliurus* sample plots and environmental factors. Abbreviations: con1~31: sample plots 1 to 31, Lat: latitude, Lon: longitude, Slo: slope, Asp: aspect, Prec: precipitation, Tem: annual temperature, LTem: lowest temperature, HTem: highest temperature, Prec: precipitation, pH: pH, SW1: 0–20 cm soil bulk density, SW2: 20–40 cm soil bulk density.

Figure 5. CCA ordination diagram of *C. paliurus* population related index and environmental factors. Abbreviations: Ri: Tree species richness, Shanon: Shannon index, Pielou: Pielou index, Simpson: Simpson index, RAb: *C. paliurus* relative abundance, Rc: *C. paliurus* relative coverage, Rf: *C. paliurus* relative frequency, IV: *C. paliurus* important value, Lat: latitude, Lon: longitude, Slo: slope, Asp: aspect, Prec: precipitation, Tem: annual temperature, LTem: lowest temperature, HTem: highest temperature, Prec: precipitation, pH: pH, SW1: 0–20 cm soil bulk density, SW2: 20–40 cm soil bulk density.

Figure 6. Environment characteristics of *C. paliurus* important value and relative abundance. (**a**), *C. paliurus* important value response to altitude. *R* = −0.54. (**b**), *C. paliurus* relative abundace response to longitude. *R* = 0.695.

4. Discussion

In this study, we investigated various communities of *C. paliurus* to identify the factors shaping its distribution. We found that the tree species composition of the studied *C. paliurus* communities varied markedly along environment gradients. Community structure is affected by many abiotic environmental factors [\[26\]](#page-13-14). Among the 12 environmental factors examined in this study, precipitation, longitude, and temperature gradients had the greatest effect on community structure, and longitude was the most representative indicators. *Swida macrophylla*, *Clerodendrum japonicum*, and *Castanea henryi* tended to be distributed in *C. paliurus* communities experiencing higher precipitation. These tree species were almost exclusively distributed in Hefeng and Wufeng counties of Hubei Province, where the annual precipitation is above 1700 mm. Similarly, Shen et al. [\[27\]](#page-13-15) have reported the presence of a *C. paliurus* forest in Yichang City, Hubei Province. Wong et al. [\[28\]](#page-13-16) have also described a *Castanea henryi*–*C. paliurus* forest community in a high-precipitation area of southeastern China. In our study, we found that *I. ficoidea*, *I. centrochinensis*, *Cinnamomum wilsonii*, *Castanopsis fargesii*, and *Diplospora dubia* were more likely to occur in *C. paliurus* communities with the highest annual minimum temperatures. These five species were mostly limited to the six sample plots in Muchuan County, Sichuan Province, where the annual minimum temperature is 1.38 ◦C. The highest IVs of *Dendrobenthamia capitata*, *B. controversum*, *A. palmatum*, and *Carpinus viminea* were recorded in the easternmost *C. paliurus* communities in the study area, mainly in sample plots in Wufeng County, Hubei Province, at longitudes of 29◦ E to 30◦ E. In a previous study, Wang et al. [\[29\]](#page-13-17) identified *C. paliurus*, *Dendrobenthamia capitata*, and *B. controversum* scattered throughout a forest community dominated by *Platycarya strobilacea* in another far-eastern location, Yuexi County, Anhui Province.

Despite the pronounced environmental gradients, the IV of *Cunninghamia lanceolata*, *Liquidambar formosana*, and *Dendropanax dentiger*, like *C. paliurus*, remained relatively constant. Of these three species, the distribution of *Liquidambar formosana* (found in seven sample plots from four regions) was more stable than that of *Cunninghamia lanceolata* (five sample plots from two regions) and *Dendropanax dentiger* (eight sample plots from three regions). In previous work, Ren et al. [\[30\]](#page-13-18) found *Liquidambar formosana* and *C. paliurus* in the Cenwanglaoshan Natural Reserve and reported that both of these species had high IVs despite their low relative abundances. This result implies that both species had entered

the community early, with consequently larger individuals. Similarly, Dong et al. [\[14\]](#page-13-6) discovered an ancient *C. paliurus*–*Liquidambar formosana* community in Anhui Province. Finally, Yi et al. [\[31\]](#page-13-19) located forest communities including *C. paliurus*, *Liquidambar formosana*, and *Cunninghamia lanceolata* on Huangshan Mountain in Anhui Province. *Liquidambar formosana* may thus be inferred to be an important tree species associated with *C. paliurus*. As a drought-tolerant tree species distributed in subtropical regions in China, *Liquidambar formosana* readily adapts to poor soil and has soil improvement capabilities [\[32\]](#page-13-20). A previous study investigated the application of mixed *Liquidambar formosana*–*Pinus massoniana* plantations to improve soil [\[33\]](#page-13-21). *C. paliurus* communities may thus benefit from the soil improvement activities of *Liquidambar formosana*. In addition to this species, *Cunninghamia lanceolata* is always associated with *C. paliurus* [\[28](#page-13-16)[,34\]](#page-13-22). Another associated species, *Dendropanax dentiger*, is a shade-tolerant, understory shrub widely distributed in southern China [\[35\]](#page-14-0). The fourth close associate of *C. paliurus*, *A. davidii*, was identified in 11 sample plots from five regions and was the most broadly ranging tree species other than *C. paliurus*. This tree species is endemic to central and southwestern China, where it often occurs in thin forests at an elevation of 500 to 1500 m and is strongly resistant to cold and drought [\[24](#page-13-12)[,36\]](#page-14-1). Jin et al. [\[25\]](#page-13-13) reported the presence of *A. davidii* and *C. paliurus* in a forest community in Zhejiang Province.

Aside from the variation in tree species in *C. paliurus* communities, the IV of *C. paliurus* increased along with increasing temperature and longitude and decreasing elevation, while the elevation was the most relevant. This variation along these environmental gradients suggests that southeastern China is more suitable as a habitat for *C. paliurus* because of its higher temperature and longitude and lower elevation. Dong et al. [\[14\]](#page-13-6) and Chen et al. [\[15\]](#page-13-7) have asserted that *C. paliurus* has a narrow ecological niche, with Dong et al. [\[14\]](#page-13-6) further considering *C. paliurus* and *Phyllostachys pubescens* to have overlapping niches. The changing climate at the end of the Quaternary ice age promoted the expansion and gene flow of *C. paliurus* into other areas [\[2\]](#page-12-1); the most suitable of which, according to our research, being Jiangxi and Anhui provinces. This trajectory is similar to that of another Quaternary relic, *Camellia sinensis*, which originated in southwestern Yunnan Province, China, and then colonized more suitable habitats in the southeast [\[37,](#page-14-2)[38\]](#page-14-3). Liu et al. [\[39\]](#page-14-4) used a MaxEnt model to analyze potential *C. paliurus* cultivation regions; he found that most regions highly suitable for planting *C. paliurus* are in southeastern China. In that study, temperature was considered to be the most important environmental factor, a finding confirmed by our research. Furthermore, Jin et al. [\[40\]](#page-14-5) found *C. paliurus* growing on a hillside near a ravine with high humidity and fertile soil in Zhejiang Province in southeastern China. Similarly, Sun et al. [\[12\]](#page-13-3) found that leaves of *C. paliurus* in Jiangxi Province have a higher triterpenoid content than those of other provinces. As a fast-growing species, *C. paliurus* requires sufficient light and water supply, but its intolerance to flooding may limit its growth in flood plains. Taking this into consideration, the low hills of southeastern China may be beneficial in terms of drainage while, at the same time, providing the higher temperature and precipitation that promote *C. paliurus* growth and regeneration.

In this study, both the relative abundance and relative coverage of *C. paliurus* increased in the same way as IV, with relative abundance increasing even more. Other than tree growth, southeastern areas are thus more suitable for *C. paliurus* regeneration. Previous research has revealed that natural recruitment of *C. paliurus* is always difficult in forest communities [\[3,](#page-12-2)[18,](#page-13-10)[36\]](#page-14-1). Areas in the distribution range of *C. paliurus* that experience more heat and precipitation should thus promote *C. paliurus* regeneration and increase its relative abundance. Furthermore, the characteristic fast growth of *C. paliurus* when provided with sufficient light and water promotes this species' successful competition for dominance, thereby leading to a high relative coverage value.

Finally, the values of species diversity indices of *C. paliurus* communities (Shannon– Wiener, Pielou, and Simpson) increased as light conditions improved due to aspect. This trend reflects the fact that *C. paliurus* communities contain a high number of light-intolerant tree species. According to our results, in addition, little correlation seems to exist between

species richness and environment. Overall, tree species composition varied along environmental gradients; however, species richness did not appear to follow any pattern in *C. paliurus* communities because of the wide range of sample plots covered. Although several tree species exhibited the same distributional pattern as *C. paliurus*, their IVs remained lower than 0.3 (compared with more than 7 for *C. paliurus*). To better understand the specificity of *C. paliurus* communities to different environments, future research should thus focus on small-scale investigation of *C. paliurus* communities.

5. Conclusions

Our analysis of *C. paliurus* communities and population distribution characteristics based on the above two CCA models revealed that the IV of many tree species in *C. paliurus* communities indeed varied according to the environment. Only three tree species in these communities, namely, *Cunninghamia lanceolata*, *Liquidambar formosana*, and *Dendropanax dentiger*, had abundances that were relatively steady across different environments, similar to *C. paliurus*. At the same time, however, the distribution of *C. paliurus* itself changed along environmental gradients. The IV, relative abundance, and relative coverage of *C. paliurus* were highest in warm, low-elevation areas at high longitudes, thus suggesting that *C. paliurus* is best adapted to these locations. Our findings should be valuable in future investigations of *C. paliurus* adaptive areas and mixed forest afforestation in different distribution areas. Further research should be carried out on a smaller scale to better understand the specificity of *C. paliurus* communities to different environments.

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