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# The leaf physiognomy of evergreen and deciduous species exhibits different responses to climate: Implications for palaeoclimate reconstruction in China

Wen-Yun Chen [a,*], Tao Su [b], Shu-Feng Li [c,*]

[a] Key Laboratory of Economic Plants and Biotechnology and the Yunnan Key Laboratory for Wild Plant Resources, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming 650201, China

[b] State Key Laboratory of Oil and Gas Reservoir Geology and Exploitation & Institute of Sedimentary Geology, Chengdu University of Technology, Chengdu 610059, China

[c] CAS Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla 666303, China

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ABSTRACT

The function and morphology of plant leaves typically differ according to leaf habit (evergreen vs deciduous), and these differences have been thought to respond divergently to climatic conditions. While the variations in leaf margins with leaf habit and their respective correlation with climate have been investigated, limited investigation has been conducted on other leaf physiognomic characters. In the present study, we studied 2111 evergreen and 1001 deciduous native woody dicotyledons, investigating how the occurrences of 21 leaf physiognomic characters vary with leaf habit in humid regions of China. We then analysed these leaf characters of evergreen and deciduous species and climate correlations using canonical correspondence analysis based on 498 and 521 calibration datasets, respectively. Our results show that most of leaf physiognomic characteristics differed significant between evergreen and deciduous species in terms of the percentage values and the ordination diagrams. The leaf physiognomic distribution of both evergreen and deciduous species exhibited remarkable differences in response to climate. The lobed, small (nano- and microphyll), obtuse apex, reflex base, wide (length: width ratio $\leq$ 2:1) and ovate shape leaves predominated in deciduous species and occurred in colder and drier climates, while untoothed, large (noto- and mesophyll), reflex apex, acute base, narrow (L:W ratio = 2–4:1) and elliptic shape leaves predominated in evergreen species and occurred in warmer and wetter climates. This distribution pattern was primarily influenced by winter temperature and precipitation. The leaf physiognomic characteristics of evergreen and deciduous species display distinct responses to winter climatic variables across humid regions of China, revealing differences in environmental tolerance between the two leaf habits. This also suggests that the East Asian winter monsoon especially influences the leaf physiognomic characters of both evergreen and deciduous species in China. Furthermore, our findings suggest that in addition to leaf margins, leaf habit could confound correlations between other leaf physiognomic characters and climate, potentially affecting the accurate prediction of paleoclimate in China using multivariate leaf physiognomy approaches.

## 1. Introduction

The morphological and functional characteristics of plant leaves have been a major subject for scientists researching plant, vegetation and ecosystem processes (Bailey and Sinnott, 1915, 1916; Wolfe, 1973, 1993; Royer and Wilf, 2006; Díaz et al., 2016; Wright et al., 2017). These characteristics reflect the adaptation mechanisms of plants to climate and make them representative indicators of climate (Givnish, 1987; Baker-Brosh and Peet, 1997). Specifically, the distribution of leaf physiognomic characters in woody dicotyledons is significantly influenced by climate (Bailey and Sinnott, 1915; Wolfe, 1971; Traiser et al., 2005; Adams et al., 2008; Yang et al., 2015; Chen et al., 2019; Reichgelt and Lee, 2021; Roth-Nebelsick and Traiser, 2024). As a result, palaeobotanists have investigated the correlation between leaf physiognomy

* Corresponding authors.
*E-mail addresses:* chenwy@mail.kib.ac.cn (W.-Y. Chen), lisf@xtbg.org.cn (S.-F. Li).

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and climate and have successfully applied these correlations to reconstruct terrestrial palaeoclimate (Bailey and Sinnott, 1916; Dilcher, 1973; Wing and Greenwood, 1993; Traiser et al., 2007; Peppe et al., 2011; Spicer et al., 2021; Nguyen et al., 2024).

Woody dicotyledons can be classified into two types of leaf habits: evergreen and deciduous. The evergreen habit is defined as retaining at least some leaves throughout the year, while species that are bare of leaves for some part of the year are considered deciduous (Kikuzawa and Lechowicz, 2011). Numerous studies have observed that leaf characters show remarkable differences in evergreen and deciduous species. Evergreen species generally have a longer leaf life span (LL) (Chabot and Hicks, 1982; Reich, 1995) and higher leaf mass per area (LMPA) (Li et al., 2022; Soh et al., 2019), leaf thickness (Givnish, 1979; Kröber et al., 2015) and leaf petiole mass (Li et al., 2008) but smaller leaf area (Sancho-Knapik et al., 2021; Vargas et al., 2021) than deciduous species. In particular, the differences in leaf physiognomic characteristics between evergreen and deciduous woody dicotyledons have long been noted. Generally, evergreen species tend to have proportionately more frequently untoothed leaf margins (Bailey and Sinnott, 1916; Wolfe, 1993; Baker-Brosh and Peet, 1997; Jacobs, 2002) and less frequently lobed margins (MacArthur, 1972) than deciduous species. Recent quantitative analyses at both the species level and site level support this conclusion. For instance, the proportion of toothed leaves in deciduous species is much higher than that in evergreen species of dicotyledonous angiosperms (Royer et al., 2012; Chen et al., 2014; Iszkuło et al., 2024). At individual sites, the deciduous species were more likely to bear teeth than evergreen species (Peppe et al., 2011; Chen et al., 2014). Despite these insights, our understanding of the differences in other leaf physiognomic characteristics of leaf habit, including leaf simple and size, type of apex and base of the blade, length-width ratio and blade shape, remains incomplete.

Different climatic conditions have been hypothesized to drive leaf characteristic variations coupled with leaf habit. Many studies have reported that leaf characteristics in evergreen and deciduous species, either globally or locally, showed different responses to temperature (Peppe et al., 2011; González-Zurdo et al., 2016; Soh et al., 2019), water accessibility (Wright et al., 2004; Reich et al., 1999; Vargas et al., 2021) and growing season length (Kikuzawa et al., 2013; Wang et al., 2023). For instance, leaf characters such as LL and LMPA from a global dataset displayed divergent temperature responses in evergreen and deciduous species. With increasing mean annual temperature (MAT), both LL and LMPA increased in evergreens but decreased in deciduous species (Wright et al., 2005; van Ommen Kloeke et al., 2012). Furthermore, LMPA from sites around the world exhibited a significant negative correlation with mean annual precipitation (MAP) in evergreen species, while showing little or no relationship with deciduous species (Wright et al., 2004, 2005). On the regional scale, leaf size in New Zealand evergreen species exhibited a significantly positively correlation with both frost-free period and MAT, while leaf size in deciduous species only displayed a weak negative correlation with these two climatic variables (Lusk et al., 2018). An analysis of oaks in Spain revealed that leaf area in evergreen species was positively correlated with the minimum temperature of the coldest month, whereas leaf area in deciduous species was negatively correlated with this climatic variable (Sancho-Knapik et al., 2021: Table 4). Additionally, this study also observed that leaf tissue density (LD) of deciduous oaks was negatively correlated with aridity period and aridity intensity, while LD within evergreen oaks exhibited a positive correlation with these two climate variables (Table 4).

Palaeobotanists have explored univariate (Bailey and Sinnott, 1915, 1916; Wolfe, 1979; Wilf et al., 1998; Su et al., 2010; Chen et al., 2014; Peppe et al., 2018) or multivariate statistical methods to analyze relationships between the percentage of leaf physiognomic characters in woody dicotyledons leaf physiognomy and climate (Wing and Greenwood, 1993; Wolfe, 1993; Gregory and McIntosh, 1996; Spicer et al., 2004; Peppe et al., 2011; Lielke et al., 2012; Chen et al., 2019; Spicer et al., 2021). Numerous studies have noted that leaf physiognomy integrates multiple characters with functional and/or physiological connections to climate (Wolfe, 1993; Wolfe and Spicer, 1999; Spicer et al., 2004, 2021; Traiser et al., 2005; Peppe et al., 2011; Kennedy et al., 2014; Yang et al., 2015; Chen et al., 2019; Wang et al., 2022). Consequently, many investigations have employed multivariate methods to concurrently analyze the relationships between various leaf characteristics and climate.

Several studies observed that leaf habit influences on leaf margins-climate correlations, due to the remarkable differences in untoothed leaf margins both evergreen and deciduous species (Peppe et al., 2011; Royer et al., 2012; Iszkuło et al., 2024). Consequently, leaf habit might affect the accuracy of estimating paleoclimate using leaf margin analysis (LMA), a univariate statistical method based on untoothed leaf margins-MAT relationship (Peppe et al., 2011; Royer et al., 2012). For instance, Chen et al. (2014) demonstrated that in cold regions of China, where deciduous species have a stronger influence on untoothed leaf margins-MAT correlations than evergreen species, and cause to the extreme overestimation temperature based on LMA model in this climatic zone. A recent study has also indicated that the LMA method for estimating palaeotemperatures is becoming increasingly inaccurate in cold regions of northern Europe, due to a negative relationship between the percentage of untoothed leaf margins in deciduous species and MAT in this region (Iszkuło et al., 2024). On the contrary, Royer et al. (2012) demonstrated that the incorporation of thickness and deciduousness into leaf physiognomy-climate models enhances the accuracy and precision of MAT estimation. However, previous studies have primarily focused on the effect of leaf habit on the correlations between toothed or tooth-related leaf characteristics and climate, as well as their impact on paleotemperature reconstructions based on these correlations. Therefore, it is essential to examine whether leaf habit could be confounding the relationships between other leaf physiognomic characters and climate, and potentially affecting the accuracy of past climate reconstructions based on multivariate leaf physiognomy-climate analysis methods.

In previous studies, the analysis of leaf physiognomy-climate correlations has commonly relied on two primary data sources: (1) data from local forest sites (Wolfe, 1993; Jacques et al., 2011; Spicer et al., 2021), and (2) assembling a 'synthetic' dataset from regional floral records (Traiser et al., 2005). The synthetic dataset offers a comprehensive floristic dataset, facilitating the exploration of distribution patterns of leaf physiognomy and their correlation with climate across numerous sampling sites. Furthermore, this approach has the potential to reduce the influence of local factors, such as edaphic conditions and microclimate factors, on leaf physiognomy (Traiser et al., 2005). Many studies have demonstrated this approach as a valuable tool for investigating the relationships between leaf physiognomy and climate (Traiser et al., 2005; Adams et al., 2008; Chen et al., 2014, 2019; Li et al., 2016; Wright et al., 2017; Reichgelt and Lee, 2021; Roth-Nebelsick and Traiser, 2024).

China hosts diverse vegetation types, including coniferous forest, mixed conifer and deciduous forest, deciduous broad-leaved forest, mixed deciduous and evergreen forest, evergreen broad-leaved forest and rainforest and monsoon forest, spanning from north to south forests (Wu, 1980). Moreover, China experiences a strong Asian monsoonal climate characterized by a wet and warm summer and a dry and cold winter (Zhang, 1991). The pronounced seasonal rainfall variations in China have a profound impact on its flora, species richness, and overall vegetation composition (Chen et al., 2018; Chen and Su, 2020; Li et al., 2021). These climatic dynamics also significantly influence the spatial distribution of Chinese leaf physiognomy (Chen et al., 2019), providing an ideal context for investigating the variations between evergreen and deciduous species in response to climatic variables, including the distinctive monsoonal climate. Despite the exceptional suitability of China as a study region, few studies have delved into the differences in leaf physiognomy (specifically leaf margins) between evergreen and deciduous species within the country (Chen et al., 2014; Li et al., 2016). Therefore, our analysis extends beyond the narrow focus on leaf margins, encompassing a comprehensive exploration of a wide array of leaf physiognomic characteristics associated with leaf habit. This broader approach enhances our understanding of how diverse leaf traits vary between evergreen and deciduous species across China, shedding light on the nuanced responses of vegetation to the unique climatic conditions prevalent in this region, which does not encompass very high latitudes where deciduousness due to light and temperature predominates over water availability.

In this study, we analysed leaf physiognomic characteristics that vary with leaf habit using a large-scale dataset across humid regions of China. We had three aims: (1) to investigate differences in leaf physiognomic characteristics between evergreen and deciduous species; (2) to analyze how the leaf physiognomy of both evergreen and deciduous species is adapted to climate variables, including the distinctive monsoonal climate; (3) to explore the effect of leaf habit on leaf physiognomy-climate correlations and its potential impact on estimating paleoclimate.

## 2. Materials and methods

### 2.1. Calibration dataset of leaf habit (evergreen and deciduous)

The dataset of evergreen and deciduous species was derived from the comprehensive database of Chinese native woody dicotyledonous species (Chen et al., 2014), which covers 3166 species across humid regions of China (the mean annual precipitation is higher than 400 mm). Among these species, 2111 are identified as evergreen, and 1001 are deciduous, while 54 have both leaf habits (see electronic Supplementary Data 1 of Chen et al., 2014). Data for each species' leaf habit (deciduous vs evergreen) were scored (0 = deciduous; 1 = evergreen; 0.5 = species with both leaf forms). All leaf habits of each species are shown in

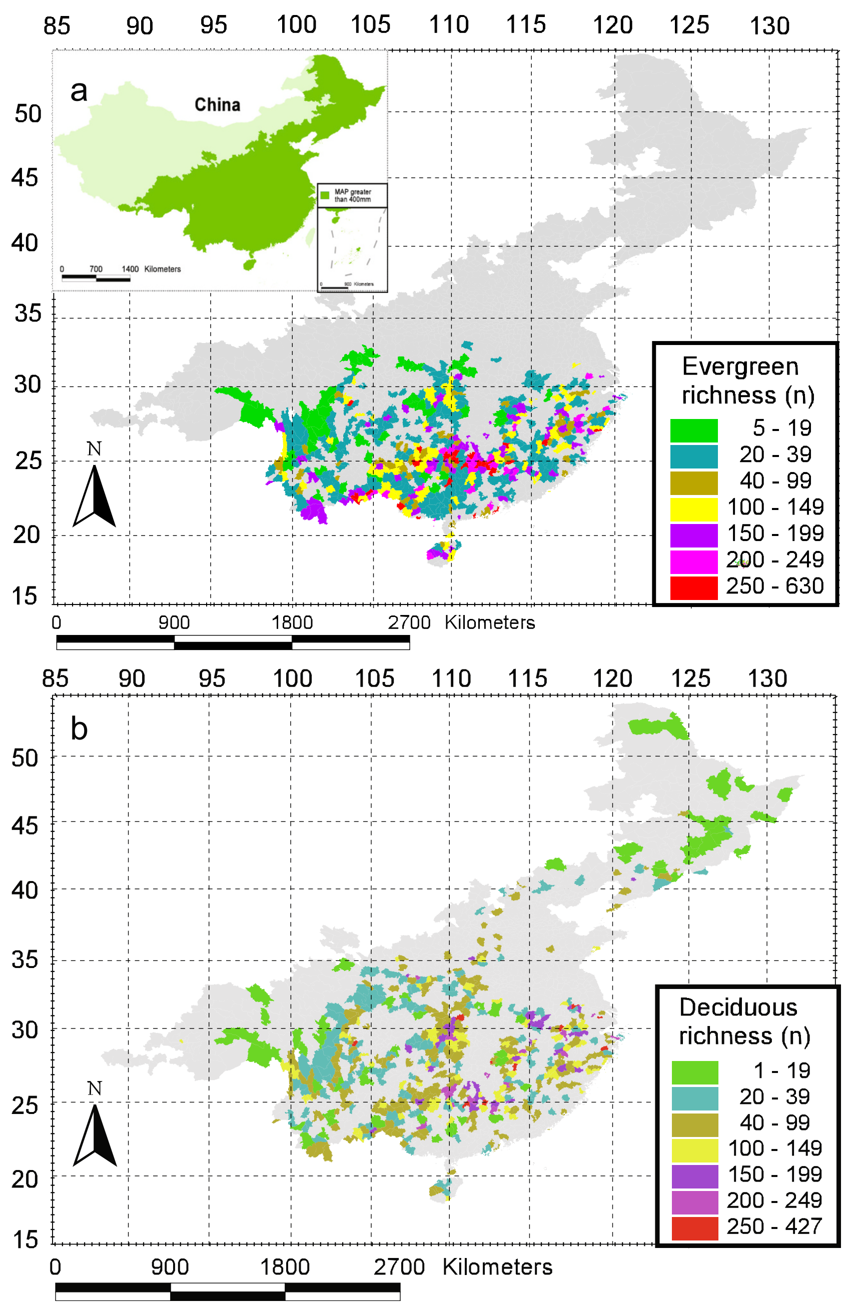


**Fig. 1.** Richness of evergreen and deciduous woody dicotyledons in humid regions of China (at county level), with a mean annual precipitation (MAP) above 400 mm. a, Evergreen species, calibration grids, $n$ = 498; b, Deciduous species, calibration grids, $n$ = 521.

Supplementary Data 1. In this study, we considered species as obligate evergreen or deciduous species, excluding intermediate categorical scores of the dependent variable (i.e., scores of 0.5). Maps of the present-day distribution of 2111 evergreen and 1001 deciduous woody dicotyledons based on presence/absence were compiled at the county level and digitised for application in a geographical information system (GIS). Following previous studies (Wolfe, 1993), we restricted our dataset to counties with at least 20 native dicotyledonous species for either evergreen or deciduous species. As a result of these restrictions, the calibration dataset used for the analysis consisted of 498 evergreen species and 521 deciduous species data units at the county level (Supplementary Data 2 and 3).

Each county in our dataset originally spanned an area ranging from 231.6 to 4931.5 km$^2$, with an average area of 2727.9 km$^2$. To mitigate the potential influence of variations in county size on species richness, we standardized each county's area to an equal size of 2500 km$^2$. Following this adjustment, the revised species richness for each county was determined as follows:

$$\text{Species richness} = \text{sum of species in each county/county area} \times 2500 \quad (1)$$

The species richness of evergreen and deciduous species of each calibration dataset can be found in Supplementary Data 2 and 3, respectively.

The distributions of the richness of evergreen and deciduous species based on the calibration dataset in humid regions of China are shown in Fig. 1a and b, respectively. The richness distribution patterns of evergreen and deciduous species show a striking difference. Evergreen species are mainly distributed in southern China and not in northeastern China (Fig. 1a). Their species richness varied from 5 to 630 per county, with an average of 109 species per county. In contrast, deciduous species occur throughout a vast region from southern to northeastern China and include almost all types of vegetation in eastern China (Fig. 1b). Their species richness varied from 1 to 427 per county, with an average of 82 species per county.

**Table 1**
Leaf physiognomic characters with number, percentages and differences as they occur in evergreen and deciduous species and the correlation coefficients ($r$) between leaf physiognomic characters and leaf habit.

| Leaf character | Abbr. | Definition | Evergreen (n) | Deciduous (n) | Evergreen (%) | Deciduous (%) | Differences (%) | Leaf habit ($r$) |
|---|---|---|---|---|---|---|---|---|
| Leaf simple | le_simp | The leaf consists of a single blade attached to a simple petiole | 1889 | 767 | 89.48 | 76.55 | 12.93 | 0.170*** |
| Leaf lobed | le_lobe | A lobe is a marginal projection with a corresponding sinus incised 25 % or more of the distance from the projection apex to the midvein | 6 | 87 | 0.28 | 8.68 | −8.40 | −0.231*** |
| Untoothed leaf margin | untooth | A leaf is no projection (teeth) along the margin and no lobes | 1355 | 302 | 64.18 | 30.17 | 34.01 | 0.342*** |
| Leaf size: nanophyll | ls_nano | Area of blade <225 mm$^2$ | 14 | 38 | 0.66 | 3.79 | −3.13 | −0.114*** |
| Leaf size: microphyll | ls_micr | Area of blade =225–2025 mm$^2$ | 577 | 382 | 27.33 | 38.12 | −10.79 | −0.110*** |
| Leaf size: notophyll | ls_noto | Area of blade =2025–4500 mm$^2$ | 880 | 311 | 41.69 | 31.04 | 10.65 | 0.102*** |
| Leaf size: mesophyll | ls_meso | Area of blade =4500–18,225 mm$^2$ | 610 | 260 | 28.90 | 25.95 | 2.95 | 0.030* |
| Apex of blade: obtuse | ap_obtu | Apex angle between 90° and 180° | 122 | 73 | 5.78 | 7.29 | −1.51 | −0.029 ns |
| Apex of blade: acute | ap_acut | Apex angle <90° | 1960 | 916 | 92.85 | 91.42 | 1.43 | 0.024 ns |
| Apex of blade: reflex | ap_refl | Apex angle >180° | 26 | 11 | 1.23 | 1.10 | 0.13 | 0.006 ns |
| Base of blade: obtuse | ba_obtu | Base angle between 90° and 180° | 319 | 285 | 15.11 | 28.44 | −13.33 | −0.158*** |
| Base of blade: acute | ba_acut | Base angle <90° | 1634 | 469 | 77.40 | 46.81 | 30.59 | 0.305*** |
| Base of blade: reflex | ba_refl | Base angle >180° | 158 | 246 | 7.48 | 24.55 | −17.07 | −0.238*** |
| Blade length: width < 1:1 | lw_1 | Ratio L/W: <1:1 | 5 | 47 | 0.24 | 4.69 | −4.45 | −0.162*** |
| Blade length: width = 1–2:1 | lw_2 | Ratio L/W: =1–2:1 | 232 | 353 | 10.99 | 35.23 | −24.24 | −0.290*** |
| Blade length: width = 2–3:1 | lw_3 | Ratio L/W: =2–3:1 | 1098 | 427 | 52.01 | 42.61 | 9.40 | 0.087*** |
| Blade length: width = 3–4:1 | lw_4 | Ratio L/W: =3–4:1 | 629 | 138 | 29.80 | 13.77 | 16.03 | 0.174*** |
| Blade length: width > 4:1 | lw_5 | Ratio L/W: >4 | 146 | 34 | 6.92 | 3.39 | 3.53 | 0.070*** |
| Shape of blade: obovate | sh_obov | Largest width in upper 2/5 of lamina | 124 | 68 | 5.87 | 6.77 | −0.90 | −0.018 ns |
| Shape of blade: elliptic | sh_elli | Largest width in middle 1/5 of lamina | 1839 | 758 | 87.12 | 75.65 | 11.47 | 0.143*** |
| Shape of blade: ovate | sh_ovat | Largest width in lower 2/5 of lamina | 146 | 173 | 6.92 | 17.26 | −10.34 | −0.160*** |

Species with a leaf habit score of 0.5 are excluded; number of evergreen species, $n = 2111$; number of deciduous species, $n = 1001$; species with an untoothed leaf margins score of 0.5 are excluded; significance correlations are indicated as *** $P < 0.0001$, * $P < 0.05$, ns $P > 0.5$; the correlation untoothed leaf margins and leaf habit, $n = 2938$; for other correlations leaf habit, $n = 3122$.

### 2.2. Leaf physiognomic data

We selected twenty-one leaf physiognomic characteristics for each evergreen and deciduous species, drawing from the datasets provided by Chen et al. (2014) and Chen et al. (2019). These characteristics encompass attributes such as simple, presence of lobes, untoothed margins, size, blade's types of base and apex, length-width ratio and blade shape. This dataset has proven valuable in recent studies on the relationship between climate and spatial distribution patterns of leaf physiognomic characters (Chen et al., 2019). Each description of evergreen and deciduous species was transformed into categorical traits. The definitions of leaf characters follow Ellis et al. (2009) are described in Table 1. Because our study was conducted only in humid regions of China, four leaf size classes were included in this study: nanophyll, microphyll, notophyll and mesophyll categories.

Following procedures by Wolfe (1993), values of 0 (the character is absent) and 1 (the character is present) were assigned to each leaf physiognomic character. The scores of leaf physiognomic characters for each species were determined using specimens in the Herbarium of the Kunming Institute of Botany (for more details on obtaining leaf physiognomic characters for each species, see Chen et al., 2014, 2019). The leaf physiognomic character scores for each evergreen and deciduous species are shown in Supplementary Data 1. The percentage of leaf physiognomic characters for evergreen and deciduous species in each county was the sum of the scores of all species divided by the number of all species. This method of investigating the relationships between the percentage of leaf physiognomy and climate was originally developed by Wolfe (1993) and was designed to reconstruct terrestrial palaeoclimate. Subsequently, it has been used to analyze leaf physiognomy-climate correlations in modern flora around the world (Jacobs, 1999; Traiser et al., 2005; Yang et al., 2015; Chen et al., 2019). The percentage of leaf physiognomic characteristics for both evergreen and deciduous species for each calibration dataset is shown in Supplementary Data 2 and 3.

### 2.3. Climatic parameters

Climate data for each county were derived from the Bristol Research Initiative for the Dynamic Global Environment (https://www.bristol.ac.uk/geography/research/bridge/), University of Bristol. Fourteen climatic parameters were included in this study: mean annual temperature (MAT), warmest month mean temperature (WMMT), coldest month mean temperature (CMMT), growing season length (GSL), mean annual precipitation (MAP), growing season precipitation (GSP), mean monthly growing season precipitation (MMGSP), precipitation of the three wettest consecutive months (P3WET), precipitation of the three driest consecutive months (P3DRY), relative humidity (RH), specific humidity (SH), vapour pressure deficit (VPD), vapour pressure deficit for the wettest season (VPD_ JJA) and vapour pressure deficit for the driest season (VPD_DJF). The definitions of the climatic variables and their units are listed in Table S1. The climatic parameters (at county level) of each calibration dataset are shown in Supplementary Data 2 and 3.

Asian monsoonal climates are outstanding, especially in terms of precipitation patterns, that is, abundant rainfall during the summer and much less rainfall during the winter (Lau and Chan, 1983). Therefore, we followed previous studies that used differences between P3WET and P3DRY as a proxy for monsoon climate (Wang et al., 2006; Jacques et al., 2011; Chen et al., 2019; Chen and Su, 2020): P3WET occurs in summer and represents summer rainfall, whereas P3DRY occurs in winter and represents winter rainfall.

### 2.4. Data analysis

To analyze leaf physiognomy-climate relationships based on a large-scale dataset covering extensive areas or including a multitude of samples, we adopted a methodology similar to previous studies that established spatial patterns of physiognomy with a high degree of resolution (Traiser et al., 2005; Chen et al., 2014, 2019; Wright et al., 2017; Reichgelt and Lee, 2021; Roth-Nebelsick and Traiser, 2024). Therefore, we followed those studies and compiled and digitised the percentages of 21 leaf physiognomic characters of both evergreen and deciduous Chinese woody dicotyledons for application using ArcGIS (ArcView GIS 3.2, ESRI, New York, USA). Eighteen leaf characters in evergreen and deciduous species were also plotted on a map at the county level (Figs. S1 and S2).

To investigate the differences in leaf physiognomic characteristics between evergreen and deciduous species for species-level, we counted the number and percentages of each leaf physiognomic characteristic as they occur in evergreen and deciduous species, respectively. Furthermore, to test the strength of the association between leaf physiognomy and leaf habit at the species level, we computed Kendall's tau-b rank coefficient with a nonparametric correlation test that accounts for ties, excluding intermediate categorical scores of the dependent variable (i.e., scores of 0.5).

Boxplot diagrams were generated to analyze the differences in the percentage of leaf physiognomic characteristics between evergreen and deciduous species on the calibration dataset. Meanwhile, the percentage of evergreen and deciduous leaf physiognomic characters did not follow a normal distribution according to the Shapiro–Wilk test (Shapiro and Wilk, 1965). Consequently, we used Mann–Whitney U statistic models (a nonparametric test) for the percentage values of each character on the calibration grids as response variables and leaf habit as the categorical explanatory variable to evaluate the significance of the differences between evergreen and deciduous species. Furthermore, we also used correspondence analysis (CA) to assess indirect ordination of the percentage of leaf physiognomic characters on the calibration dataset to evaluate the difference in the distribution of leaf characters in both evergreen and deciduous species (Hill, 1973). CA is a method for the visual display of information from two-way contingency groups (Riani et al., 2022), which has been found to be useful for comparing the distributions of functional groups (Stegner and Holmes, 2013; Diogo et al., 2021; Wang et al., 2022).

To investigate the relationships between the percentages of leaf physiognomic characters and climatic parameters based on all calibration datasets together and evergreen and deciduous calibration grids separately, we used canonical correspondence analysis (CCA) (Ter Braak, 1986). The CCA, a widely used multivariate statistical method for examining leaf characteristics-climate correlations, followed the methodology outlined by Ter Braak (1986) and has been employed in prior studies (Wolfe, 1993; Wolfe and Spicer, 1999; Yang et al., 2015; Luong et al., 2021; Wang et al., 2022). As for the above-mentioned fact that the percentage of evergreen and deciduous leaf physiognomic characters did not follow a normal distribution, we applied a "hellinger" transformation to the percentages of leaf physiognomic characters for both evergreen and deciduous species before conducting the CCA analysis. Additionally, the climatic variables, which exhibited varying scales, were standardized using the "standardize" function. In the ordination diagram, sample sites are represented by points and climatic factors by vectors. Sites with similar leaf characters plot together, while dissimilar sites plot apart. The relative significance of various climatic factors is judged by the relative length of the vectors. The statistical significance of the CCA relationships between climate and each leaf characteristic variable on the calibration dataset was tested by an Anova like permutation test with 999 permutations, which is adequate for a test at the 5 % significance level. Furthermore, to evaluate the relationship between climate variables and leaf physiognomy while accounting for potential effects due to different leaf habits among species, we fitted a quadratic regression model. In this model, the correspondence analysis (CA) of leaf physiognomy served as the response variable, with climate variables treated as independent variable. All CCAs were made using the R package 'vegan' (Oksanen, 2015).

All statistical analyses were performed with SPSS 25 (SPSS Science, Chicago, IL, USA) and R (v.3.6.1) (R Core Team, 2019).

## 3. Results

### 3.1. Differences in leaf physiognomic characteristics between evergreen and deciduous species at the species level

Table 1 provides an overview of the number, percentages and differences in leaf physiognomic characteristics that occur in evergreen and deciduous species in humid regions of China. In general, there are significant differences in leaf characteristics between evergreen and deciduous species. The values of species number and species percentages for these leaf character occurrences on evergreen species are higher than those of deciduous species, including simple, untoothed, large (noto- and mesophyll), acute and reflex apexes, acute base, narrow (L:W ratio $\geq$ 3:1) and elliptic shape leaves. Nevertheless, these leaf characters in evergreen species are lower than those of deciduous species, including lobed, small (micro- and mesophyll), obtuse apex, obtuse and reflex bases, wide (L:W $\leq$ 2:1) and obovate and ovate shapes leaves.

Moreover, except for the apex and obovate shape leaves, which are not correlated with leaf habit ($P > 0.05$), other leaf physiognomic characteristics are significantly correlated with leaf habit (Table 1). The simple, untoothed, large (noto- and mesophyll), acute base, narrow (L:W $\geq$ 3:1) and elliptic shape leaves are more associated with evergreen species than deciduous species ($r > 0$, $P < 0.05$), whereas lobed, small (nano- and microphyll), obtuse and reflex bases, wide (L:W $\leq$ 2:1) and ovate shape leaves are less associated with evergreen species than deciduous species ($r < 0$, $P < 0.001$). In general, these significant differences in leaf characteristics between evergreen and deciduous species are consistent with the results of Kendall's tau-b rank correlation analysis, indicating that the differences in leaf physiognomic characteristics with two leaf habits exist at both the species level and the site level.

### 3.2. The differences in leaf physiognomic characteristics between evergreen and deciduous species at the sites

The boxplots show that the percentages of leaf physiognomic characters for both evergreen and deciduous species based on the 1019 calibration grids significantly differ apart from the very smallest leaves (nanophyll) in humid regions of China (Fig. 2, $P < 0.001$). Among the significant differences in leaf characters between evergreen and deciduous species, the average percentage values of leaf characters in evergreen species are higher than those in deciduous species, including simple, untoothed, large (notophyll), acute and reflex apexes, acute base, narrow (L:W $\geq$ 3:1) and elliptic shape leaves (coloured green in Fig. 2). In contrast, these average percentages of leaf characters in evergreen species are lower than those in deciduous species, including lobed, small (microphyll) and very larger (mesophyll), obtuse apex, obtuse and reflex bases, wide (L:W $\leq$ 2:1), obovate and ovate shapes leaves (Fig. 2: orange).

The CA axes 1 vs 2 show the distribution patterns of leaf physiognomic characters for both evergreen and deciduous species based on the 1019 calibration grids (Fig. 3). Axis 1 has an eigenvalue of 0.047 and accounted for 44.49 % of the leaf physiognomy percentage variance; axis 2 has an eigenvalue of 0.014 and accounted for 13.16 % of the percentage variance of leaf physiognomy (Table S2). In the CA ordination diagram (Fig. 3), the distributions of leaf characters between evergreen and deciduous species are clearly divided into two groups, with leaf characters of evergreen species (coloured green) mostly distributed on the left of the graph and leaf characters of deciduous species (coloured orange) grouped in the middle of the right-hand side of the graph. These distribution patterns reflect significant differences in leaf characteristics between evergreen and deciduous species. Moreover, at the first CA axis, simple, untoothed, large (notophyll), reflex apex, acute base, narrow (L:W $\geq$ 3:1) and elliptic shape leaves are more associated with evergreen species, whereas lobed, small (nanophyll), wide (L:W $\leq$ 2:1), obtuse apex, obtuse and reflex bases, obovate and ovate shapes leaves are more associated with deciduous species. This result indicates that most leaf characters' dominance in evergreen and deciduous species show significant differences.

### 3.3. Climate shaping the distributions of leaf physiognomic characteristics for evergreen and deciduous species

The CCA results show that climatic variables strongly affect the distributions of leaf characters for all evergreen and deciduous species

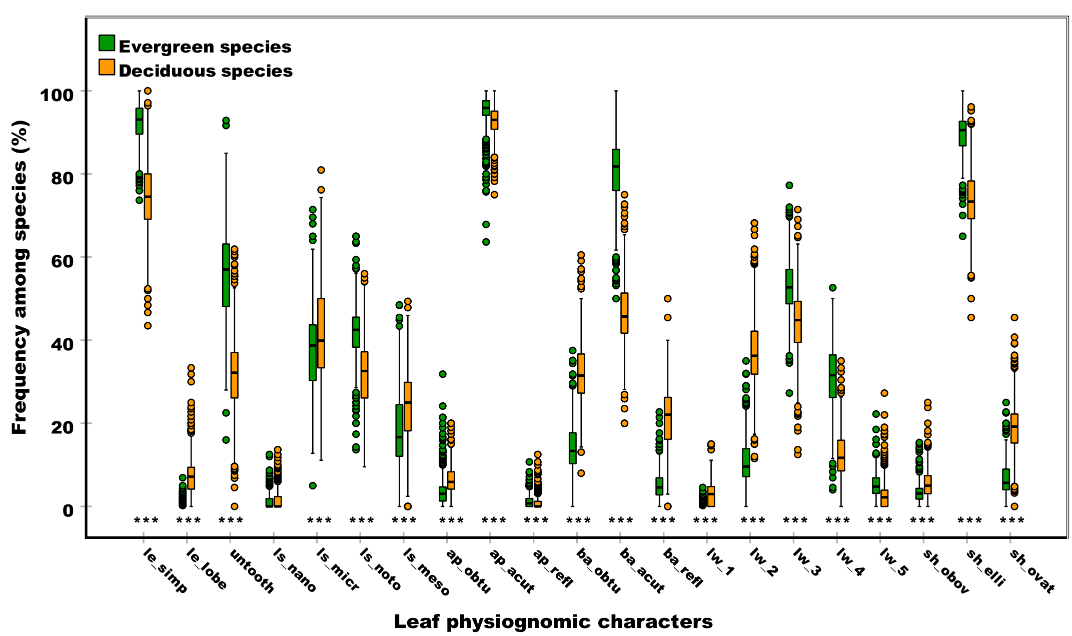


**Fig. 2.** Box plots of leaf physiognomic characteristics from both evergreen and deciduous species at the sites. Box plots show median (centreline), interquartile range (IQR), whiskers the 5th and 95th percentiles (horizontal lines below and above the boxes), and outliers (black dots); asterisks under the bar groups indicate significantly different evergreen and deciduous species groups based on U Mann–Whitney tests (***$P < 0.001$); evergreen species calibration grids, n = 498; deciduous species calibration grids, n = 521; leaf character abbreviations are given in Table 1.

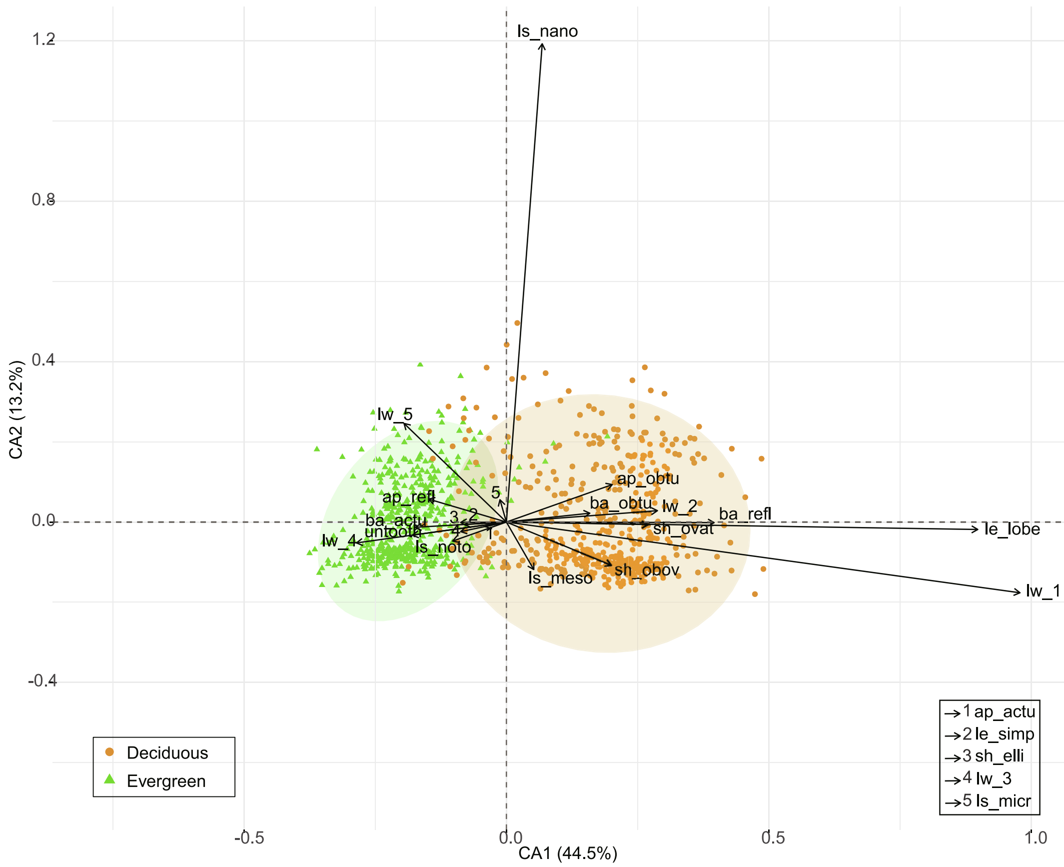


**Fig. 3.** Correspondence analysis (CA) plot for leaf physiognomic characters. Axes 1 and 2 account for 44.5 and 13.2 % of the variance in leaf physiognomy, respectively; for calibration grids, $n = 1019$; leaf character abbreviations are given in Table 1.

together, with the first three axes of the CCA models explaining 18.34 % of the variation in leaf character distributions (Table S3). Among them, the first axis explains 14.11 % of the variation. The eigenvalue of the first axis is 0.015, and the second axis has a low eigenvalue of 0.003. Therefore, these results indicate that the first axis is the most important, representing the main climate-constrained leaf character variations. A permutation test for CCA under the reduced model shows that the canonical relationship between leaf characters and climatic factors is significant ($\chi 2 = 0.02$, $F = 30.40$, $P < 0.001$). These climatic parameters of CMMT, P3DRY, SH, MAT, RH, GSP, MAP and WMMT are significantly correlated with all leaf character distributions ($P < 0.009$). Among them, CMMT and P3DRY are the most important climatic factors that influence these distributions, and the F values are 145.53 and 42.97, respectively (Table 2). The CCA ordination diagram (Fig. 4) shows that the distributions of leaf characters of both evergreen and deciduous species are clearly divided into two separate groups on the first axis, with evergreen species samples (green colour) scored on the right-hand side of the first axis and deciduous species samples (orange colour) distributed on the left-hand side of this axis. All climatic parameters are positively correlated with the first axis. With increasing temperature and moisture (precipitation or humidity) on the first axis, the characters are arranged from smaller (nano- and microphyll) to larger leaves (noto- and mesophyll); from obtuse apex to reflex apex leaves; from obtuse and reflex bases to acute base leaves; from wider (L:W $\leq$ 2:1) and very narrowest (L:W $>$ 4:1) to narrower leaves (L:W = 2–4:1); and from obovate and ovate shapes to elliptic shape leaves. Lobed leaves predominantly occur in colder and drier climates, while untoothed leaves mainly occur in warmer and wetter climates. Simple and acute apex leaves do not show such a clear pattern. This indicates that most of the leaf characteristics are associated with the leaf habits along the climate gradients. These distribution patterns are largely replicated in leaf characters both evergreen and deciduous in CAs, reflecting the shifts in the dominance of leaf character distributions between evergreen and deciduous species. Therefore, the leaf characteristics of both evergreen and deciduous species show contrasting patterns in response to climatic factors.

In addition, CCA is used to explore the relationship between climatic variables and separate distributions of leaf characters between evergreen and deciduous species. For evergreen species, the first two axes of the CCA models can explain 15.17 % of the variation in leaf character distributions (Table S4). The permutation test shows that most of the climatic parameters are significantly correlated with leaf characters, and WMMT and MAT are the most important climatic factors that affect the distributions of leaf characters in evergreen species, with *F* values of 39.17 and 28.12, respectively (Table 2). The CCA ordination diagram (Fig. 5a) shows that the leaf characteristics of evergreen species are significantly negatively correlated with WMMT, P3DRY, GSP and MMGSP on the first CCA axis and significantly positively correlated with CMMT, GSL, MAT and SH on the second CCA axis. For each leaf characteristic, lobed, wide (L:W $<$ 1:1), small (nanophyll), obtuse apex and reflex base leaves are negatively correlated with climatic variables on the first axis, while large (mesophyll) leaves are positively correlated and lobed, small (nano- and microphyll) leaves are negatively correlated with climatic variables on the second axis (Fig. 5a; Table S4).

Consequently, the first two axes of the CCA models can explain 26.36 % of the variation in the leaf character distributions in deciduous species (Table S5). The permutation test shows that nine climatic factors are significantly correlated with the leaf characters of deciduous species, and SH and P3DRY are the most important climatic factors affecting the leaf character distributions of deciduous species, with *F* values of 123.91 and 35.74, respectively (Table 2). The CCA ordination diagram (Fig. 5b) shows that the leaf characters of deciduous species are positively

**Table 2**
The permutation test for canonical correspondence analysis (CCA) of all, evergreen and deciduous calibration dataset.

| All dataset | *Chi-square* | *F*-value | *Pr* (>*F*) |
|---|---|---|---|
| coldest month mean temperature (CMMT) | 0.0122 | 145.5302 | 0.001*** |
| precipitation of the three driest consecutive months (P3DRY) | 0.0036 | 42.9653 | 0.001*** |
| specific humidity (SH) | 0.0014 | 16.9487 | 0.001*** |
| mean annual temperature (MAT) | 0.0010 | 11.4004 | 0.001*** |
| relative humidity (RH) | 0.0007 | 8.7422 | 0.001*** |
| growing season precipitation (GSP) | 0.0006 | 7.3333 | 0.001*** |
| mean annual precipitation (MAP) | 0.0005 | 6.2137 | 0.001*** |
| warmest month mean temperature (WMMT) | 0.0003 | 4.0374 | 0.008** |
| CCA model | 0.0204 | 30.3964 | 0.001*** |
| | | | |
| Evergreen dataset | | | |
| warmest month mean temperature (WMMT) | 0.0050 | 39.1665 | 0.001*** |
| mean annual temperature (MAT) | 0.0036 | 28.1271 | 0.001*** |
| vapour pressure deficit for the driest season (VPD_DJF) | 0.0016 | 12.3474 | 0.001*** |
| precipitation of the three driest consecutive months (P3DRY) | 0.0013 | 10.5981 | 0.001*** |
| vapour pressure deficit (VPD) | 0.0009 | 7.1044 | 0.001*** |
| relative humidity (RH) | 0.0008 | 6.6120 | 0.001*** |
| specific humidity (SH) | 0.0007 | 5.7081 | 0.001*** |
| vapour pressure deficit for the wettest season (VPD_ JJA) | 0.0007 | 5.5761 | 0.001*** |
| growing season length (GSL) | 0.0005 | 3.9250 | 0.002** |
| coldest month mean temperature (CMMT) | 0.0005 | 3.8494 | 0.002** |
| growing season precipitation (GSP) | 0.0004 | 3.4357 | 0.002** |
| mean monthly growing season precipitation (MMGSP) | 0.0004 | 3.2087 | 0.002** |
| precipitation of the three wettest consecutive months (P3WET) | 0.0004 | 3.0047 | 0.008** |
| CCA model | 0.0169 | 10.2050 | 0.001*** |
| | | | |
| Deciduous dataset | | | |
| specific humidity (SH) | 0.0117 | 123.9148 | 0.001*** |
| precipitation of the three driest consecutive months (P3DRY) | 0.0034 | 35.7430 | 0.001*** |
| coldest month mean temperature (CMMT) | 0.0022 | 23.3565 | 0.001*** |
| relative humidity (RH) | 0.0010 | 10.4256 | 0.001*** |
| warmest month mean temperature (WMMT) | 0.0007 | 6.8783 | 0.001*** |
| growing season length (GSL) | 0.0006 | 6.4261 | 0.001*** |
| mean monthly growing season precipitation (MMGSP) | 0.0004 | 5.8010 | 0.001*** |
| precipitation of the three wettest consecutive months (P3WET) | 0.0006 | 3.9195 | 0.002** |
| growing season precipitation (GSP) | 0.0004 | 3.9031 | 0.002** |
| CCA model | 0.0211 | 22.2410 | 0.001*** |

The significance of constraint variables was tested by performing 999 permutations; the results show the significance of specified climate factors for leaf physiognomic characters; *Pr* represents the significance: $^{***}Pr < 0.001$, $^{**}Pr < 0.01$; calibration grids for all species, n = 1019; calibration grids for evergreen species, n = 498; calibration grids for deciduous species, n = 521.

correlated with all climatic factors on the first CCA axis. For each leaf characteristic, untoothed, large (mesophyll), reflex apex and narrow (L:W = 3–4:1) leaves are positively correlated with climatic variables, such as SH, P3DRY, CMMT, RH, WMMT, GSL, MMGSP, P3WET and GSP, while lobed, small (nano- and microphyll), and very narrowest (L:W > 4:1) leaves are negatively correlated with these climatic variables (Fig. 5b; Table S5).

Due to the fact that the sampling data sources in our study use the assembly of a 'synthetic' dataset from regional floral records, our CCA analysis results indicate relatively low correlations between climate and leaf physiognomic characters. This is partially attributed to the variations in leaf physiognomic characters and climate data in each calibration dataset.

## 4. Discussion

### 4.1. Significant differences in leaf physiognomic characteristics occur in leaf habit (evergreen vs deciduous)

Our results reveal significant differences between evergreen and deciduous species in leaf physiognomic characters, evident not only in the percentage values of individual species levels (Table 1) and the calibration dataset (Fig. 2) but also in leaf physiognomic distributions of indirect ordination of CA (Fig. 3). This demonstrates that, beyond leaf margins and lobed leaves, various other leaf physiognomic characters exhibit substantial differences between evergreen and deciduous species. This observation is consistent with previous results highlighting that marked variations in the morphology and function of leaf characters have striking differences between evergreen and deciduous species (Wolfe, 1993; Wright et al., 2004; Sancho-Knapik et al., 2021; Wang et al., 2022). While leaf longevity has traditionally been considered the most pivotal trait for distinguishing between evergreen and deciduous species (Chabot and Hicks, 1982; Kikuzawa and Ackerly, 1999), our study demonstrates that leaf physiognomic characters, encompassing simple, lobed, margin type, size, apex, base, L:W ratio and shape, exhibit noteworthy differences between evergreen and deciduous species. Thus, leaf physiognomic characters are closely associated with leaf habit, and serve as indicators of differences in the morphology of evergreen and deciduous habits.

### 4.2. Climate drives leaf physiognomy distribution in both evergreen and deciduous species

Our CCA results highlight that the distribution of leaf physiognomic characteristics for evergreen and deciduous species is deeply shaped by climate (Figs. 4 and 5; Table 2). Specifically, the leaf physiognomic characters in both evergreen and deciduous species respond different climatic variables: the latter is positively correlated with these leaf characters that occur at a high proportion in evergreen species and negatively correlated with those leaf characters that occur at a high proportion in deciduous species. Previous studies on the global scale showed that MAT is the primary climatic factor driving the patterns of LL (Wright et al., 2005; van Ommen Kloeke et al., 2012) and LMPA (Soh et al., 2019) for different leaf habit types. Instead, our data showed that CMMT is the most important climatic variable driving the dominance of leaf character distribution shifts in deciduous and evergreen species in China. This finding is in line with some local-scale observations, in which leaf characteristics for evergreen and deciduous species showed different response to winter temperature (González-Zurdo et al., 2016; Sancho-Knapik et al., 2021). The impact of low winter temperatures on plants is multifaceted, affecting the leaf net photosynthetic rate, enzyme function, membranes and cellular processes and potentially causing irreparable tissue damage (Jones, 2014). Consequently, extremely low or winter temperatures act as constraints on the distribution of plants or vegetation types (Woodward, 1990; Wang et al., 2011), as well as the distribution of leaf form (Chen et al., 2014, 2019), ultimately driving the dominance of leaf character distributions showing different patterns in deciduous and evergreen species in China.

We assume that low-temperature tolerance differences between evergreen and deciduous species lead to their different leaf characteristics–climate correlations in humid regions of China. The leaves of evergreen woody dicotyledons could have function throughout the growing season and are exposed to climate throughout the year. During winter, the leaves of evergreen species need to endure low temperatures and are thus more affected by winter temperatures. The leaf characters of evergreen species in our datasets are mainly distributed in southern China, and vegetation types primarily belong to the evergreen broadleaved forest (Wu, 1980). In eastern China, previous studies showed that winter low temperature was not only the upper and northern limit of the distribution of evergreen broadleaf forest (Fang and Yoda, 1991) but

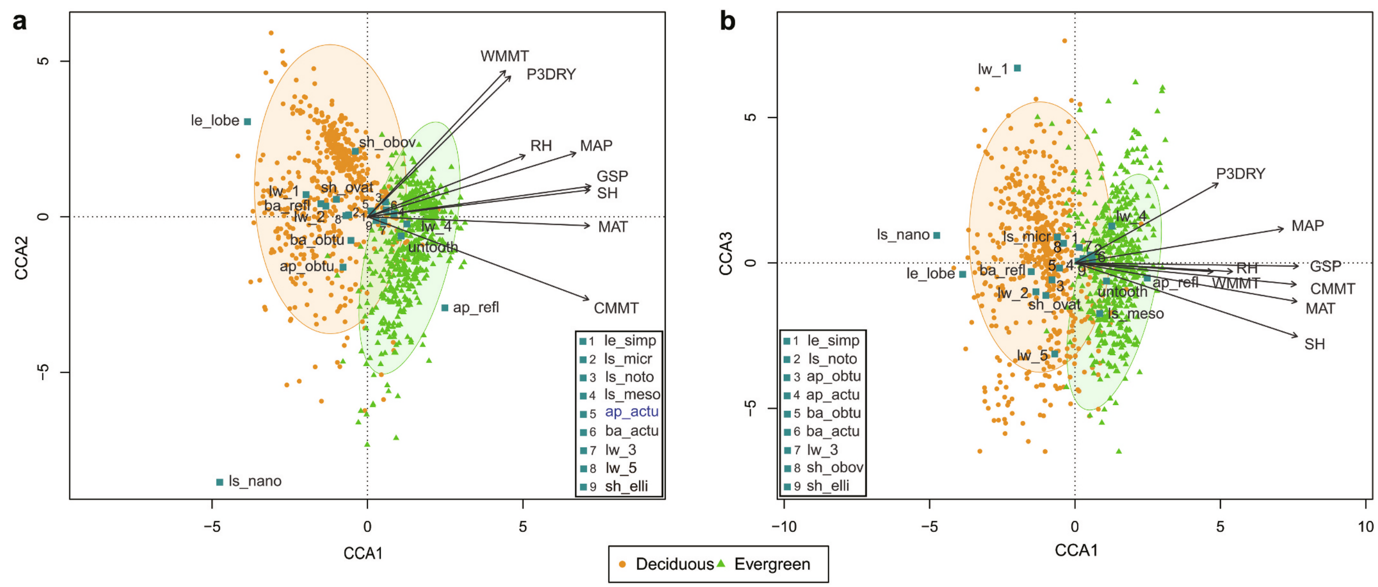


**Fig. 4.** Canonical correspondence analysis (CCA) plots show evergreen and deciduous species sites positioned on axes 1–3 spaces. a, CCA1 vs CCA2; b, CCA1 vs CCA3; for calibration grids, n = 1019; climate variables are mean annual temperature (MAT), warmest month mean temperature (WMMT), coldest month mean temperature (CMMT), mean annual precipitation (MAP), growing season precipitation (GSP), precipitation of the three driest consecutive months (P3DRY), relative humidity (RH) and specific humidity (SH); leaf character abbreviations are given in Table 1.

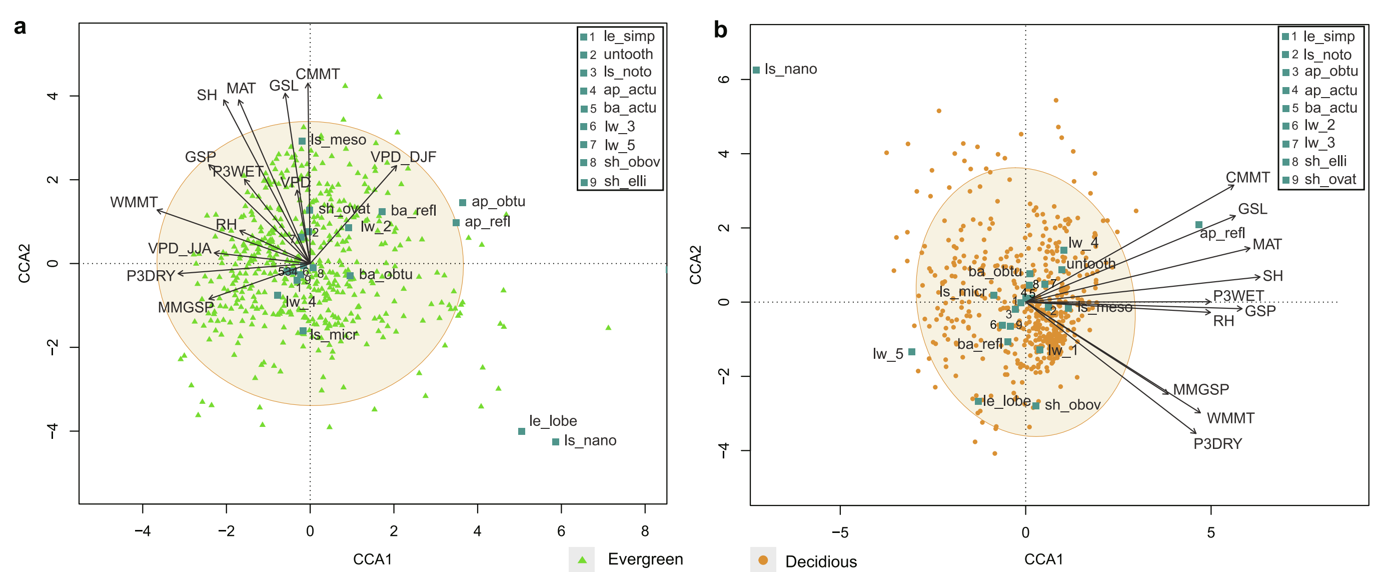


**Fig. 5.** Canonical correspondence analysis (CCA) plots show separately evergreen and deciduous species sites positioned on axes 1–2 spaces. a, Evergreen species, calibration grids, n = 498; b, Deciduous species, calibration grids, n = 521; climate variables are mean annual temperature (MAT), warmest month mean temperature (WMMT), coldest month mean temperature (CMMT), length of the growing season (GSL), mean annual precipitation (MAP), growing season precipitation (GSP), mean monthly growing season precipitation (MMGSP), precipitation during three wettest consecutive months (P3WET), precipitation during three driest consecutive months (P3DRY), relative humidity (RH), annual mean specific humidity (SH), vapour pressure deficit (VPD), vapour pressure deficit for the driest season (VPD_DJF) and vapour pressure deficit for the wettest season (VPD_JJA); leaf physiognomic characters abbreviations see Table 1.

also the northern limit of evergreen broadleaved species (Song et al., 2014; Qian et al., 2016). In particular, winter low temperature is a major climatic factor strongly driving latitudinal directional shifts in evergreen and deciduous broadleaved tree species in forests across subtropical China (Ge and Xie, 2017). Consequently, winter low temperature could strongly influence the distribution of leaf physiognomic characteristics in evergreen species in China. Our canonical correspondence analysis (CCA) reinforces the influence of winter low temperature (CMMT) on the leaf physiognomic distributions of evergreen species in China. While the most critical climatic variable affecting leaf characters is WMMT, CMMT significantly influences the second axis of leaf physiognomy distributions (Table 2). For instance, CMMT prominently constrains the distribution of leaf size in evergreen species in China, showing a significant positive correlation with large leaves (mesophyll) and a significant negative correlation with small leaves (nano- and microphyll) (Fig. 5a). This highlights how winter low temperature acts as a restricting factor for the distribution of evergreen broadleaved forests and shapes the leaf physiognomies in evergreen species in China.

In contrast to evergreen species, deciduous woody dicotyledons, although distributed in almost all humid regions of China, undergo leaf shedding during winter, allowing them to avoid low temperatures. Consequently, the leaves of deciduous species are less affected by the winter low temperatures. The CCA analysis for leaf characters of deciduous species identifies SH as the most critical climate factor controlling the distribution of leaf physiognomy (Table 2, $F = 123.92$), with a relatively weaker influence from CMMT ($F = 23.36$) on this distribution pattern. This distinction in the response to winter low temperature aligns with our findings that winter low temperature is positively correlated with leaf characters of evergreen species and negatively correlated with leaf characters of deciduous species. These results are consistent with previous reports indicating a significant positive correlation between winter low temperature and leaf area in evergreen species, and significantly negative (Table 4; Sancho-Knapik et al., 2021) or weakly negative (Lusk et al., 2018) correlation with leaf area in deciduous species. Therefore, our study suggests that differences in low-temperature tolerance between evergreen and deciduous species in China, possibly involving physiological mechanisms, lead to a divergent response to winter low temperature.

Furthermore, P3DRY strongly affected the leaf physiognomic distributions (Table 2), demonstrating that winter precipitation also contributes to the shifts in the dominance of leaf character distribution in deciduous and evergreen species in humid regions of China. Previous studies showed that increasing winter rainfall could lead to a transition from deciduous broadleaf vegetation to evergreen broadleaf vegetation in southeastern Asia from the Palaeogene to the early Neogene, and then evergreen broad-leaved vegetation dominated across southeastern Asia in the Neogene (Li et al., 2021). This suggests that distinctions in winter drought tolerance between evergreen and deciduous species in China lead to their distinct leaf characteristics–climate correlations. The leaves of evergreen species must withstand drought stress during low winter precipitation, making this a significant factor strongly influencing leaf characteristics in evergreen species. In contrast, deciduous species shed their leaves during the winter, avoiding drought pressures associated with low winter precipitation, which has a lesser impact on the leaf characters of deciduous species during that season. Our CCA results for leaf characters of evergreen species show that in addition to temperature, P3DRY strongly affects leaf physiognomy distributions (Fig. 5a; Table 2). At the same time, the CCA analysis for leaf characters of deciduous species also shows that compared to SH, P3DRY has a relatively weaker impact on leaf physiognomy distributions (Fig. 5b; Table 2). Thus, marked drought-intolerant differences between evergreen and deciduous species in China contribute to the varying responses of leaf characteristics to winter precipitation.

In general, our results demonstrate that the distributions of the physiognomy of evergreen and deciduous species in China are mainly controlled by winter temperature and precipitation. This indicates that the leaf physiognomic characteristics between evergreen and deciduous species are driven by differences in their tolerance to winter low temperature and drought between these two leaf habits. Leaf characteristics of evergreen species may have to help confer resilience to winter low temperature and drought climates and be influenced by these climates, while leaf characteristics of deciduous species may avoid the challenges posed by these climates and be less influenced by these unfavorable climatic conditions. Therefore, we suggest that the leaf physiognomic characteristics of evergreen and deciduous species exhibit remarkable differences in their response to climate across humid regions of China, revealing differences in environmental tolerance between these two leaf habits.

### *4.3. The impact of the Asian winter monsoonal climate on leaf physiognomy distribution in both evergreen and deciduous species*

Our results reveal that low-temperature winter, accompanied by winter precipitation, has a significant influence on the distribution of the physiognomic characteristics in both evergreen and deciduous species in humid regions of China. In China, they are predominantly influenced by the East Asian monsoon, which is characterized by wet and warm summers (East Asian summer monsoon) and dry and cold winters (East Asian winter monsoon) (Wang and Ho, 2002). Thus, this finding implies that the East Asian winter monsoon might shape the distribution of leaf physiognomic characters in both evergreen and deciduous species in humid regions of China.

The East Asian monsoon, with its strong seasonal contrast, is believed to have developed its modern-like pattern after the middle Miocene (Spicer et al., 2017). Previous studies have observed the impact of the East Asian winter monsoon on the distribution of species, plant diversity and vegetation types in China (Su et al., 2013; Chen and Su, 2020; Li et al., 2021). The East Asian winter monsoon also exerts a significant impact on the distribution of the leaf characteristics in China. Under prolonged exposure to these monsoonal conditions, plant species must adapt to the extremes low temperature and drought during winter, resulting in distinctive "monsoon fingerprints" encoded within their leaf characteristics (Spicer et al., 2017). These adaptations have contributed to the formation of unique leaf physiognomic spectra in China (Jacques et al., 2011; Spicer et al., 2016; Chen et al., 2019).

Our findings show that evergreen and deciduous species exhibit distinct leaf physiognomic adaptations to the East Asian winter monsoonal climate. For instance, evergreen species commonly display leaf characteristics such as untoothed, large (noto- and mesophyll), reflex apex, acute base, narrow (L:W = 3–4:1) and elliptic shape leaves, which mainly occur in warmer and wetter winter climates. In contrast, deciduous species predominantly present leaf characteristics such as lobed, small (nano- and microphyll), obtuse apex, obtuse and reflex bases, wide (L:W $\leq$ 2:1), obovate and ovate shapes of leaves, which are primarily found in colder and drier winter climates. These divergent responses illustrate how the variations in low temperature and drought tolerance between the two leaf habits are finely tuned to the climatic conditions imposed by the East Asian winter monsoon. This suggests that the East Asian winter monsoon especially affects the leaf physiognomic characteristics of both evergreen deciduous and deciduous species and drives the shifts in the dominance of leaf character distribution between these two leaf habits in the humid regions of China.

### *4.4. The effect leaf habit (evergreen vs deciduous) on estimating palaeoclimate using leaf physiognomy methods*

Our findings demonstrate that the majority of leaf physiognomic characteristics between evergreen and deciduous species in humid regions of China show significant differences (Figs. 2 and 3; Table 1) and remarkable variations in response to climatic variables (Fig. 4; Table S3). This indicates that in addition to leaf margins, leaf habit could confound correlations between other leaf physiognomic characters and climate in China. The quadratic regression model reveals that the response of leaf physiognomic characteristics in evergreen species to climate is inconsistent with that of deciduous species (Fig. 6). This result suggest that leaf habit may influence the accuracy of paleoclimate reconstructions in humid regions of China when using a multivariate physiognomy-climate approach. As for the climatic parameter of mean annual temperature (MAT), the CCA analysis of leaf characters identifies that MAT also significantly influences the variations in leaf characteristics for both evergreen and deciduous species (Fig. 4; Table 2). The quadratic regression fitted to MAT also reveals that the relationship between leaf characteristics in evergreen species and climate differs from that of deciduous species (Fig. 6c). This suggests that the leaf habit also has a significant impact on the precision of estimating paleo-MAT in China based on the multivariate physiognomy-climate method. This result confirms the previous proposition that in regions of northeastern China with extremely cold temperatures, it may not be appropriate to estimate paleotemperature using the multivariate leaf physiognomy-temperature model due to the influence of leaf habit. They observed that large overestimates of MAT (6.0–10.5 °C) occur in this particular region despite the application of the multiple linear regression model (Chen et al., 2019). The previous studies have also observed that leaf habit might affect the accuracy of estimating paleoclimate based on LMA

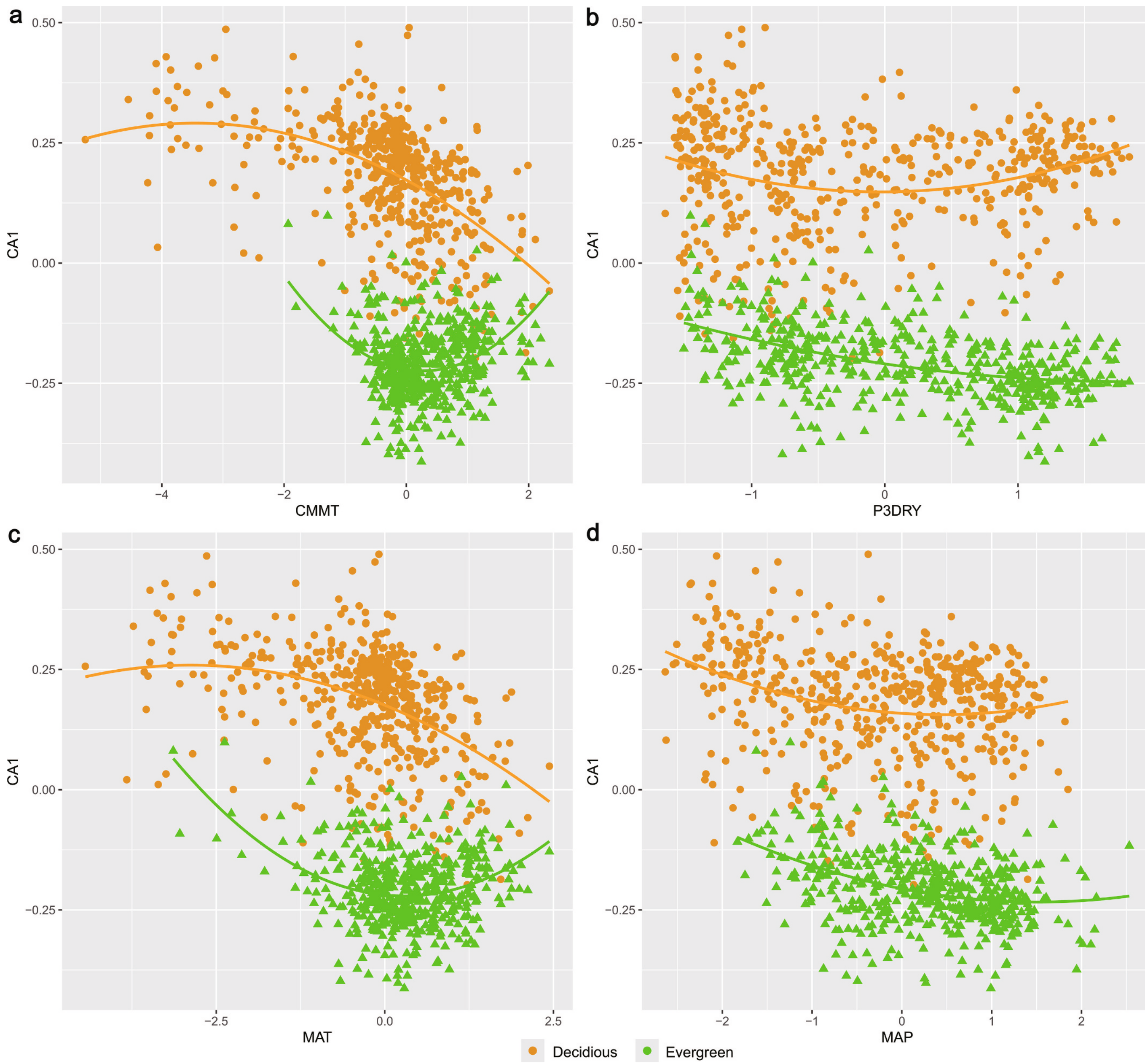


**Fig. 6.** Scatter plots of leaf physiognomic characters of both evergreen and deciduous species on calibration datasets and the coldest month temperature (CMMT), precipitation of the three driest consecutive months (P3DRY), mean annual temperature (MAT) and mean annual precipitation (MAP). The fitted lines are estimated using a quadratic regression, with climate variables treat as independent variable and the y-axes represent the scores from the first axis of correspondence analysis (CA); calibration grids, $n = 1019$.

methods (Peppe et al., 2011; Royer et al., 2012; Iszkuło et al., 2024). Therefore, whether utilizing univariate or multivariate leaf physiognomy-climate models to infer paleoclimate, leaf habit might affect the accurate of paleoclimate reconstruction. However, it is more difficult to determine whether a fossil leaf was evergreen or deciduous based on leaf morphology. Therefore, although leaf habit, to a certain extent, could confound leaf physiognomy-climate correlations (Peppe et al., 2011; Royer et al., 2012; Iszkuło et al., 2024), leaf physiognomy-climate methods still remain one of the most reliable and prevalent tools for reconstructing terrestrial palaeoclimate, as demonstrated in the previous study (Bailey and Sinnott, 1916; Wolfe, 1993; Adams et al., 2008; Peppe et al., 2011, 2018; Royer, 2012; Kennedy et al., 2014; Yang et al., 2015; Chen et al., 2019; Spicer et al., 2021). Overall, our results demonstrate that leaf habit not only could confound leaf margins-climate correlations, but also confound other leaf physiognomy-climate correlations, thereby potentially affecting the accurate prediction of paleoclimate in China using leaf physiognomy approaches. One feasible way to refine the leaf physiognomy methods is to classify the leaves of evergreen and deciduous woody dicotyledons, which appears to be a challenge to the current knowledge.

## 5. Conclusions

In the present study, we analysed leaf physiognomic characteristics that vary with leaf habit using a large-scale dataset based on 2111 evergreen and 1001 deciduous native dicotyledon trees in humid regions of China. Our results show that there are significant differences in the majority of leaf characteristics between evergreen and deciduous species. This indicates that these leaf physiognomies could represent differences in the morphology of evergreen and deciduous habits. The leaf physiognomy distributions for both evergreen and deciduous species are deeply shaped by climatic variables. Specifically, the leaf physiognomic characters with leaf habit respond remarkably differently to winter temperature and precipitation. This reveals that the leaf physiognomic characteristics of evergreen and deciduous species in China are driven by differences in their tolerance to winter low temperature and drought between these two leaf habits. This also suggests that the East Asian winter monsoon especially affects the leaf physiognomic characteristics of both evergreen deciduous and deciduous species in China. Furthermore, the significant differences in most leaf physiognomic characters with leaf habit exhibit a remarkable distinct response to climate in humid regions of China, indicating that leaf habit could potentially confound leaf physiognomy-climate correlations. Therefore, we suggest that leaf habit might have an impact on the accurate prediction of paleoclimate in China using a multivariate physiognomy-climate approach. Nonetheless, phylogeny also may contribute to variations in leaf characteristics between evergreen and deciduous species (Vargas et al., 2021; Wang et al., 2022). Further research could be improved by examining the impact of evolutionary processes on the variations of leaf characteristics in both evergreen and deciduous groups.

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## CRediT authorship contribution statement

**Wen-Yun Chen:** Writing – review & editing, Writing – original draft, Software, Methodology, Formal analysis, Data curation, Conceptualization. **Tao Su:** Writing – review & editing, Funding acquisition, Conceptualization. **Shu-Feng Li:** Writing – review & editing, Software, Funding acquisition.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

I have shared the data at the Attach File step.

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