

Climatic envelope of evergreen sclerophyllous oaks and their present distribution in the eastern Himalaya and Hengduan Mountains

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Abstract Evergreen sclerophyllous oaks (the E.S. oaks, *Quercus* section *Heterobalanus*) are the dominant species of the local ecosystem in the eastern Himalaya and the Hengduan Mountains, southwest China. In this study, we document the climatic envelope of the seven E.S. oak species and examine the relationships between climate and their distribution. This was done using a principal components analysis (PCA) and multiple regression analysis (MRA) of nine climatic indices. The main climatic envelope of the E.S. oaks were: mean temperature of the warmest month (MTW)=12.0–19.5 °C, warmth index (WI) = 33.2–88.9 °C month, annual biotemperature (BT)=–6.9– –0.3 °C, coldness index (CI)=–30.4– –10.1 °C month, mean temperature of the coldest month (MTC)=–3.7–3.0 °C and annual precipitation (AP)=701–897 mm at the lower limits; and MTW=8.3–16.1 °C, WI=15.7–59.1 °C month, BT=3.6–8.9 °C, CI=–55.4– –19.3 °C month, MTC=8.3–16.1 °C and AP=610–811 mm at the upper limits. The climatic range of the E.S. oaks is wide and includes two climatic zones, the cool-temperature zone and the subpolar zone. The PCA and MRA results suggest that the thermal climate plays a major role and precipitation plays a secondary role in controlling the large-scale distribution of the E.S. oaks, except *Quercus monimotricha*. In thermal regimes, BT and/or MTW are most important for both lower and upper limits of the E.S. oaks. Furthermore, our results indicate that the upper distribution limits of the E.S. oaks are less determined by low temperatures and their duration (CI) than by other factors.

Key words climatic indices, distribution limits, multiple regression analysis, principal components analysis, *Quercus* section *Heterobalanus*.

Evergreen sclerophyllous oaks (hereinafter referred to as the E.S. oaks) of China are also known as *Quercus* section *Heterobalanus* Menitsky. They are a distinct and natural group including eight species, *Quercus aquifolioides* Rehder & Wilson, *Quercus guyavifolia* Lévl., *Quercus longispica* A. Camus, *Quercus monimotricha* Hand.-Mazz., *Quercus pannosa* Hand.-Mazz., *Quercus semecarpifolia* Smith, *Quercus senescens* Hand.-Mazz., and *Quercus spinosa* David Rehder & Wilson (Camus, 1936–1954; Menitsky, 1984; Huang et al., 1999; Pu, 2002; Zhou et al., 2003). They are typically gregarious, forming pure forests on the upper slopes and summits of ridges in the eastern Himalaya and the Hengduan Mountains (Jin, 1980; Zhou et al., 2003). The E.S. oaks can stand cold and dry climates and poor soils, conditions that limit the growth of most other evergreen broad-leaved trees, such as other evergreen Fagaceae members, Magnoliaceae, Theaceae and Lauraceae, all very common in the evergreen broad-leaved forests of East Asia (Jin, 1980; Yang, 1990a). Due

to their wide distribution and dominance in the eastern Himalaya and the Hengduan Mountains, the E.S. oaks play a key role in water and soil conservation in the upper reaches of the Yangtze, Mekong and Salween Rivers (Jin, 1980; Zhou et al., 2003) and in shaping many vegetation types in southwest China (Jin, 1980; Yang, 1990a; Li, 1996; Li et al., 2000).

Understanding factors that determine the distribution and abundance of species is a central goal of ecology and biogeography (Ohsawa, 1990, 1991; Rosenzweig, 1995; Cavender-Bares et al., 2004). A significant contribution to this goal is to determine what factors underlie the remarkable variation in range exhibited by most taxonomic groups (Fang et al., 1996; Gaston, 1996; Cavender-Bares & Bazzaz, 2000). Climate is treated as a major abiotic factor that determines plant species' geographical range (Woodward, 1987; Larcher, 1995; Ni & Song, 1997; Cox & Moore, 1999), especially in extra-tropical regions (Huntley et al., 1989; Latham & Ricklefs, 1993; Dynesius & Jansson, 2000; Fang, 2000), due to its influence on plant physiology. Many studies have also shown a correlation between taxon distribution limits and climatic variables (Prentice et al., 1992; Cao et al., 1995; Sykes et al., 1996; Cao & Peters, 1997; Cavender-Bares et al., 2004;

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Fang & Lechowicz, 2006). Furthermore, understanding the relative roles of climate in controlling plant distribution is also a basis for predicting plant responses to potential climatic changes in the future (Loehle & LeBlanc, 1996; Fang, 2000; Austin, 2002). As an important element in the local ecosystem, the E.S. oaks are of special interest to botanists and ecologists (Yang, 1990a; Zhou et al., 1995; Li, 1996). Although research into its leaf morphological characters related to environment (Zhou et al., 1995), physiological features (Zhang et al., 2005) and vegetation types (Yang, 1990a) has been carried out, little effort has focused on the limiting factors that determine the present distribution of the E.S. oaks. Some thermal indices of the E.S. oak forests were calculated by Fang and Yoda (1989), but their vegetation data corresponding to meteorological stations were limited. The objective of the present study is to investigate the effects of climate on the distribution limits of the E.S. oaks. This was achieved by reassessing the climatic envelope of seven E.S. oak species in the eastern Himalaya and the Hengduan Mountains, and determining the main climatic factors that limited their distribution using principal components analysis (PCA) and multiple regression analysis (MRA).

1 Material and methods

1.1 Environment and vegetation of study sites

The principal study sites are situated at the eastern Himalaya and the Hengduan Mountains, southwest China (26–33°N, 90–103°E), which correspond to regions belonging mainly to three provinces: southeast of Tibet (Xizang); northwest of Yunnan; and west of Sichuan (Fig. 1). The regions are very typical in environmental heterogeneity and in vegetation types (Liu et al.,

1985; Zhang, 1998). The altitude ranges from 500 m to 5000 m except for some very high mountains, such as Namjagbarwa summit (7756 m) and Kawadgarbo summit (6740 m) (Yang, 1990b). The climate varies from the northern tropical dry-hot and humid climates to subtropical, temperate and highland climates. The vegetations include monsoon forests in the tropical areas, broad-leaved forests and evergreen coniferous forests in subtropical areas, deciduous broad-leaved forests and coniferous forests in the temperate areas, alpine brushes, alpine meadows and alpine desert (Liu et al., 1985; Yang, 1990b). We mainly focused on the E.S. oak species found in these regions, except *Q. semecarpifolia* for which only a few specimens were recorded.

1.2 Distribution data for E.S. oaks

The distribution ranges of the E.S. oaks were determined by a combination of field surveys, specimen records in three herbaria, namely KUN, PE and CDBI, and our specimen database (the Information System of Seed Plant Specimens), local floras (including Hsu & Jen, 1983; Hsu et al., 1985; Huang et al., 1999), local vegetation references (including Jin, 1980, 1987; Chen, 1988), and numerous relevant scientific papers (including Hsu & Jen, 1976; Jin, 1981; Yang, 1990a; Zhou, 1993; He et al., 1995; Li, 1996) were used as supplementary materials. As a result, geographical locations, lower and upper elevation limits, and other information (e.g., topography and community characteristics) were determined throughout the range of each species (Appendix S1). We surveyed 269 sites at the lower elevation limits and 252 sites at the upper elevation limits of the E.S. oak species in the study areas.

1.3 Sources of climatic data

The climatic data used were supplied by the China Meteorological Data Sharing Service System (<http://cdc.cma.gov.cn/>) based on information from 82 meteorological stations. We used three climatic variables: annual mean temperature; monthly mean temperature; and annual precipitation.

Temperature, at the upper and lower elevation limits of the E.S. oaks, was estimated for each site using a mean lapse rate of 0.71 °C per 100 m in the eastern Himalaya and the Hengduan Mountains (Zhang, 1998) together with data from the nearest meteorological station. The sites where oaks occurred were typically less than 0.5° of latitude and 1.0° of longitude (approximately 50–100 km radius) from a meteorological station. In those instances where there was no meteorological station close to a site, monthly temperature was calculated following the equations of Fang (1992). Annual precipitation (AP) at the upper and lower elevation limits was



Fig. 1. Location of the study areas. Map of China was supplied by the State Bureau of Surveying and Mapping.

calculated following the regression equation.

$$\begin{aligned} AP = & 2487.86 - 0.166 \times ALT - 4.734 \\ & \times LON - 27.201 \times LAT \\ (n = & 97, r = 0.44, P < 0.01) \end{aligned} \quad (1)$$

where ALT, LON and LAT indicate altitude, longitude and latitude of surveyed sites, respectively.

1.4 Determination of climatic indices

As shown in previous studies, distribution limits of plant species are correlated to the following climatic factors: growth season temperature (Holdridge, 1947; Kira, 1977, 1991; Prentice et al., 1992; Sykes et al., 1996), winter temperature (Woodward, 1987; Sykes et al., 1996; Pederson et al., 2004), and precipitation (Yagihashi et al., 2007; Cole et al., 2008). Thus, we considered all of these climatic factors.

Most climatic indices we used were standard in the pertinent published reports (Woodward, 1987; Fang & Yoda, 1989, 1991; Prentice et al., 1992; Sykes et al., 1996; Fang & Lechowicz, 2006). The thermal indices were Kira's warmth index (WI) and coldness index (CI) (Kira, 1945, 1971; cf. Hsu, 1985), and Holdridge's annual biotemperature (BT) (Holdridge, 1967; cf. Chang et al., 1993):

$$WI = \sum (T - 5) \quad (\text{for months in which } T > 5^\circ\text{C}) \quad (2)$$

$$CI = \sum (T - 5) \quad (\text{for months in which } T < 5^\circ\text{C}) \quad (3)$$

$$BT = \sum T/12 \quad (\text{for months in which } 0 < T < 30^\circ\text{C}) \quad (4)$$

Single climatic indices, such as mean temperature of the coldest month (MTC), and mean temperature of the warmest month (MTW) were also used.

The moisture regime was characterized using AP, Kira's arid index (K) (Kira, 1945, 1971) and Holdridge's potential evapotranspiration ratio (PER) (Holdridge, 1967):

$$\begin{aligned} K = & AP/(WI + 20) \\ & (\text{for } 0 < WI < 100^\circ\text{C month}) \text{ or} \\ K = & 2 * AP/(WI + 140) \\ & (\text{for } WI > 100^\circ\text{C month}) \end{aligned} \quad (5)$$

$$PER = APE/AP = 58.93 * BT/AP \quad (6)$$

where APE is annual potential evapotranspiration.

All climatic indices were calculated for the seven species individually. The influence of each climatic index on the distribution of the E.S. oak species was determined using PCA and MRA in the SPSS 12.0 software package (SPSS Inc., 2003).

2 Results

2.1 Climate envelope of the E.S. oak species

In the eastern Himalaya and the Hengduan Mountains, average thermal indices of the E.S. oaks' growth season warmth at the lower limits are between 12.0 (*Q. pannosa*) and 19.5 °C (*Q. spinosa*) for MTW, between 33.2 and 88.9 °C month for WI, and between 6.1 and 11.9 °C for BT (Table 1). Indices at the upper limits are: MTW=8.3–16.1 °C, WI=15.7–59.1 °C month, BT=3.6–8.9 °C (Table 1). The indices of growth season warmth have large fluctuations within and among species, and it means the E.S. oaks occur under very heterogeneous conditions. It is also verified by annual mean temperature (AT), with a range of 5.2–11.8 °C at the lower limits and 1.5–8.5 °C at the upper limits (Table 1). And based on WI, the E.S. oaks occur under cool to cold conditions in the eastern Himalaya and the Hengduan Mountains.

Average thermal index of winter temperature at the lower limits of the E.S. oaks is between –30.4 (*Q. pannosa*) and –10.1 °C month (*Q. senescens*) for CI, and between –55.4 and –19.3 °C month at the upper limits. Average MTC is between –3.2 to 3.0 °C at the lower limits, and –6.9– –0.3 °C at the upper limits. It indicates that the E.S. oaks have a strong cold tolerance.

With regard to moisture regimes, the E.S. oaks have an average AP range from 701 mm to 897 mm at the lower limits and 610–811 mm at the upper limits, indicating humid or semi-humid conditions. These characteristics are verified by K, with a range of 9.0–14.5 at the lower limits and 11.3–19.1 at the upper limits, and by PER, which was 0.50–0.77 at the lower limits and 0.33–0.62 at the upper limits (Table 1).

2.2 Climatic factors controlling distribution

All climatic indices except AT were used to identify the limiting factors for the distribution of the E.S. oaks in the PCA. The first two principal components in the PCA analyses accounted for more than 90% of overall variance for lower and upper limits of six species, except *Q. spinosa* (Table 2). The first PCA axis represented a growth season warmth gradient and the loadings of BT and WI were the largest (Table S1). The second was always a precipitation gradient (Table S1). In these two principal components, the first principal

Table 1 Average for climatic indices at distribution limits for evergreen sclerophyllous oaks

Species	Limits	AT	MTW	WI	BT	CI	MTC	AP	K	PER	Climatic zone
<i>Quercus aquifolioides</i>	Lower	9.0	16.5	62.4	9.3	-14.7	0.2	775.4	10.7	0.67	C
	Upper	3.3	11.1	22.7	4.5	-42.9	-5.7	654.4	15.5	0.44	S
<i>Q. guyavifolia</i>	Lower	9.3	15.9	63.3	9.5	-13.2	1.1	799.8	10.3	0.69	C
	Upper	4.8	11.4	29.9	5.7	-32.4	-3.4	689.6	14.8	0.48	S
<i>Q. longispica</i>	Lower	10.6	17.3	75.3	10.7	-10.3	2.3	812.8	9.0	0.77	C
	Upper	6.9	13.6	43.6	7.3	-20.8	-1.4	723.8	11.8	0.59	S
<i>Q. monimotricha</i>	Lower	9.8	17.8	70.6	10.0	-14.3	0.9	814.6	9.8	0.72	C
	Upper	5.2	12.8	34.6	6.1	-32.4	-3.7	702.2	14.2	0.51	S
<i>Q. pannosa</i>	Lower	5.2	12.0	33.2	6.0	-30.4	-3.2	701.4	14.5	0.50	S
	Upper	1.5	8.3	15.7	3.6	-55.4	-6.9	609.7	19.1	0.33	S
<i>Q. senescens</i>	Lower	10.9	17.5	77.9	11.0	-10.1	2.6	876.2	9.7	0.74	C
	Upper	7.5	14.4	49.1	7.9	-19.3	-0.9	784.9	12.3	0.59	S
<i>Q. spinosa</i>	Lower	11.8	19.5	88.9	11.9	-12.4	3.0	896.5	9.0	0.75	C
	Upper	8.5	16.1	59.1	8.9	-20.8	-0.3	810.9	11.3	0.62	C

AP, annual precipitation; AT, annual average temperature; BT, annual biotemperature; C, cool temperature zone (WI=50–90 °C month) defined by Fang and Yoda (1989); CI, coldness index; K, arid index; MTC, mean temperature for the coldest month; MTW, mean temperature for the warmest month; PER, potential evapotranspiration ratio; S, subpolar zone (WI = 15–50 °C month); WI, warmth index.

Table 2 Proportion (%) of cumulative variance on the first three principal components in a principal components analysis of distribution limits for evergreen sclerophyllous oak species

Species	Lower limit			Upper limit		
	PC1	PC2	PC3	PC1	PC2	PC3
<i>Quercus aquifolioides</i>	82.09	91.30	98.47	75.35	88.84	95.71
<i>Q. guyavifolia</i>	85.88	96.20	99.04	88.44	97.09	98.46
<i>Q. longispica</i>	82.79	97.25	99.03	84.93	96.47	99.07
<i>Q. monimotricha</i>	76.54	88.24	98.10	81.28	91.05	97.74
<i>Q. pannosa</i>	82.74	95.16	98.46	83.19	96.83	99.04
<i>Q. senescens</i>	83.56	94.90	98.56	82.21	94.22	98.13
<i>Q. spinosa</i>	57.91	79.68	97.30	68.27	86.18	97.12

PC1, first principal component; PC2, second principal component; PC3, third principal component.

component (PC1) always played a main role and accounted for more than 80% of overall variance (Table 2). However, the first two principal components in the PCA analyses accounted for less than 90% of overall variance for both limits of *Quercus spinosa* (Table 2). Mean temperature of the warmest month was always the third principal component. However, for *Q. monimotricha*, the third principal component was annual precipitation (Table S1). And the first three principal components accounted for more than 95%, even 99% of overall variance for both limit of all the E.S. oaks.

To identify the correlation between the principal components and distribution limits, a multiple regression analysis (MRA) was carried out. To preserve the information of original data as much as possible, the first three principal components were chosen. In the MRA results, *P*-values indicated whether there was a relationship between the three principal components and the distribution of the E.S. oaks, and standardized coefficients (BETA) showed what the relationship was (Table 3). The first principal component (PC1) showed the largest negative coefficient at both limits of *Q. aquifolioides*, *Q. guyavifolia*, *Q. longispica* and *Q. pannosa* (Table 3), and the PC1 of the four species was a growth season warmth gradient (Table S1). For *Q. monimotricha* and

Q. spinosa, the third principal component (PC3), a precipitation gradient of the former and a mean temperature of the warmest month gradient of the latter, showed the largest negative coefficient (Table 3). For *Q. senescens*, the conditions were different: the third principal component (PC3), a precipitation gradient, was the largest negative coefficient at lower limits; and the second principal component (PC2), a growth season warmth gradient, was the largest at upper limits (Table 3). Furthermore, *P*-values of all these principal components having largest standardized coefficients were less than 0.01, that is, the relationship between the principal component and the distribution was highly significant. Both PCA and MRA results indicated that climatic factors strongly influenced the large-scale distribution of the E.S. oaks. Specifically, thermal indices always showed larger loadings at both lower and upper limits for most species, and precipitation generally played the second role.

3 Discussion

Although the study areas belong to the subtropical region, the E.S. oaks in fact grow in climatic regimes

Table 3 Regression coefficients[†] and significance of a multiple regression analysis of distribution limits for evergreen sclerophyllous oaks

	Lower limit			Upper limit		
	B	BETA	P	B	BETA	P
<i>Quercus aquifolioides</i>						
Constant	2763.78	NA	0.00	3491.09	NA	0.00
PC1	-195.08	-0.60	0.00	-252.44	-0.63	0.00
PC2	-100.44	-0.31	0.00	-97.64	-0.24	0.01
PC3	-144.24	-0.44	0.00	-171.24	-0.43	0.00
<i>Q. guyavifolia</i>						
Constant	2750.50	NA	0.00	3336.50	NA	0.00
PC1	-212.30	-0.78	0.00	-271.57	-0.79	0.00
PC2	-48.84	-0.18	0.11	-86.38	-0.25	0.07
PC3	-111.61	-0.41	0.00	88.63	0.26	0.06
<i>Q. longispica</i>						
Constant	2736.67	NA	0.00	3138.46	NA	0.00
PC1	-187.04	-0.67	0.00	-269.89	-0.79	0.00
PC2	-145.37	-0.52	0.00	-135.81	-0.40	0.00
PC3	-43.25	-0.15	0.23	-76.04	-0.22	0.02
<i>Q. monimotricha</i>						
Constant	2514.80	NA	0.00	3120.00	NA	0.00
PC1	-139.68	-0.42	0.00	-236.00	-0.58	0.00
PC2	2.04	0.01	0.96	-62.16	-0.15	0.16
PC3	-218.34	-0.66	0.00	-258.19	-0.63	0.00
<i>Q. pannosa</i>						
Constant	3287.50	NA	0.00	3751.67	NA	0.00
PC1	-262.03	-0.64	0.00	-301.22	-0.66	0.00
PC2	-256.22	-0.63	0.00	-281.43	-0.62	0.00
PC3	-106.66	-0.26	0.00	-124.08	-0.27	0.00
<i>Q. senescens</i>						
Constant	2425.68	NA	0.00	2848.25	NA	0.00
PC1	-98.04	-0.34	0.00	-112.43	-0.34	0.00
PC2	-164.66	-0.57	0.00	-242.46	-0.74	0.00
PC3	-177.92	-0.62	0.00	-155.04	-0.48	0.00
<i>Q. spinosa</i>						
Constant	1956.25	NA	0.00	2477.63	NA	0.00
PC1	-27.51	-0.05	0.60	-26.43	-0.06	0.50
PC2	70.70	0.13	0.19	95.22	0.23	0.02
PC3	-388.77	-0.74	0.00	-278.32	-0.67	0.00

[†]Dependent variable, distribution limits/m. B, unstandardized coefficients; BETA, standardized coefficients; NA, not applicable; PC1, first principal component; PC2, second principal component; PC3, third principal component.

different from those of the subtropical climatic zone (Table 1). The E.S. oaks concentrated within a climatic range of 33.2–88.9 °C month for WI at the lower limits, and 15.7–59.1 °C month at the upper limits. It means that the lower boundaries of most E.S. oaks are in the cool-temperate zone (WI=50–90 °C month) defined by Fang and Yoda (1989) and the upper limits are in the subpolar zone (WI=15–50 °C month) (Table 1). Except *Q. pannosa* and *Q. spinosa*, the E.S. oaks always occupy two climatic zones: the cool-temperate zone and the subpolar zone. *Quercus pannosa*, with a WI value between 15.7 and 33.2 °C month, occurs completely in the subpolar zone. On the contrary, *Q. spinosa* (WI=59.1–88.9 °C month) only occurs in the cool-temperate zone.

The climatic zone characteristics of the E.S. oaks are consistent with the environment of high mountains in the eastern Himalaya and the Hengduan Mountains. These high mountains always cause a low temperature environment, especially in the E.S. oaks occurrence sites, and the E.S. oaks also suit a low temperature en-

vironment by various morphological characters. First, foliar trichomes are an important trait for the E.S. oaks to suit the cool environment, and the character is a main factor for plant distribution (Jones, 1986; Zhou et al., 1995). The species with foliar trichomes can tolerate lower temperatures than the species without hairs, and all E.S. oaks' young leaves have hair underneath. Second, a dwarfing effect is another main approach of these oaks to suit the environment and many E.S. oak forests are coppiced in subalpine sunny slopes (Jin, 1980; Yang, 1990a). For example, *Q. monimotricha* is the only dwarf small shrub and occurs at higher altitudes than *Q. senescens*, although both of them have gray hair under the leaves. Thus, low temperature in high mountains does not restrict the E.S. oaks occurring at their upper limits. This is also verified by low CI values, with a range of -55.4 – -19.3 °C month at the upper limits.

It has been argued in previous studies that low temperatures and their duration (CI) rather than growth season warmth (WI) limits the upward and northward

distribution of the evergreen broad-leaved tree species (Kira, 1976, 1977; Hattori & Nakanishi, 1985; Fang & Yoda, 1991). However, our PCA and MRA analysis results do not support this viewpoint, indicating that CI is a more significant factor affecting the upper distribution of the E.S. oaks than WI. In contrast, for *Q. aquifolioides*, *Q. guyavifolia*, *Q. longispica* and *Q. pannosa*, PC1 was a growth season warmth gradient not only at the lower limits but also the upper limits. It indicates that the growth season warmth is very important for the large-scale distribution of the four species. In another example, PC3 plays a key role in controlling the upward distribution of *Q. monimotricha* and *Q. spinosa*. Therefore, AP mainly controls distribution of *Q. monimotricha* at the upper limits and MTW mainly controls distribution of *Q. spinosa*. And for *Q. senescens*, the upper limits are closely related to AP. Therefore, for most of the E.S. oaks, growth season warmth but not winter temperature is the most important factor controlling their upward distributions.

However, strong correlation among different climatic indices precludes identification of a single, dominant aspect of thermal regime that affects the distribution of E.S. oaks. And all thermal regimes, including growth season warmth (WI, BT and MTW) and winter low temperature (CI and MTC), show almost equal loadings at the first PCA axis (Table S1). Given the complexity of interaction between various indices, the relationships between climatic factors and distribution of the E.S. oaks are less than perfect. This highlights the need to incorporate other physiological attributes such as leaf tolerance to low temperature, and more accurate climatic data from their real sites. This study serves as a useful starting point and forms the basis to initiate further investigations into the co-relationships between climatic factors and the distribution of the E.S. oaks.

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Supplementary Material

The following supplementary material is available for this article:

Appendix S1. Locations and elevation of distribution limits of evergreen sclerophyllous oak (*Quercus* section *Heterobalanus*) species used in the present study. –, no available records.

Table S1. Loadings of 8 climatic indices derived from principal components analysis for the first three principal components for distribution limits of the evergreen sclerophyllous oak species. AP, annual precipitation; BT, annual biotemperature; CI, coldness index; K, arid index; MTC, mean temperature for the coldest month; MTW, mean temperature for the warmest month; PC1, the first principal component; PC2, the second principal component; PC3, the third principal component; PER, potential evapotranspiration ratio; WI, warmth index.

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