

Climatic seasonality is linked to the occurrence of the mixed evergreen and deciduous broad-leaved forests in China

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Abstract. Evergreen and deciduous broad-leaved tree species can coexist across the globe and constitute different broad-leaved forests along large-scale geographical and climatic gradients. A better understanding of climatic influence on the distribution of mixed evergreen and deciduous broad-leaved forest is of fundamental importance when assessing this mixed forest's resilience and predicting potential dynamics of broad-leaved forests under future climate change. Here, we quantified the horizontal distribution of this mixed forest in mountains in relation to climate seasonality by compiling vegetation information from the earlier records and our own field sampling on major subtropical mountains of China. We found that the probability of occurrence of this forest in subtropical mountains was positively associated with the latitude but not the longitude. The occurrence probability of this forest was observed at high-temperature but not precipitation seasonality mountains. Temperature seasonality was five times more important than precipitation seasonality in explaining the total variation of occurrence of this mixed forest. For its distribution, our results shed light on that temperature seasonality was generally a more powerful predictor than precipitation seasonality for montane mixed forest distribution. Collectively, this study clearly underscores the important role of temperature seasonality, a previously not quantified climatic variable, in the occurrence of this mixed forest along geographical gradients and hence yields useful insight into our understanding of climate–vegetation relationships and climate change vulnerability assessment in a changing climate.

Key words: leaf habit; mixed forest; subtropical mountains; temperature seasonality; transition zone; vegetation zonation.

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INTRODUCTION

Leaf habit, for example, the property of being deciduous or evergreen, is a key functional attribute of tree species, which is regarded to be an adaptation to drought or low temperatures around the world (Kikuzawa and Lechowicz 2011, Ouédraogo et al. 2016). Tree species with different leaf habits occur widely in many regions and potentially have many cascading

consequences for ecosystem processes and functioning in a range of different forest ecosystems. For example, the property of being deciduous or evergreen may for different tree species contribute to the seasonal changes in carbon and nutrient cycling that have been documented in many tropical and temperate forests (Baldocchi et al. 2010, Guan et al. 2015, Ge and Xie 2017). Thus, a better understanding of how climate shapes the geographic distribution and

community assembly of tree species with different leaf habits is crucial to predict the potential dynamics of forest biomes under changing environment conditions (Ouédraogo et al. 2016, Zanne et al. 2018).

The relative dominance of evergreen vs. deciduous tree species varies across the large-scale geographical gradient, constituting distinct types of forest climaxes, and consequently various forest physiognomies: evergreen, deciduous, and in-between, corresponding to evergreen forests, deciduous forests, and mixed evergreen–deciduous forests, respectively (Woodward et al. 2004, Suzuki et al. 2015, Ge and Xie 2017). And physiognomic alterations for a specific forest could be seen as an early-warning signal of potential shifts in tree species distribution. For example, the distribution of this mixed forest is an indicator of climatic conditions, on which the prediction of large-scale vegetation distribution patterns can be based (Bohlman 2010, Kikuzawa and Lechowicz 2011). Patterns in the relative dominance of evergreen and deciduous tree species and climate correlates such as temperature and precipitation variables have attracted much interest in the past decades (Givnish 2002, Buitenwerf and Higgins 2016, Wu et al. 2017, Zanne et al. 2018). Considerable research effort has revealed that the evergreenness (or deciduousness) of tree species is tightly linked with climate-related variables. Some earlier studies have described the patterns of evergreen or deciduous species in a qualitative fashion and demonstrated the bimodal pattern of evergreen forests along the latitudinal gradient around the globe (Woodward et al. 2004, Kikuzawa and Lechowicz 2011), while recent studies have attempted to quantify these relationships in a direct way (Buitenwerf and Higgins 2016, Ouédraogo et al. 2016). For example, Ouédraogo et al. (2016) have investigated the deciduousness of tropical forests in central Africa and identified the crucial role of dry season length. Combined, these previous studies have significantly extended our understanding of the patterns and climatic correlates of evergreenness or deciduousness of forests over a broad geographical scale.

Despite the growing number of studies aiming to predict consequences of global change for broad-leaved forest distributions, our understanding of quantitative relationships between

evergreenness or deciduousness of forests and climate is usually somewhat rough and remains constrained in the following broad aspects. First, earlier studies have largely focused on the evergreenness or deciduousness of tree species either on the level of individual tree species or on the level of functional groups. For example, some studies have mainly quantified leaf life span of evergreen and deciduous species (a key indicator of evergreenness) at the species or functional group level, but ignored community-level patterns (Givnish 2002, Kikuzawa and Lechowicz 2011, van Ommen Kloeke et al. 2012). Second, previous studies have heavily biases toward the single forest such as the evergreen forest or deciduous forest and geographical biases also occur in that most studies have focused on broad-leaved forests within tropical and temperate regions where existing records are often more readily available (Gilliam 2016, Evans and Brown 2017). We lack an integrated understanding of the relationship between climatic variables and the transitional forest, namely the mixed evergreen and deciduous broad-leaved forest (MEDBF) in subtropical regions, which can rapidly expand or contract under directional shifts in abiotic drivers but play a dominant role in ecosystem functioning (Baldocchi et al. 2010, Ge and Xie 2017, Su et al. 2019a). Furthermore, existing studies have mainly used mean annual values for climatic variables when exploring the evergreen/deciduous forest–climate relationship, with very little explicit attention on the seasonality of climate (Allen et al. 2017, Vico et al. 2017). Such knowledge on effects of climatic seasonality on forests is particularly important, given that a growing body of evidence documenting that the dominant role of this variation in climatic seasonality is driving forest structure and functioning, particularly for mountain ecosystems (Stephenson 1998, Ernakovich et al. 2014, Rudgers et al. 2018). To our knowledge, few studies have made attempts to examine regional patterns of these mixed forests vs. climatic seasonality from a quantitative point of view. Moreover, temperature and precipitation seasonality may work simultaneously on the geographical distribution of these mixed forests (Cuba et al. 2013, Suzuki et al. 2015). However, while such knowledge is of fundamental importance for understanding the link between tree leaf habits and ecosystem

functioning at large geographical scales, the relative role of temperature and precipitation seasonality has remained largely understood. These shortcomings above have hindered forecasts of how global climate change or cascading effects of changing leaf habits may affect the geographical distribution of different forest types.

Seasonal changes in temperature and precipitation are typical features of the monsoon climate prevailing in subtropical China. Evergreen and deciduous broad-leaved tree species form fundamental components of subtropical forests, and their co-occurrence has been pointed out to be one of the outstanding properties of subtropical forests (Wu 1980, Fang et al. 2002, Ge and Xie 2017). The dominance of these tree groups with different leaf habits could alter with elevation along the horizontal gradients. They can form stable MEDBFs in different mountains along latitudinal gradients (Box and Fujiwara 2015, Ge and Xie 2017). The evergreenness and deciduousness are key functional unique attributes for this targeted mixed forest, and fractional alteration of the evergreen vs. the deciduous may reflect climatic perturbations and impact forest different seasonal physiognomies. Therefore, this montane forest provides an ideal model to investigate the relationships between climate seasonality and forest vegetation distribution.

Furthermore, existing observational and model studies have indicated that the subtropics have experienced an increasing unpredictability in climatic seasonality over the past decades, which consequently have shown more prominent effects on forest distribution in high-altitude mountain areas than in low-altitude regions (Seddon et al. 2016, Alexander et al. 2018). Future climate change is anticipated to shift the ranges of evergreen and deciduous broad-leaved tree species, resulting in expansion and/or contraction of spatial extent for various broad-leaved forests. Therefore, mixed forests are extremely vulnerable to climate fluctuations. Current empirical knowledge of the quantitative relationships between variability in climatic seasonality and evergreenness/deciduousness of forests allows for more accurate forecasting of climate change impacts. Specifically, comparative analyses of these mixed forests on mountain vegetation zonation along latitudinal gradients could offer more insight into the potential long-term

responses of these montane mixed forests to future climate change and bridge the linkage between evergreen and deciduous broad-leaved forests. Therefore, it is urgent to understand the defined relationship between climate seasonality and these mixed forests.

In this study, we explored horizontal distribution of the mixed forest in relation to climatic seasonality in subtropical China by literature survey and field investigation of mountain vegetation zonation. Specifically, we aimed to (1) quantify horizontal pattern of the occurrence of this mixed forest in mountain vegetation zonation and (2) to determine how climatic seasonality affects this pattern and parse the relative importance of temperature and precipitation seasonality in geographical distribution of this mixed forest in subtropical China.

MATERIALS AND METHODS

Data collection

We have compiled a database of vegetation zonation of distinct mountains in subtropical China and combined it with climatic information from a global climate database (Hijmans et al. 2005). Information on the description of forest distribution for each mountain used in this study was collected from published literature including peer-reviewed papers and monograph publications since the 1980s and our own previous fieldwork in subtropical China (Appendix S1). We collected these data on geographical locations of the mountains, climatic conditions, and vertical distribution of natural vegetations for each mountain. Our definitions of both mountain and the targeted mixed forest followed the earlier studies (Wu 1980, Ge and Xie 2017, Körner et al. 2017). To ensure data quality and comparability among various studies, we critically reviewed all sources of data from the multiple pathways. For example, to identify the altitudinal zonation of forest formations on subtropical mountains, we have checked different references of various sources, consulted the various local experts, and collated other ancillary information. Specifically, the data we included in our database were strictly filtered according to the following criteria. First, this mixed forest must be climax vegetation at the corresponding altitudinal zones of the mountains usually occurring above 1000 m,

so we excluded these mountains lower than 1000 m (Chen et al. 1997, Körner et al. 2017). Second, we discarded mountains where vegetation partly or completely consisted of plantations. Third, for each mountain typical plantations were excluded from the vegetation zonation. After imposing these criteria, we obtained data for altitudinal distribution of mountain forests for in all 52 mountains from 71 publications covering the most important mountain systems across subtropical China. The location of analyzed sites ranged from 23.3° to 34.0° N in latitude and from 98.9° to 119.7° E in longitude. See Appendix S2 for additional information on geographical locations of study sites and Appendix S3 for the ideal paradigm of altitudinal distribution of different montane forests in subtropical China.

We extracted climatic variables such as temperature and precipitation seasonality from a global climate database at the highest resolution (30 arc-seconds; <http://worldclim.org/>; Hijmans et al. 2005) and inferred data for temperature (TS) and precipitation seasonality variables (PS) using the geographic location of each mountain, which has been a common practice in previous studies (Elsen et al. 2018). No corrections for elevation were applied for both TS and PS, assuming that they are not affected by elevation, as indicated by previous studies (Jobbágy and Jackson 2000, Ghalambor et al. 2006). TS was defined as the standard deviation of monthly mean temperature multiplying by 100, whereas PS was defined as coefficient of variation of monthly precipitation. Both variables present how evenly dispersed temperature and rainfall is throughout the year and is usually used as a surrogate for climatic seasonality intensity relevant to forest distributions. The choice of climatic seasonality was made according to the adaptive reasoning used in this study. The evergreen and deciduous broad-leaved tree species display seasonal patterns so the mixed forest presents different physiognomies as climate changes. We therefore expect the horizontal distribution of this montane mixed forest may be potentially coupled with climate seasonality along the large-scale spatial gradients (Appendix S4). In our study region, TS ranged from 422.1 to 941.4 and PS from 49.2 to 105.3. We also displayed the quantitative

relationships between climatic seasonality and geographical positions of sampling mountains in Appendix S5.

Data analysis

We constructed a matrix of presence–absence data of the mixed evergreen and deciduous forest along the elevational gradient for different subtropical mountains of China. We developed our models using occurrence data of this mixed forest as dependent variable and the corresponding climatic seasonality as independent variables. We implemented a generalized linear model (GLM), which is generalization of ordinary least squares regression-based technique to explore the relationship between occurrence and climatic seasonality variables. We performed single and multiple logistic regressions to explore the effects of temperature and precipitation seasonality on the occurrence of this forest. This method has been developed and tested elsewhere (Lehmann et al. 2011, Grünig et al. 2017).

Specifically, we developed the logistic models by the backwardly and forwardly selected variable approaches. First, we tested the contribution of each climatic variable to the logistic model by removing that term from the full model (this model including both climatic variables). Second, we followed a forward selection approach to model development. We thus assessed whether adding each of the factors in turn to the null model (a model without any factor) showed a significant effect. We selected the best fit models by calculating Akaike's information criterion (AIC) and following the methods of previous similar studies (Ge and Xie 2017). The model with the lowest AIC values among all models within the candidate set of models was considered to possess the greatest support (Zuur et al. 2009). Since both approaches resulted in the same main terms in the final model, only results for the first approach are presented in main texts. Some additional information could be found in Appendix S6.

Before performing the statistical analysis, we checked the collinearity between TS and PS and spatial autocorrelation between sampling data points. First, we have checked the collinearity using a bivariate correlation plot based on Pearson's correlation coefficient. According to Dormann et al. (2013), collinearity is reached, if

$|r| > 0.7$; however, this was not the case here. We also calculated variance inflation factor (VIF) for TS and PS to evaluate the significance of collinearity within our statistical models. Generally, collinearity between predictors is considered to be significant when VIF is greater than five (Zuur et al. 2009). Here, we found VIF was less than five. Therefore, both these results have illustrated the collinearity between TS and PS is not considered a major concern here. Second, we verified the significance of spatial autocorrelation in the occurrence of mixed forests using Moran I test because Moran's test indicated significant spatial autocorrelation ($P < 0.05$), we hence included an auto-covariate that represented the influence of neighboring observations as an additional term to the set of independent variables. We used a method illustrated by Dormann et al. (2007) to construct auto-covariate that accounted for inherent and induced spatial autocorrelation in non-normal data. Here, we applied GLM that explicitly taking spatial autocorrelation into account, the spatial GLM was found to be similar to GLM that did not account for spatial autocorrelation by model selection methods. So we did not display the results of spatial GLM. More information could be seen in Appendix S6. To allow the comparison of model parameter estimates, we standardized TS and PS to have a mean of zero and a standard deviation one given TS and PS differing in their ranges.

To further disentangle the relative importance of TS and PS and their interaction, we ranked the effect size of TS and PS using hierarchical partitioning analysis. Hierarchical partitioning analysis isolates the percentage independent and joint contribution of TS and PS to the total explanatory power of the model. The joint effect could also quantify the collinearity between model variables. Highly collinear variables have a large joint effect relative to their independent effects (Shen et al. 2015). We conducted all statistical analyses in R 3.0.0 (R Core Team 2013).

RESULTS

Horizontal patterns of occurrence of the montane mixed forest

We have retrieved that the MEDBF occurred for 37 mountains among 52 investigated mountains in subtropical China. We performed the single logistic regression and found that the occurrence of MEDBF in mountains was positively correlated with latitude ($P < 0.05$), but not significantly associated with longitude ($P > 0.05$) of the mountains (Fig. 1).

Relationships between the probability of this mixed forest occurrence and climatic seasonality

We quantified the relationships between the probability of occurrence of mixed forest and temperature and precipitation seasonality by

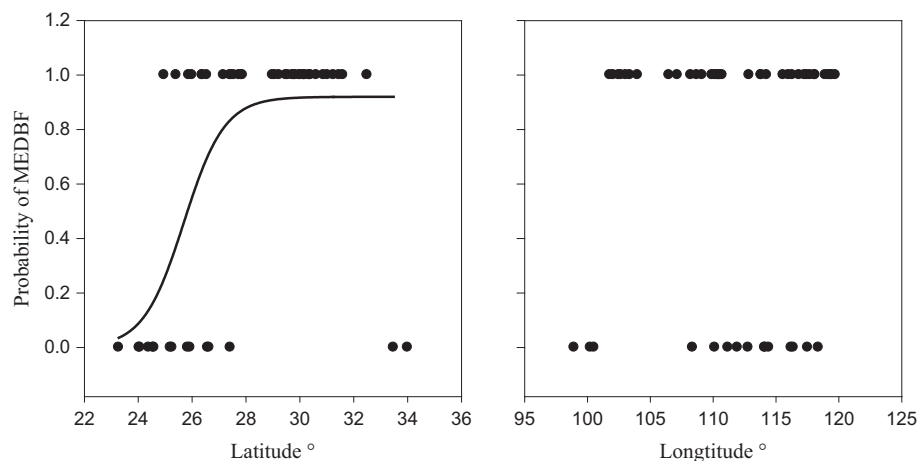


Fig. 1. The relationships between the occurrence of the mixed evergreen and deciduous broad-leaved forest (MEDBF) and the geographical location of mountain. The black solid circles represent the sampling mountains in subtropical regions, and the solid line represents the predictions of a logistic regression model.

single and multiple logistic regression analyses (Table 1). We found the occurrence probability of the mixed forest was positively related to temperature seasonality ($P < 0.05$) but not precipitation seasonality ($P > 0.05$; Fig. 2). There was no significant interaction between temperature and precipitation seasonality on the occurrence of this forests ($P > 0.05$). We also isolated the relative role of these two climatic variables and found the independent effect of temperature seasonality contributed much more than that of precipitation seasonality to above-mentioned geographical pattern (temperature vs. precipitation: 14.99% vs. 2.00%). The interaction of TS with PS only accounted for 1.31% of the explained variance (Fig. 3).

DISCUSSION

To the best of our knowledge, this is the first study to quantify the occurrence of MEDBFs and explore its correlation with temperature and precipitation seasonality in subtropical China. Although growing studies have indicated that climatic seasonality is closely linked to forest distribution in subtropical regions, there indeed exists a knowledge gap for MEDBFs and only a few published studies have included quantitative data on the occurrence of this targeted mixed forest (Wu 1980, Chen et al. 1997). Besides, despite the well-recognized importance of this mixed forest, our current quantitative understanding of the geographical patterns in the occurrence probability shift in the mixed forests is still surprisingly poor (Ge and Xie 2017). Therefore, our study expands existing work that only focuses on evergreen broad-leaved forests and/or deciduous broad-leaved forests. Our results have

demonstrated that our targeted mixed forest occurred on the most of mountains (37/52) and displayed high probability of occurrence at high-latitude mountains in subtropical China. This finding, which has not been previously quantified, is largely in accord with earlier qualitative studies that showed MEDBF is distributed widely on mountainous areas in subtropical China (Wu 1980, Fang et al. 2002, Song 2013). Results from this study offer important advances both in the ability to quantify the probability of occurrence of this mixed forest over a wide range of climatic combinations and in the identification of climatic factors previously largely overlooked. Specifically, we have further explored and untangled the key role of temperature seasonality in the geographical distribution of the mixed forest. This is in contrast with the previous findings that precipitation seasonality plays a much more important role in the geographical distribution of this kind of forest with beech/oak forests as an example (Guo and Werger 2010, Shen et al. 2015). Additionally, our findings add to a growing body of studies that highlight the key role of climate variability in controlling distinct vegetation distributions across different biomes (Stephenson 1998, Seddon et al. 2016, Vázquez et al. 2017). Therefore, this study has broadened our understanding of climate–vegetation relationships on mountain vegetation zonation by considering the crucial but largely overlooked aspects of climate such as temperature and precipitation seasonality.

Higher occurrence probability of mixed evergreen and deciduous broad-leaved forests in subtropical high-latitude mountains

Here, we found that low-latitude mountains have lower occurrence probability of this mixed forest than their corresponding high-latitude counterparts; this is, the probability of the mixed forest occurrence was much higher in the mountains located more to the north. This result is in accord with previous qualitative descriptions in China (Wu 1980, Fang et al. 2002). A general paradigm of differentiation for mountain forest zonation in subtropical China is from evergreen broad-leaved forest, MEDBF, deciduous broad-leaved forests, mixed deciduous broad-leaved and coniferous forests, and finally coniferous forests with increasing elevation, which

Table 1. Results of a multivariate model detecting the relationship between the occurrence of this mixed forest and temperature (TS) and precipitation seasonality (PS) in subtropical mountains in China.

Parameters	Slope	Standard error	P value
TS	1.35424	0.50238	0.00703*
PS	−0.09216	0.48871	0.85042
TS × PS	−0.56649	0.40069	0.15743

Note: TS and PS are standardized before statistical analyses.

* Significant level at $P < 0.05$.

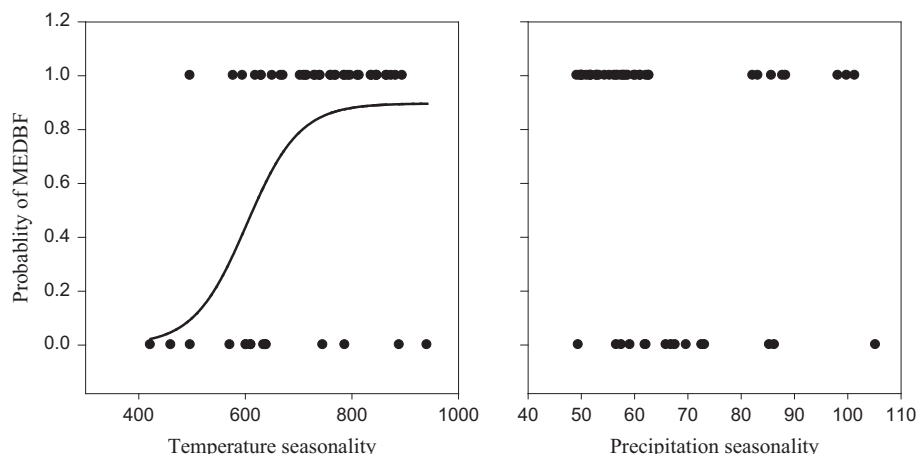


Fig. 2. The relationships between the occurrence of the evergreen and deciduous broad-leaved mixed forest (MEDBF) and climatic seasonality of different mountains. The black solid circles represent the sampling mountains in subtropical regions, and the solid line represents the predictions of a logistic regression model.

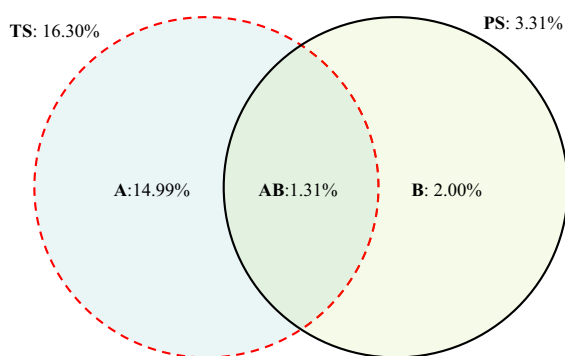


Fig. 3. Venn diagrams of variance partitioning of temperature (TS) and precipitation seasonality (PS) in accounting for geographical distribution of the mixed evergreen and deciduous broad-leaved forest in subtropical mountains. *A* and *B* denotes the independent effects of TS and PS, respectively; *AB* represents the interactive effects between TS and PS.

corresponds to latitudinal patterns of these forests (see Appendix S4 and S7 for more information). Along a gradient of decreasing mean annual temperature and increasing climate seasonality, evergreen broad-leaved species occupied warmer and less seasonal extreme climatic axis, followed by deciduous broad-leaved species, then evergreen conifers, and finally deciduous conifers. This MEDBF constitutes an indispensable and important vegetation type in mountains, which

corresponds to zonal forests in northern subtropical regions (Box and Fujiwara 2015, Ge and Xie 2017). However, this kind of forests could be replaced by other forest types in mountains of different regions (Walter 1973, Ohsawa 1993). For example, this kind of montane mixed forest is generally replaced by deciduous broad-leaved forests or evergreen coniferous forests in Taiwan (Chiu et al. 2014). We did not observe that this forest could occur along elevational gradients for each mountain here. Specifically, only 37 out of 52 mountains had this mixed forest, with higher occurrence probability at higher-latitude mountains. Therefore, this finding supports the prevailing belief that mountain vegetation pattern does not simply reflect horizontal zonation of vegetations across the latitude (Troll 1972, Wu 1980). Moreover, we further linked and quantified this observed horizontal pattern to climatic variables. This phenomenon could be largely attributable to the factors we have investigated here, including geographical locations of surveyed mountains, climate variables such as temperature and precipitation seasonality (Appendix S5 and S7).

The higher importance of temperature than precipitation seasonality

Previous research on zonation of mountain vegetation has mainly concentrated on tropical and temperate regions, with less attention being paid to the transitional zone between them, such

as the subtropical region. In East Asia, and especially in subtropical China, temperature usually synchronizes with precipitation, co-determining the distribution of mountain vegetation zonation (Fang et al. 2002, Guo and Werger 2010, Ge and Xie 2017). Nevertheless, the relative importance of these two climatic factors remains largely unclear as to when it comes to in shaping different mountain vegetations such as the formation of MEDBFs. Furthermore, earlier studies that have explored climate–vegetation relationship only focus on climatic means such as mean annual temperature and precipitation (Woodward et al. 2004, Rudgers et al. 2018), and seldom account for the effects of climate seasonality within a quantitative framework (Ernakovich et al. 2014, Moles et al. 2014, Vázquez et al. 2017). Furthermore, while the importance of climate seasonality in controlling the distribution of mountain vegetation zonation has been recognized in some earlier studies (Shen et al. 2015, Souza et al. 2016), there have been few attempts to link altitudinal patterns of these specific mixed forests to temperature and precipitation seasonality in a direct and quantitative manner.

Here, we found that the occurrence of this mixed forest in subtropical mountains increases significantly with temperature seasonality. Moreover, temperature seasonality was five times more important role than precipitation seasonality. Our results clearly suggest at mountains with high-temperature seasonality intensity this mixed forest is favored. This result quantitatively supports previous studies that temperature seasonality is one of important determinants of tree lines across different mountains at the global and regional scales (Jobbágy and Jackson 2000, Cudlín et al. 2017) and largely aligns with the earlier qualitative studies showing that temperature seasonality works well on the altitudinal differentiation of mountain vegetations in South and East Asian (Ohsawa 1993, Chiu et al. 2014). This result also coincides with some studies of temperate mountain vegetation zonation (Troll 1972). However, this finding is in striking contrast with the general conclusion that temperature seasonality plays a minor role in the differentiation of mountain vegetations in tropical regions where lack significant obvious year-around temperature changes (Guan et al. 2015, Ouédraogo et al. 2016, Singh and Chaturvedi

2018), while a few studies also have already revealed the higher importance of temperature than precipitation seasonality in shaping the deciduousness of forests in the tropics (Cuba et al. 2013, Gaviria et al. 2017). Our finding also appears at odds with the result of previous studies obtained in Mediterranean environments which have implicitly demonstrated water stress but not temperature restricted the formation of MEDBFs (Baldocchi et al. 2010, Di Paola et al. 2017).

We propose the following underlying mechanisms that could account for the occurrence of this mixed forest in mountains along the temperature seasonality gradient. Generally speaking, temperature seasonality reflects the degree to which tree species of different leaf habits experience temporal temperature fluctuations and includes two key aspects that affects tree completion of life cycles and thus the occurrence of this mixed forest: minimum low temperature and high summer temperature (Vázquez and Stevens 2004, Harrison et al. 2010, Chan et al. 2016). Previous studies have indicated that in the Northern Hemisphere markedly high seasonality at high latitudes is primarily driven by low winter temperatures while fluctuations of seasonal temperature sum are relatively minimal at low latitudes (Vázquez and Stevens 2004, Ghalambor et al. 2006). Latitudinal shifts in the relative roles of these two temperature variables drive the formation of mixed forest. Tree species of different leaf habits can adapt and/or acclimatize to these temperature conditions differentially, which thus alter the respective competitive performance of tree species within forests and formations of our targeted mixed forest (Woodward et al. 2004, Liang et al. 2013, Zanne et al. 2018). In other words, evergreen broad-leaved tree species and deciduous broad-leaved tree species respond to climate in unique ways, especially to temperature variables. For example, in low seasonal temperature regimes at the low-latitude mountains, evergreen broad-leaved tree species usually could photosynthesize and thrive across the whole year, while deciduous trees do not thrive due to the lack of normal temperature triggers for leaf onset and abscission (Ohsawa 1993, Givnish 2002, Harrison et al. 2010, Kong et al. 2017). The observed ecological differences between leaf habits favor the seasonal competitive advantage

of evergreen broad-leaved species over co-occurring deciduous counterparts at low-latitude forests. Evergreen broad-leaved tree species could not prevail at the high-temperature seasonality region where low temperature hampers the establishment success of evergreen broad-leaved species (Zanne et al. 2018, Kong et al. 2019). Thus, increasing temperature seasonality along the increasing latitude gradient of mountains is also likely to favor deciduous tree species over their evergreen counterparts, and lead to the higher occurrence of this targeted mixed forest at high-latitude mountains. Our arguments are also well supported both by the previous empirical study highlighting that leaf life span, the key trait differentiating evergreen from deciduous broad-leaved tree species, was only driven by temperature variable (van Ommen Kloeke et al. 2012, Zanne et al. 2018) and these theoretical studies from the carbon budget perspective at the leaf and whole-plant levels, which assumed the evergreen species occurred at high climatic seasonality environments (Givnish 2002, Buitenwerf and Higgins 2016). Temperature variation could occur at various temporal scales (Chan et al. 2016). Here, we only focused on the influences of the long-term seasonal temperature variation and ignored the short-term effects of temperature variation such as daily temperature variation, one key component that quantify climate variability that may also influence the earlier stage of long-lived tree species of different leaf habits (Ge et al. 2015, Chan et al. 2016). These short-term climatic variables should be included in following studies to explore their effects on the potential dynamic shift in the mixed forest.

Somewhat surprisingly, the probability of occurrence of this mixed forest we studied correlated weakly with precipitation seasonality across our studied mountains, despite a similar change in this climatic variable to temperature seasonality across our study region. Specifically, we have detected the minor role of precipitation seasonality in the occurrence of this mixed forest in subtropical Chinese mountains. This result has demonstrated that this climatic variable did not reach a significant level in explaining the distribution of our target forest. This finding is contradictory to previous model studies, which have suggested that precipitation seasonality has defined the stability of tropical dry forests where

evergreen and deciduous tree species could co-occur (Allen et al. 2017, Vico et al. 2017). Besides, we have not detected any significant interaction of temperature and precipitation seasonality in controlling the large-scale geographical distribution of these mixed forests in different mountains. These findings seem to be in contrast with previous work elsewhere in the subtropics and other regions with the general conclusions that the simultaneous availability of temperature and precipitation was more important than the individual climatic variable (Stephenson 1998, Ge and Xie 2017). For example, Fang et al. (2002) have concluded that thermal conditions and water availability greatly affect forest transitions across an evergreen–deciduous broad-leaved forest ecotone in eastern China. Our finding has indicated that temporal distribution of water resource around the year did not restrict the coexistence of evergreen and deciduous broad-leaved tree species. One of the plausible explanations for the above-observed pattern is due to the overriding effect of temperature seasonality. Despite the relatively high seasonal fluctuation of precipitation through the year at the East Asian monsoon region, the amount of temporal precipitation is sufficient to sustain the life cycle and thus the relative success of both evergreen and deciduous broad-leaved tree species. Another interesting possibility is that the high levels of precipitation seasonality in the subtropics might not always translate into high variability in water availability for evergreen and deciduous broad-leaved tree species (Moles et al. 2014, Su et al. 2019a). For example, much precipitation could be not available for tree species roots owing to runoff during the growing season or tree dormancy during the winter. This argument has been supported by various vegetation–climate relationship studies (van Ommen Kloeke et al. 2012, Moles et al. 2014).

It is worth noting that the minor contribution of precipitation seasonality does not mean less importance of other facets of precipitation regime in determining the geographical pattern of these montane mixed forests, while the straightforward annual or seasonal climatic indices did not contribute much to the occurrence of this mixed forest on mountain vegetation zonation. For instance, temporal shortages of water availability inhibit the establishment and high-altitude

upward of evergreen broad-leaved trees species in the north of subtropical regions (Fang et al. 2002, Vico et al. 2017, Su et al. 2019a). We also need to point out that available precipitation estimates from global circulation models may contain high uncertainties in comparison with temperature estimates (Wang et al. 2012, Grünig et al. 2017, Wu et al. 2017). Therefore, more rigorous analysis of seasonal distribution of precipitation regime will offer more detailed insight into the role of water-related variables in governing spatiotemporal dynamics of this mixed forest using high-resolution climate data (Stephenson 1998, Guan et al. 2015).

Climate change-related implications

Our results have two broad aspects of profound implications. On one hand, a growing body of studies has suggested that substantial shifts in climate seasonality patterns have been observed across the subtropical region over the past decades and are projected to continue and intensify as a consequence of the ongoing climate change (Feng et al. 2013, Xu et al. 2013). Current vegetation–climate models for subtropical regions suffer from a lack of ecological data and mechanistic understanding of the factors shaping current forest distributions, particularly for this targeted montane mixed forest, which is thought of as one of the most threatened of forest ecosystems under current predicted global warming scenarios (Woodward et al. 2004, Seddon et al. 2016, Ge and Xie 2017). Such knowledge that temperature seasonality, together with the unique sensitivity of tree species of different leaf habits to temperature, is a better climatic factor influencing the distribution patterns of subtropical targeted mixed forests will help to improve the accuracy and specificity of predictions of mountain vegetation shifts under global change scenarios (Alexander et al. 2018, Pouteau et al. 2018). On the other hand, these results presented here have shed light on the key role of temperature seasonality for the occurrence of this montane mixed forest and demonstrate that future changes in seasonal temperature regimes will have ecological cascading effects on species ranges, community dynamics, and associated ecosystems functioning and services in mountainous areas (Pouteau et al. 2018, Sun et al. 2018, Su et al. 2019b). For example, numerous

lines of evidence have indicated that the phenological match between litterfall for evergreen and deciduous species and the soil matrix affects decomposition rates (Ernakovich et al. 2014, Ge et al. 2017a). As future climate seasonality regimes are predicted to alter in subtropical regions, such a phenological match is likely to shift temporally and spatially when dominant tree species of contrasting leaf habits have very different timing of leaf senescence. Therefore, these changes will exert great cascading consequences for carbon and nutrient cycling-associated ecosystem services (Xie et al. 2015, Faucon et al. 2017, Ge et al. 2017b).

CONCLUSIONS

Our work comprehensively documented geographical distribution of the MEDBF in mountains in relation to temperature and precipitation seasonality in subtropical China. We found that higher occurrence probability of MEDBFs in subtropical high-latitude than low-latitude mountains and temperature seasonality played a more important role than precipitation seasonality and the former climatic variable that should be taken into account when attempting to better understand the geographical distribution of this mixed forest along the spatial gradient. This work advances the quantitative analysis of this mixed forest in mountains and illustrates the need for better understanding of the impact of climate seasonality on climate–vegetation relationship. By identifying the importance of temperature seasonality in predicting the occurrence of this mixed forest, it leads us a step closer toward determining how the evergreen–deciduous tree species may shift given that species of different leaf habits may respond to climatic seasonality with contrasting manners as the climate changes in the coming future (Ge et al. 2017b, Zanne et al. 2018). Future research should focus on geographically comparative studies that quantify structural and functional properties of evergreen and deciduous tree broad-leaved tree species and the effects of climatic seasonality among various mixed forests and ecoregions by integrating previous sparse forest plot information data and sampling much more forest plots, which can provide further more detailed empirical evidence to refine our understanding to

forecast how this mixed forest responds to climate change at different spatial and temporal scales.

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