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Original Research Article

Precipitation is the most crucial factor determining the distribution of moso bamboo in Mainland China

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A B S T R A C T

Moso bamboo is widespread in natural forests and is cultivated over large areas in China. This study investigated how climate controls its distribution, about which little is known. We collected moso bamboo presence-absence data from 674 sites with long-term climate data in Mainland China. Generalized additive models that included location and climate variables were used to test the effects of these predictors on the species' occurrence. We identified the best model as the one with the lowest Akaike's Information Criterion value that contained only statistically significant predictors. We found precipitation, especially the mean (APRE) and interannual standard deviation (SDPRE) of the annual precipitation at each site, rather than temperature, to be the main factors determining the distribution of moso bamboo in Mainland China. In addition, we found that there was a significant power law relationship between the mean and interannual variance of precipitation, which made it possible to make long-term predictions. The SDPRE in climate scenarios of changes in the APRE could then be calculated using the fitted power law relationship. We simulated six climate scenarios, in which the APRE increased/decreased by 25, 50, and 75%. We used the 0.5 and 0.9 probability contour lines of model predictions to represent the suitable and core distributions, respectively, of moso bamboo under each scenario. The current core distribution of moso bamboo in Mainland China predicted by our model agreed with actual observations. Our model suggested that the middle and lower reaches of the Huaihe River Plain in eastern China should be climatically suitable for the growth of moso bamboo; it seems likely that its current absence there has resulted from intensive land use. Our model predicted that changes in APRE can strongly alter the distribution of moso bamboo. Increased APRE would expand the core distribution of moso bamboo into southern Shandong Province and over all of Chongqing and most of Guizhou Provinces, which are areas not currently in the species' core distribution. Conversely, decreased APRE

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would shrink the core distribution of moso bamboo to the junction of Anhui, Fujian, Jiangxi, and Zhejiang Provinces. We showed that the current distribution of moso bamboo is mainly determined by annual precipitation rather than temperature. The deviations between the moso distributions predicted by the climate model and the current distribution in some plain areas might have resulted from human activities. Future changes in annual precipitation will probably change the distribution of moso bamboo considerably.

1. Introduction

Moso bamboo, *Phyllostachys edulis* (Carriere) J. Houzeau, is widely distributed in southern China, and has been introduced into other countries in Southeast Asia (Flora of China Editorial Committee, 1996; Fu, 2001). Moso bamboo was also introduced to several parts of South America and Europe. China is considered to be the original source of this bamboo species. Moso bamboo is the most important bamboo species in southern China, where it is often used in forestry, industry, landscape design, and in people's daily lives because of its biological characteristics (Zhou, 1998; Fu, 2001). Moso bamboo grows and produces biomass quickly, and it can exclude most tree species to form forests dominated by this single species (Fukushima et al., 2015). Cheng et al. (2015) reported that the mean diameter at breast height (DBH) of moso bamboo ranges from 2 to 16 cm, with a median of ca. 11 cm, in the main areas producing it in Mainland China, including Hunan, Jiangxi, Zhejiang, Fujian, Hubei, southern Anhui, and southern Jiangsu Provinces. In addition, the bamboo shoots of this species are popular as an expensive vegetable in southern China both in winter and spring, and thus have a high economic value. In southern China, the establishment of plantations of pure moso bamboo forests (i.e., single species-dominated forests or monocultures) was advocated by local governments in the 1980s to increase the incomes of farmers in mountainous areas (Cheng et al., 2015). The original trees growing in such areas were cut down to promote the propagation of moso bamboo. This plant quickly dominates vacant patches resulting from human disturbance because of its efficient and complex underground rhizome system, which can also efficiently prevent other woody plants from regenerating. To enhance the productivity of moso bamboo forests, farmers usually cut off a portion of the new shoots to provide sufficient light and water for the growth of the remaining shoots. As a result, the mean individual biomass of moso bamboo in well-managed stands is greater than that in stands that are poorly controlled or not managed (Liu, 2009; Cheng, 2015). In fact, in a bamboo forest without human disturbance the bamboo population density will increase, but mean individual biomass will decrease through self-thinning (Liu et al., 2016).

However, despite moso bamboo's economic importance and recent history of propagation and management, little is known about its historical distribution in China. In central and northern Jiangsu and Anhui Provinces, where intensive agricultural activities have occurred, no considerable stands of moso bamboo are currently present, yet, strangely, the local inhabitants are still accustomed to using materials made from moso bamboo as necessities in their daily lives. This may imply that moso bamboo existed in these places at a previous period in their history, although there is so far no evidence to support this hypothesis.

If climate factors like temperature and precipitation significantly affect the distribution of moso bamboo, one could expect to be able to predict the past and future distributions of this plant by adjusting these climate variables' values over the ranges that different sites might experience. Li et al. (2019) used a model based on the maximum entropy principle to study the influence of climate change on bamboo distributions in China. However, they pooled all bamboo species together, ignoring interspecific differences, and also did not collect sufficient information on bamboo distributions in China. The former of these shortcomings is problematic because different bamboo species differ in their responses to climate variables, and this might result in differences in their distributions, especially in the more climatically extreme northern areas of China and Japan (Takano et al., 2017). The latter issue occurred because their selected bamboo stands did not represent the full potential distributions of all bamboo plants. Specifically, they only defined regions where there were large areas of bamboo forests as bamboo distributional areas, while they discarded regions that had only small areas of bamboo forest. However, human activities, especially agriculture, have led to large reductions in the extents of bamboo forest areas in China. It is well-known that many areas that are highly suitable for bamboo survival have been developed for various economic and ecological uses, for example being developed as agricultural fields, residential areas, and plantation forests. When bamboo plants appear in large numbers in such areas, they are immediately removed. Finally, Li et al. (2019) only examined 314 bamboo forest sample plots, in which they assessed the combined abundance of many bamboo species. This approach could have potentially underestimated or overestimated the actual distributions for particular uncommon or unusual bamboo species. Meanwhile, Takano et al. (2017) studied the distributions of two *Phyllostachys* species (*P. edulis* and *P. bambusoides*) in central and northern Japan using a logistic regression approach based on presence-absence (1-0) data. They found that bamboo stands in this region could not exist where the mean maximum annual temperature was below 28.8 °C, the mean annual temperature was below 8.6 °C, and the mean minimum annual temperature was below −16.8 °C. However, they did not find a significant influence of precipitation on the distributions of these two bamboo species.

In general, temperature, especially temperature extremes, has notable impacts on the distributions of poikilotherms (Guschina and Harwood, 2006). Temperature has been directly observed to affect the development and growth of arthropods and plants, especially in temperature-dependent development experiments performed on plants and agricultural insect and mite pests (Shi et al., 2016, 2019b; Quinn, 2017). The minimum annual temperature was previously demonstrated to determine the northern distributional limits of several insects in the Northern Hemisphere (Uvarov, 1931; Ungerer et al., 1999; Shi et al., 2012). Temperature can also directly influence the development times of bamboo plants, including the durations of seed germination and leaf unfolding (Lin et al., 2018; Shi et al., 2019b). Low temperatures can even result in the development of more leaf teeth, lobes and dissections in temperate plants (Peppe et al., 2011). In addition, temperature is regarded as the most important climate factor determining the phenological timing of important life cycle events, such as flowering in many plants and egg hatching time in overwintering insects (Shi et al., 2017a,b). Several previous studies showed that climatic extremes usually have more significant effects on plant physiology and distributions than annual means (Brando et al., 2019 and references therein). When focusing on the distribution, physiology, growth, and mortality of plants, precipitation rather than temperature is often the dominant controlling factor; insufficient precipitation can be expressed in the form of different drought indices (Vicente-Serrano et al., 2010). Prolonged droughts (i.e., periods with insufficient rainfall) were shown to be is the key factor determining tree growth (Chen et al., 2017; Brando et al., 2019). Long-term drought events can lead to lasting functional changes in tropical forests (Aguirre-Gutierrez et al., 2019). Drought has been further shown to be a more important variable than temperature in inducing bamboo plants to flower (Campbell, 1987). The globally increasing temperatures and more frequent and severe droughts related to global warming were further already shown to lead to higher background tree mortality rates and die-off, even in environments that traditionally were not considered to be water limited (Allen et al., 2010; Adams et al., 2009; Williams et al., 2013). It thus seems worthwhile to test if and how the mean and variability of annual precipitation influence the distributions of certain plant species such as bamboos, considering that droughts frequently occur in many areas of the Northern Hemisphere and are projected to further increase in frequency. To date, only a few studies of plants have presented analyses of the joint influence of such precipitation characteristics on their distributions, although some studies have reported this for insects (Ungerer et al., 1999; Shi et al., 2012).

In studies of ecological measures, the existence of a power law relationship between the mean and variance of a non-negative random variable has been confirmed in many fields of study, and this relationship has come to be referred to as Taylor's power law (TPL; Taylor, 1961). Taylor (1961) found a power law relationship between the mean and variance of insect spatial densities in different quadrats. This law was then further confirmed to also hold true for time series of population densities. Cheng et al. (2017) and Shi et al. (2019a) found that measurements reflecting individual energy allocation or release can also be fit well by TPL. Precipitation results when atmospheric water vapour condenses, accumulates, and then falls under the influence of gravity. Atmospheric water vapour originates from the evaporation of surface water on land or sea, and from the transpiration of terrestrial plants. In areas with a marine monsoon climate, the amount of precipitation falling at a site is mainly affected by the interplay between heating and cooling air masses, which reflects the interaction of different energetic entities resulting from sea-land temperature differences (Webster et al., 1998). Thus, the mean-variance relationship of interannual changes in precipitation in a region is likely to follow a TPL relationship, since differences in regional precipitation can reflect variability in interannual differences in such atmospheric energy interactions among regions. The exponent of TPL ranges from 1 to 2 for most ecological and physical measures (Eisler et al., 2008; Fronczak and Fronczak, 2010; Cohen and Xu, 2015). If the mean and interannual variance of annual precipitation affect the distribution of moso bamboo, this provides an opportunity to explore the impact of changes in mean precipitation on the distribution of this bamboo species because the corresponding viability in interannual precipitation could be estimated using a fitted TPL relationship.

In this study, we used 674 sites in Mainland China for which $\geq$40 years of climate data and corresponding data for the presence-absence of moso bamboo were available to analyse the distribution of this species and the influences of different climate variables (and scenarios of how they could change) on its distribution.

2. Material and methods

2.1. Climate and moso bamboo distribution data

We chose 674 of the climate sites listed on the website of the National Meteorological Information Center of China (http://data.cma.cn/) for which $\geq$ 40 years of climate data were available from 1951 to 2012 as study sites. Data for the minimum annual air temperature (i.e., the minimum temperature on the coldest day in winter) and annual precipitation (i.e., the cumulative precipitation in each year) at each site were downloaded and used to calculate the mean and standard deviation of the minimum annual temperature across years (AMAT and SDMAT, respectively) and the mean and standard deviation of annual precipitation across years (APRE and SDPRE, respectively); these were the climate predictors tested in this study. The longitude, latitude, and altitude of each site were also recorded, and tested as location predictors.

In the summer of 2014, we collected the official telephone numbers of the local departments of forestry at the 674 chosen sites. We then carried out a telephone survey to assess the distribution (presence-absence) of moso bamboo. We designed the following three questions for use in each telephone survey: (1) Is there a moso bamboo forest in your region at present? (2) If moso bamboo is present, how much area is occupied by moso bamboo forests? (3) If moso bamboo is present, is the moso bamboo in your region native, introduced, or both? In the analyses done in the present study, we did not distinguish native moso bamboo from introduced plants because we were mainly attempting to examine the areas suitable for this species'

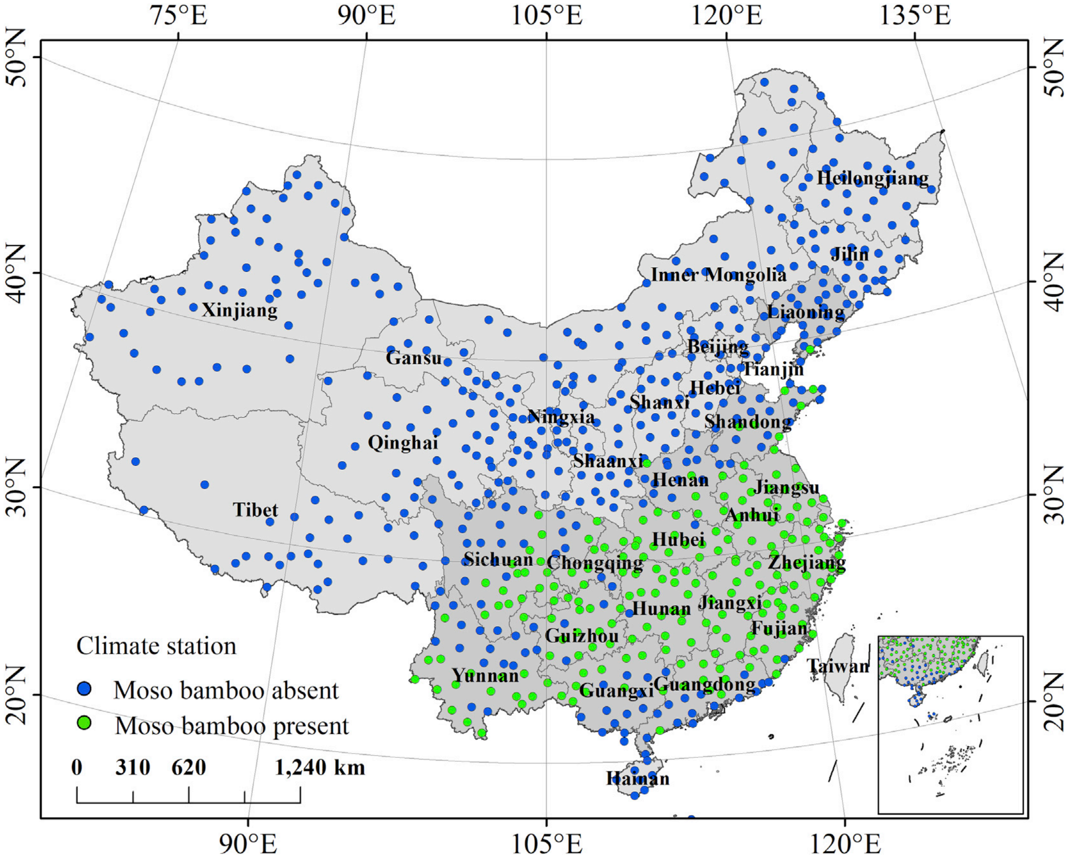

Fig. 1. The climate sites investigated and information on the distribution of moso bamboo (presence-absence) at them in Mainland China.

survival, including those to which moso bamboo can potentially adapt and become established. We recorded a value of '1' when moso bamboo was present at a site, and recorded a '0' when it was absent in the year of the survey. Fig. 1 shows the reported presence and absence of moso bamboo at the studied sites in Mainland China.

Table S1 in the online supplementary data lists the presence-absence of moso bamboo at each site, the site information (including site code, longitude, latitude, and altitude), and the climate data for each site (including the AMAT, SDMAT, APRE, and SDPRE).

2.2. Analytical methods

If the realizations of a climate variable follow a normal distribution at a site during a period, it implies that the variability in this climate variable the plant therein has experienced could be reflected well by the standard deviation of the climate variable. This means that the range of variations in this climate variable could be easily calculated by its mean and standard deviation under a normal distribution (e.g., the 95% confidence interval of a normal random variable equals its mean plus/minus 1.96 standard deviations). Thus, for each site, we used the Shapiro-Wilk test to check whether the minimum annual temperature and cumulative annual precipitation data followed a normal distribution, and this hypothesis was rejected when the test returned $P < 0.05$.

To explore which factors determine the distribution of moso bamboo, we used the following predictors to fit the presence-absence data ($Y = 1$ or 0, respectively): the longitude, latitude, altitude, AMAT, SDMAT, APRE, and SDPRE for each site. We fitted 11 generalized additive models (GAMs) to the data with a logit link function to represent the relationship between moso bamboo presence-absence and different sets of predictors (Table S2 in the online supplementary data). We chose the best model as the one with the lowest value of Akaike's Information Criterion (AIC) out of all those tested that also contained only statistically significant predictors. After finding the best model, we divided the predicted probabilities of moso bamboo presence into ten classes at 0.1 increments (0.0–0.1, 0.1–0.2, 0.2–0.3, …, 0.9–1.0) and the corresponding proportion of sites matching these probability of occurrence classes (observed fraction) was calculated as the number of sites where moso bamboo was present divided by the number of the sites in each class. We then used a reliability diagram, which was a scatter plot of the observed fraction (with its 95% confidence interval) vs. the predicted probability class, to assess the goodness-of-fit of the model and check whether there were outliers for each predicted probability class. We calculated the standard error (SE) for each observed fraction as follows:

$$\mathrm{SE} = \sqrt{\frac{p(1-p)}{n}} \tag{1}$$

where p is the observed fraction in a class and n is the number of observations in that class. The observed fraction was then plotted $\pm 1.96 \times$SE, which represented its corresponding approximate 95% confidence intervals.

To examine whether TPL holds true for the relationship between the mean (APRE) and variance (VPRE) of annual precipitation across years, the following linearized equation was used:

$$y = c + b\,x \tag{2}$$

where $y = \ln(\mathrm{VPRE})$, $x = \ln(\mathrm{APRE})$, and c and b are fitted constants. The coefficient b is equivalent to the exponent of TPL, which fell in the range of 1–2 in previous studies of many ecological and physical measures.

To explore the sensitivity of the reaction of the distribution of moso bamboo to climate change, we hypothesized the following six climate scenarios: (1) APRE increases by 25%; (2) APRE decreases by 25%; (3) APRE increases by 50%; (4) APRE decreases by 50%; (5) APRE increases by 75%; and (6) APRE decreases by 75%. We did not consider the impacts of changes in the AMAT and SDMAT because these two variables were not included in the best model obtained (see Results).

R version 3.6.1 (R Core Team, 2019) was used to carry out all statistical analyses, and the package 'mgcv' (version 1.8–28; Wood, 2019) was used to fit generalized additive models to the data. Maps of the (observed and predicted) distribution of moso bamboo were plotted using ArcGIS version 10.5 (Esri China Information Technology Co. Ltd., Beijing, China).

3. Results

We found that the minimum annual temperature and annual precipitation data of 72.1 and 76.3% of sites, respectively, passed the normality test (see Table S1). This indicates that both the minimum annual temperature and annual precipitation data for most sites followed a normal distribution. The 95% confidence interval of any climate variable during the period could thus be calculated by its mean plus/minus 1.96 standard deviations. This also suggests that the standard deviation could be regarded as a typical representation of the variability in this climate variable for most sites.

Among the 11 GAMs tested, the lowest AIC values were found for model 4 [y ~ te(Long, Lat, Alt) + te(AMAT) + te(APRE, SDPRE); AIC = 256.83] and model 6 [y ~ te(Long, Lat, Alt) + te(APRE, SDPRE); AIC = 257.30], where y represents the moso bamboo presence-absence (1-0) response variable, te are semi-parametric smooth functions (tensor product smooths) within GAM formulae, and the deviance explained by each of these models was 75.58 and 74.98%, respectively (see Table S2). Considering that the AMAT predictor in model 4 was not statistically significant ($P > 0.05$), we finally chose model 6 as the best one out of those tested. The odds of moso bamboo occurrence increased with longitude, especially from 100°E to 120°E (Fig. 2A), and also increased with latitude from 20°N to 30°N (Fig. 2B), but decreased with increasing altitude from 0 to ca. 800 m above sea level, above which it stabilized (Fig. 2C). The odds of moso bamboo occurrence sharply increased with the APRE, with it sharply increasing from 0 to 700 mm, and then slowly increasing from 700 to 1500 mm (Fig. 2D). The odds of moso bamboo occurrence also rapidly increased with increasing SDPRE from 0 to 120 mm, and then the effect of increasing SDPRE on moso bamboo occurrence tended to be constant above 120 mm (Fig. 2E). From Fig. 2F, it can clearly be observed that in the region with an APRE within 0–700 mm and SDPRE within 0–120 mm the probabilities of moso bamboo occurrence are small, but increase rapidly as these precipitation values increase. However, in the region with an APRE within 500–1000 mm and SDPRE within 100–200 mm the probabilities of moso occurrence become abnormally high.

The data in Fig. 3 show that there is a significant power law relationship between the mean and variance of annual precipitation across years because the 95% confidence interval of the slope does not include zero. The values of the natural logarithms of these two variables were also strongly correlated. However, dropping either the APRE or SDPRE predictor from model 6 would considerably increase the model's AIC, in which case it seems necessary and reasonable to keep these two correlated predictors together in the best model.

Fig. 4 shows the predicted probabilities of moso bamboo occurrence in Mainland China based on the current climate scenario. The 0.5 probability contour line predicts the potential distribution of this species, and the 0.9 probability contour line predicts the areas of its core distribution. Fujian, Zhejiang, Jiangxi, most of Hunan, central and eastern Hubei, southeastern Henan, a small area in southwestern Yunan, a small area in northwestern Guizhou, central and southern Anhui, and Jiangsu Provinces were predicted to be included in the core distribution of moso bamboo. The species' potential distribution, which was reflected by the 0.5 probability contour line, was predicted to extend northward into southeastern Shandong, northern Anhui and Jiangsu, southeastern Henan, and central and northern Sichuan Provinces, westward into central and southern Yunan Province, and southward into central Guangxi and Guangdong Provinces.

Fig. 5 shows the reliability diagram produced based on model 6. The predicted probabilities for the 0.0–0.4 and 0.5–1.0 classes appeared to give a good fit to the observed values, whereas the probabilities for the 0.4–0.5 class deviated greatly from the expected 45° (1:1) straight line, although their 95% confidence interval still included the 45° line.

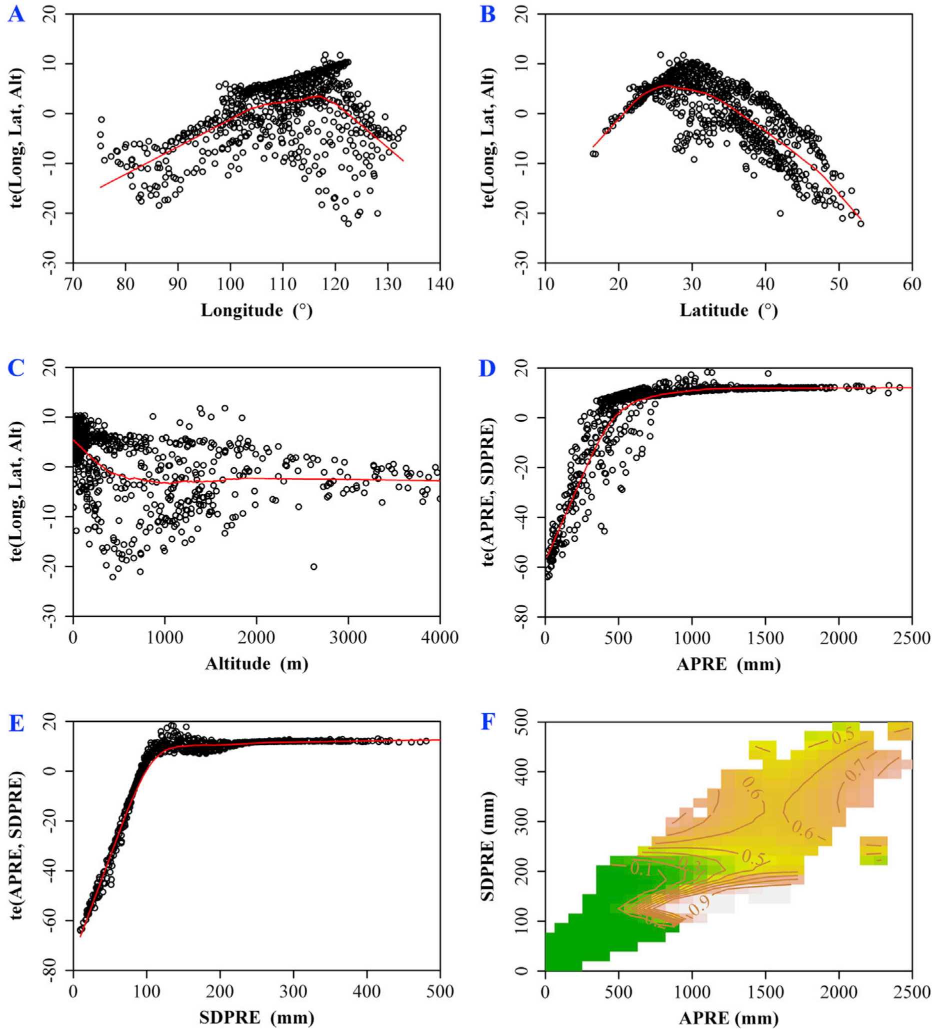

Fig. 2. Partial residuals and smoothed curves of the predictor variables and the surface representing the predicted probability of moso bamboo occurrence. Predictors included (A) longitude (Lon) in °E, (B) latitude (Lat) in °N, (C) altitude (Alt) in m above sea level, (D) average annual precipitation (APRE) in mm, (E) interannual standard deviation in precipitation (SDPRE) in mm, and (F) the surface of the predicted probability of occurrence based on the APRE and SDPRE. In panels A–E, the open circles are partial residuals, and the dark solid curve is the curve fitted by using Friedman's super smoother. In panel F, the numbers on the contour lines are the predicted occurrence probabilities.

Fig. 6 and Fig. S1 in the online supplementary data show the predicted distributions of moso bamboo in Mainland China under each of six hypothesized climate scenarios. A 25% increase in the APRE (scenario 1) was predicted to expand the core distribution northward by 60–150 km past the current northern distributional limits, westward by 90–120 km past the current western distributional limits, and southward by 0–90 km past the current southern distributional limits. At the same time, this scenario led to the disappearance of the core distributional area in northwestern Guizhou Province. A 25% decrease in the APRE (scenario 2) was predicted to shrink the core distribution southward by 120–180 km from the current northern distributional limits, eastward by 180–270 km from the current western distributional limits, and northward by 30–75 km from the current southern distributional limits, while the whole of northern Guizhou Province became more suitable for moso bamboo survival in this scenario. Increasing the APRE by 50% (scenario 3) was predicted to expand the current core distribution northward by 90–150 km, westward by 150–300 km, and southward by 0–150 km, but led to the disappearance of the current core distributional area in northwestern Guizhou Province. However, a new core distributional area in northern Sichuan Province (close to Gansu and Qinghai Provinces) formed in this scenario. Decreasing the APRE by 50% (scenario 4) was predicted to shrink the current core distribution to a smaller area made up of Zhejiang, northern Fujian, southern Anhui and Jiangsu, and northeastern Jiangxi Provinces. This would shift the core distribution of moso bamboo southward by 180–330 km from the current northern distributional limits, eastward by 330–600 km from the current western distributional limits, and northward by 120–300 km from the current southern distributional limits. A 75% increase in the APRE (scenario 5) was predicted to expand the current core distribution northward by 90–150 km, westward by 240–480 km, and

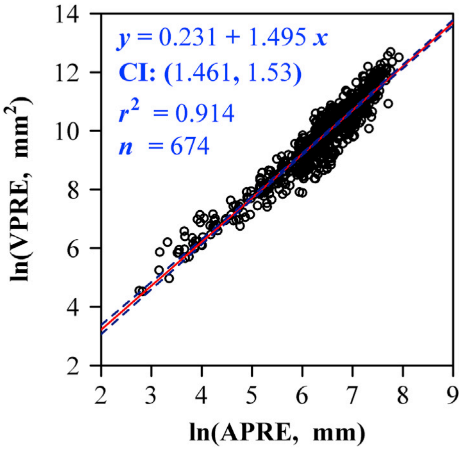

Fig. 3. Linear fit of the relationship between the log$_e$-transformed interannual variance in precipitation (VPRE) and the log$_e$-transformed mean annual precipitation (APRE). The open circles represent the values of each combination of ln(VPRE) vs. ln(APRE), where each point represents a climate site; the straight line represents the regression line; and the two blue dashed lines represent the 95% confidence intervals for the regression line. On this figure, y represents ln(VPRE), x represents ln(APRE), CI represents the 95% confidence interval of the slope, r^2 is the coefficient of determination that measures the regression's goodness-of-fit, and n represents the sample size (the number of sites). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article).

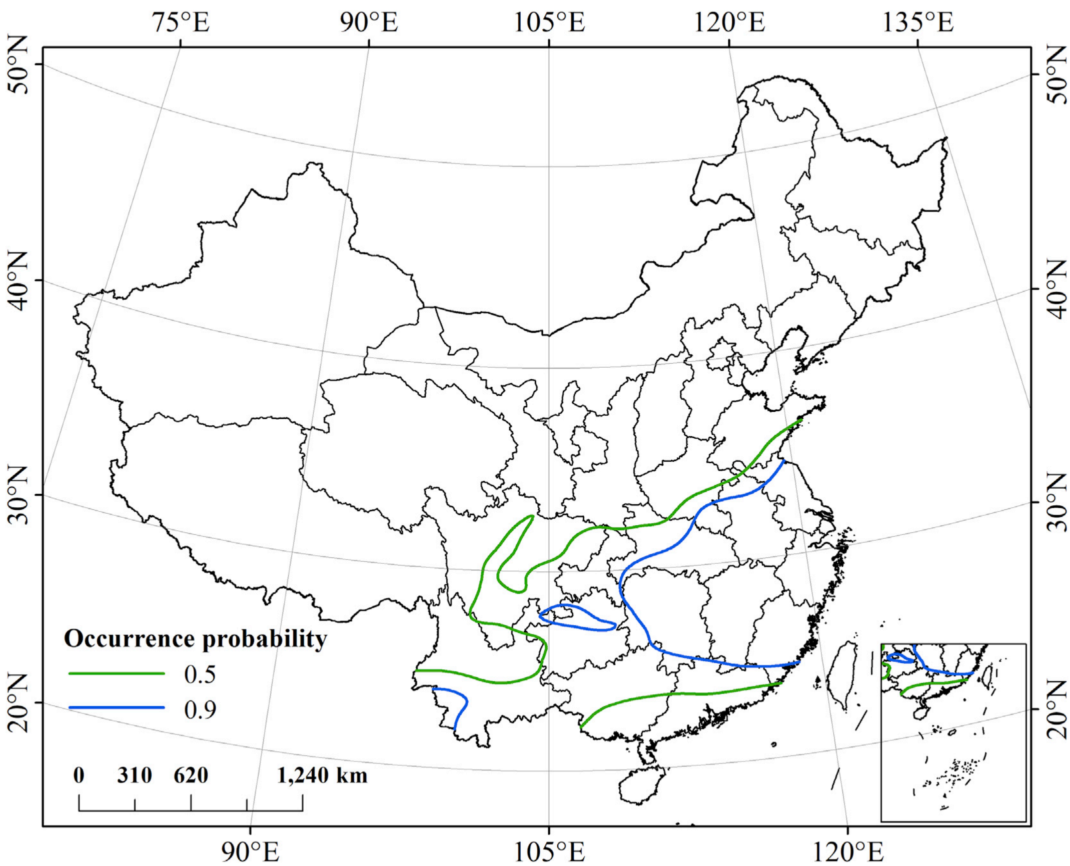

Fig. 4. Predicted probabilities of moso bamboo occurrence in Mainland China. The contour lines representing occurrence probabilities of 0.5 and 0.9 are shown, which represent the limits of the species' potential distribution and core distribution, respectively.

southward by 0–300 km; additionally, in the junction of Sichuan, Qinghai, and Gansu Provinces, a new core distributional area of moso bamboo appeared under this scenario. A 75% decrease in the APRE (scenario 6) was predicted to reduce the

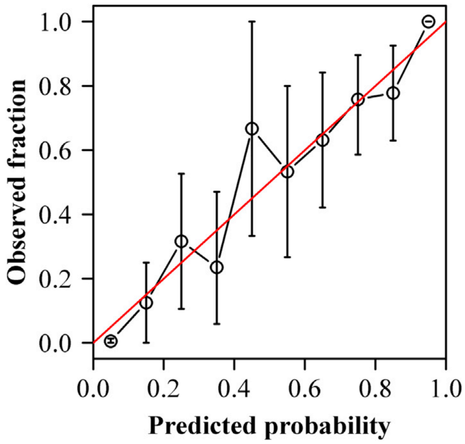

Fig. 5. Reliability diagram for the generalized additive model fit of moso bamboo distribution (presence-absence) data. The predicted probabilities were divided into ten classes at 0.1 increments (0.0–0.1, 0.1–0.2, 0.2–0.3, ..., 0.9–1.0), and the corresponding observed fraction was calculated as the number of the sites where moso bamboo was present divided by the total number of sites (moso present + absent) in each class.

current core distribution to a very small area lying along the junction of Anhui, Jiangxi, Zhejiang, and Fujian Provinces, with a total area of less than 35000 km^2; the entire potential distribution also shrank greatly under this scenario. In the sixth climate scenario, several current core distributional areas, including those in central and southern Fujian and Jiangxi, eastern Hubei, Hunan, and central and southern Anhui and Jiangsu Provinces, were predicted to become unsuitable for moso bamboo survival.

4. Discussion

4.1. Influence of the interannual variability in precipitation on moso distribution

Species distribution models (SDMs) are widely used to make statistical inferences about the drivers of species' distributions under different conservation, ecological, and evolutionary scenarios and address questions relevant to these processes (Zimmermann et al., 2010). In previous studies, the mean annual temperature, rather than the minimum annual temperature, has been the climate variable that was most often used as a predictor of species' distributions. Many species' ranges were hypothesized to be closely related to the mean annual temperature they experienced (e.g., Preisler et al., 2012; Li et al., 2019). However, the influence of the variability in climate variables on species' distributions has largely been neglected by all but a few studies that realized the important role of the variability in these climate variables. For instance, Ungerer et al. (1999) found that minimum annual temperatures at most sites in the eastern United States of America followed the normal distribution. They further found that changes in the standard deviation of the minimum annual temperature could significantly affect the northern distributional limits of *Dendroctonus frontalis* Zimmermann, an important forest pest insect in North America. Changes in the variability of minimum annual temperatures in particular were found to relax the climatic constraints on the northern distributional limits of this forest pest insect. Shi et al. (2012) used the same approach to study the northern distributional limits of *Scirpophaga incertulas* Walker, a rice pest insect in East Asia, and they also found that the mean and standard deviation of minimum annual temperature were the crucial climate factors delimiting the distribution of *S. incertulas* in Mainland China. Takano et al. (2017) examined the influence of the minimum annual temperature on the distributions of two bamboo species in central and northern Japan, and they confirmed that the minimum annual temperature was a limiting factor for bamboo distributions there, whereas precipitation had no significant influence on bamboo distributions.

However, in comparison with animals, the survival of plants, especially trees, has been demonstrated to be limited by the lack of precipitation (namely drought) in temperate and subtropical areas (Allen et al., 2010; Aguirre-Gutierrez et al., 2019). Rather than long-term averages, extreme events are usually the most crucial determinants of biological adaptation and speciation (Leigh et al., 2012). For instance, Zeppel et al. (2014) found that when soil water content increases or decreases, extreme precipitation events can have a powerful influence on the aboveground net primary productivity of plants. They found that reductions in precipitation in spring or summer generally negatively affected plants, whereas subsequent reductions in autumn or winter did not have significant influences on them. In addition, they found that increased summer precipitation affected plants more significantly than increased winter precipitation. In our study, we did not analyse the influences of seasonal changes in precipitation on the distribution of moso bamboo because the distribution data used were only presence-absence (1-0) data, which therefore required us to assume that the absence or presence of moso bamboo at a site was constant from 1951 to 2014. Thus, seasonal analyses were not performed. However, interannual variability in precipitation is an important factor that affects species' distributions and functional diversity, but which has a negative effect on

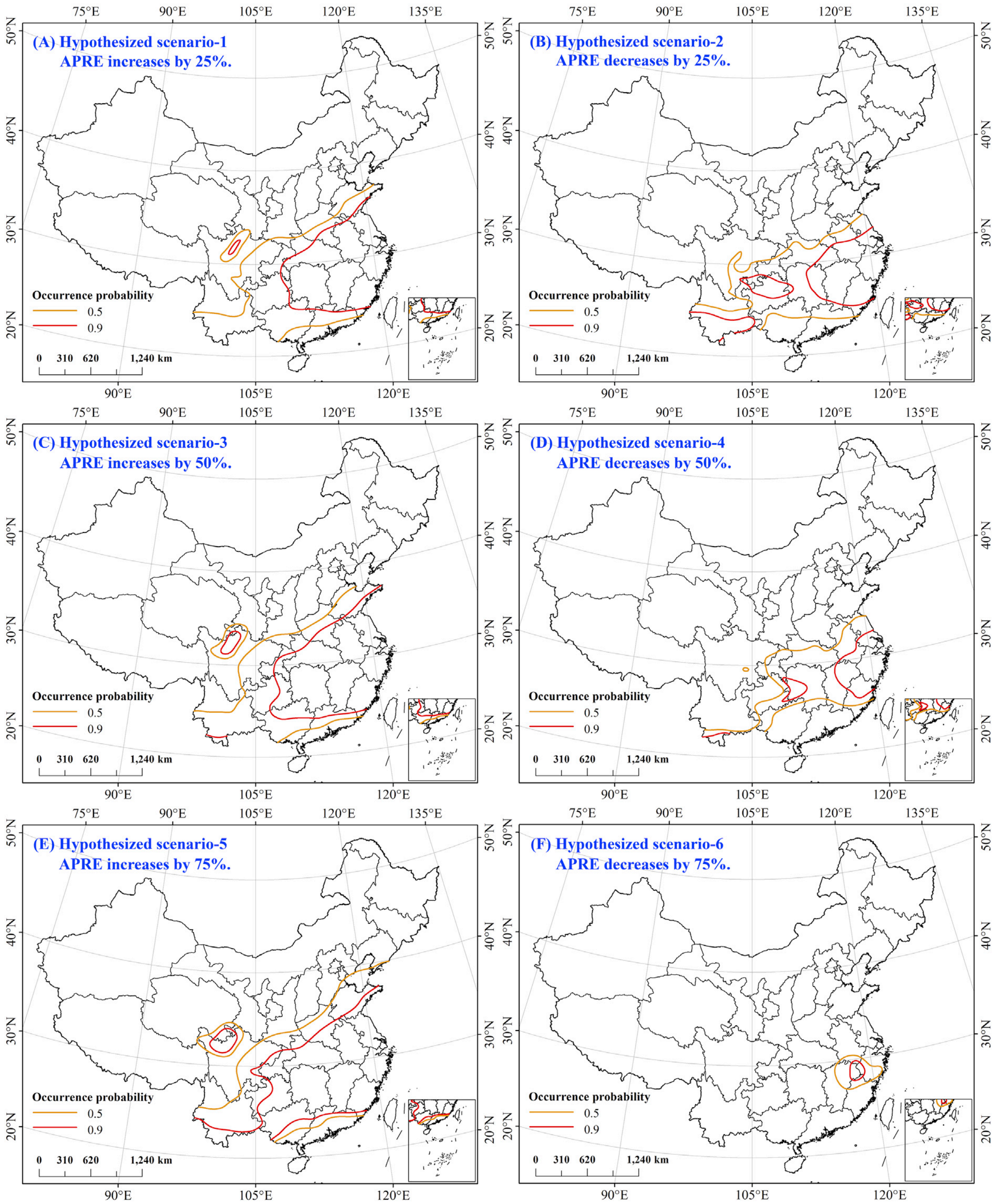

Fig. 6. Predicted probabilities of moso bamboo occurrence in Mainland China based on the following six hypothesized climate scenarios: (A) APRE increases by 25%; (B) APRE decreases by 25%; (C) APRE increases by 50%; (D) APRE decreases by 50%; (E) APRE increases by 75%; and (F) APRE decreases by 75%.

the stability of productivity (Gherardi and Sala, 2015). In a recent experimental study, Groves and Brudvig (2019) demonstrated that the magnitude of the interannual variability in precipitation can have an important influence on seedling establishment in sown plant communities. Moso bamboo propagates via a complex underground rhizome system, and it expands its population by producing new shoots from these rhizomes (Wei et al., 2017). Whether bamboo shoots can grow up to become adult bamboo plants and how much biomass adult bamboo plants can produce mainly depends on the mean rainfall and the extent of its variation over the growing season. Our study showed that precipitation plays a more important role in limiting the distribution of moso bamboo than temperature, which is in accordance with the results of previous studies that also reported the importance of precipitation to plant distributions (Song et al., 2016; Chen et al., 2017). Indeed, by regulating plant gas exchange and its long-term response to climate change, changing precipitation rather than global warming could have a more prominent impact on the productivity of grasslands (Song et al., 2016).

Although our study was focused on the distribution of moso bamboo as inferred from presence-absence (1-0) data, the small sizes of the viable areas of moso bamboo at specific sites caused by changing precipitation conditions there might drive the bamboo to become extinct or extirpated on a regional scale. Takano et al. (2017) found that precipitation had no significant influence on the distributions of *P. edulis* and *P. bambusoides* in Japan, which could have resulted from the climatic characteristics of Japan. Specifically, Japan is a long and narrow country from south to north, and is surrounded by the sea on all sides. The long-term average annual precipitation in most areas of Japan exceeds 1000 mm, so insufficient rainfall is not generally a problem for bamboos in Japan (Yue and Hashino, 2003). Under conditions with sufficient precipitation, temperature becomes a relatively more important and limiting factor for bamboo distributions. However, droughts frequently occur in central-northern China, which tends to lead to precipitation being more important than temperature in determining the distribution of moso bamboo in Mainland China.

4.2. Interactions among predictors and contribution rates of two tensor product smooths within the GAM

In the 11 tested GAMs (see the Material and methods section), we did not consider the possible impacts of interactions between the location and climate variables. Since the GAM approach was proposed (Hastie and Tibshirani, 1986), the question of how to accurately account for interactions among predictors in these models has always been difficult to answer. If there is clear evidence of the occurrence of interactions among the predictors or if the predictors have the same linked characteristics, then the use of the tensor product of the predictors to reflect the influence of their interactions on the response variable is usually recommended. Even though using a tensor product, which effectively combines the interactions among predictors, can improve the goodness-of-fit of a GAM, this can also sometimes result in over-fitting the data. Because no mechanisms of any possible interactions between the location and climate variables tested were known, we did not consider the interactions between these two types of variables in our analyses. We deemed it preferable to exclude such interactions when the evidence thereof from biophysics or biochemistry is lacking. In fact, the interaction between the location and climate variables is usually neglected by most studies of species' distributions using GAMs (e.g., see the papers in Volume 157, Issues 2–3 of *Ecological Modelling* in 2002). For instance, in the marine realm, Wood and Augustin (2002) used GAMs to analyse the effects of location (i.e., longitude and latitude), seabed depth, sea-surface temperature, and the distance from the 200 m isobath on the egg density of Atlantic mackerel (*Scomber scombrus* Linnaeus), and these predictors were all treated as independent in that study. However, to explore which factors might be more important than other factors in controlling the response variable, it is necessary to explore the role of each type of independent variable in explaining the deviance in the data (Legendre and Legendre, 1998).

We used the following method to calculate how much of the deviance in the response variable was explained by each of the main classes of predictors in our models: first, we calculated the deviance in the data explained (*DE*) by model 6, which we represented as DE_0; second, we calculated the *DE* values for each class of predictors; third, we calculated the contribution rates (*CR*s) of the two classes of variables using the formula:

$$CR_i = \frac{DE_i}{\sum_{j=1}^{2} DE_j}, \tag{3}$$

where DE_i (i = 1 and 2) and DE_j represent the deviance explained using a GAM with the location or climate variables, respectively; fourth, we then calculated the contribution of each class of predictors to the deviance explained (PDE_i) as:

$$PDE_i = DE_0 \times CR_i. \tag{4}$$

For the location variables (longitude, latitude, and altitude) and the climate variables in model 6 (APRE and SDPRE), the contribution rates were similar (55 and 45%, respectively), while the corresponding portions of the total deviance explained (75%) by each of them were 41% and 34%, respectively (Fig. 7). This demonstrates that these two classes of variables together accounted for more than three quarters of the deviance in the data. However, 25% of the deviance remained unexplained. In our study, we did not investigate soil properties, but there are significant differences in the spatial distributions of soil pH, cation exchange capacity, organic carbon, nitrogen (N), phosphorus (P), and potassium (K) in China (Wei et al., 2013). According to Wei et al. (2013), the distribution of moso bamboo appears to be similar to the spatial distributions of soil pH, organic carbon, available N, and available K. Soil type and soil properties can significantly affect plant growth and distributions (Jobbágy and Jackson, 2001). In addition, soil properties can modulate the responses of plants to enhanced rainfall (Eskelinen and Harrison, 2015). We already have spatial location in the model, and part of the reason location explains so much of the variability is probably caused by soil. Soil and location are highly confounded. Actually, the location term is likely

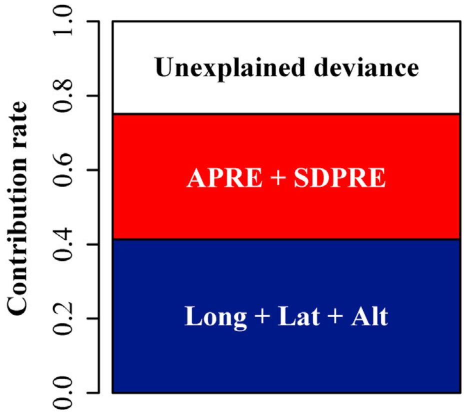

Fig. 7. Contribution rates (%) of each of the two main classes of predictor variables to explaining variation in the data. 'Long + Lat + Alt' represents the location variables, and 'APRE + SDPRE' represents the climate variables in the best model (model 6).

to be a surrogate for other spatially explicit variables such as soil. The other role of the location variable is in representing spatial contiguity. For instance, moso bamboo might tend to disperse to nearby locations (Zhou, 1998). Although the effect of soil was probably already included in our model, this is worth being further investigated by using detailed soil factors in the models.

4.3. Taylor's power law and the predicted interannual variability in precipitation

In previous studies of the effects of climate change on species' distributions, climate change scenarios were usually projected using time series or regression methods. The mean value of a key climate variable is usually predicted under different scenarios, but the variability of the variable has seldom been considered in such studies. In our opinion, extant climate models might have led to incorrect projections of the influence of climate change on species' distributions since they were used without considering the agreement between the changes in the variability of climate variables with their predicted mean changes. TPL has been demonstrated to apply in many study areas (Eisler et al., 2008; Fronczak and Fronczak, 2010; Cohen and Xu, 2015; Shi et al., 2017c, 2019a), and thus it cannot be neglected when modelling climate change scenarios, including changes in precipitation, which was demonstrated to be an important limiting factor in the present study. Empirical estimates of the exponent of TPL usually range from 1 to 2. TPL reflects the individual differences in energy allocation or energy release (Shi et al., 2019a), and the range of the empirical values of the exponent of TPL represent the actual universal limits to such mean-variance relationships. In this study, we first verified that the mean-variance relationship of interannual precipitation changes followed a TPL relationship with a scaling exponent unequal to unity; that is, increases in the interannual variation in precipitation did not keep pace with increases in the APRE. In this case, the influence of SDPRE (i.e., the square-root of the variance) on the probability of moso occurrence should not be neglected when making long-term predictions. Assuming the APRE increases by k, based on Eq. (2) we can assume that:

$$V_{\text{new}} = aM_{\text{new}}^{b} \Leftrightarrow V_{\text{new}} = a(1+k)^{b}M^{b}, \tag{5}$$

where V_{new} represents the interannual variance in precipitation associated with an APRE that has increased by k (i.e., M_{new}), and a and b are the normalized intercept constant and the exponent of TPL, respectively. We then know that:

$$\text{SDPRE}_{\text{new}} = \sqrt{a(1+k)^{b}\text{APRE}^{b}}. \tag{6}$$

The percentage increase (IP) in the SDPRE can then be calculated as:

$$\begin{aligned} \text{IP} &= \frac{\sqrt{a(1+k)^{b}\text{APRE}^{b}} - \text{SDPRE}}{\text{SDPRE}} \times 100\% \\ &= \left(\sqrt{(1+k)^{b}} - 1\right) \times 100\% \end{aligned} \tag{7}$$

From the above, we could calculate the percent increase in the SDPRE based on the percent increase in the APRE, since the estimated b value was equal to 1.495 and k was also known (±25%, ±50%, and ±75%) in each of the respective climate scenarios. The corresponding percentage increases in the SDPRE were equal to −19.4, 18.2, −40.4, 35.4, −64.5, and 52.0% for the six climate scenarios. Fig. 8 shows the effect of the percent increase in the APRE on the SDPRE.

4.4. Validity of the data and model

In this section, we discuss the validity of the data and model tested with regard to the following three points: (1) the reliability of the data source; (2) the representativeness of the presence-absence data we analysed; and (3) the outliers identified in the reliability diagram.

Climate data were downloaded from the authoritative official climate website of China, and we chose to examine climate sites for which more than 40 years of consecutive records were available. Thus, the mean and standard deviation values calculated for the minimum annual temperature and precipitation data we calculated should have been robust.

We used a telephone survey approach to obtain information on the distribution of moso bamboo in Mainland China. We cannot exclude the possibility that some interviewees could not distinguish moso bamboo from other species, especially in southern China, where there are many other bamboo species. However, fortunately, moso bamboo is a tall, large-sized type of monopodial bamboo, while all other large bamboos in China are sympodial bamboos, so it is thus easy to distinguish them. In addition, we chose to call professional staff working in local forestry departments, who should know the forest species and conditions at these sites well. Thus, we believe that the investigated data are reliable. There is some uncertainty regarding whether the one-time investigation of the presence-absence of moso bamboo can reasonably represent its actual long-term distribution. A successful colonization by or introduction of moso bamboo in an area usually requires many years. Indeed, observations over 6–8 years (i.e., 3–4 generations) are required to demonstrate whether moso bamboo can adapt sufficiently to local climates to become established (Zhou, 1998). In the 1970s, some northern provinces in China attempted to introduce moso bamboo, but most failed because of the frequent occurrence or severity of drought there, especially in winter, which further demonstrates that bamboo stands of this species cannot form over short time periods, especially in stressful conditions (Liaoning Academy of Forestry Sciences, 1977). In our survey, the presence of moso bamboo actually denoted that there was at least one moso bamboo forest at a site, meaning that moso bamboo had existed there for at least 6–8 years. Although our study showed that changes in the APRE could result in the expansion or contraction of this species' distribution, the time series of annual precipitation data pooled across the region with longitude $\geq$97.5°E and latitude $\leq$35°N did not show any overall increasing or decreasing trend (Fig. 9). In our analysis of the normality of annual precipitation data, 76.3% of sites passed the normality test (Table S1). In other words, at those sites, the changes in annual precipitation during the past 60 years could be regarded as different random realizations of a normally distributed variable (see example in Fig. 10). Thus, we believe that the distribution of moso bamboo during the investigated 60 years has been stable. Whether its distribution will change in the future will mainly depend on whether the APRE in this region changes. In that case, the data we obtained in our one-time investigation of the presence and absence of moso bamboo could in fact reflect the actual long-term distribution of this plant.

With regard to the reliability diagram (Fig. 5), there is an outlier in the 0.4 to 0.5 probability class. We noted above that in the region in Fig. 2F where the APRE ranged from 500 to 1800 mm and the SDPRE from 100 to 200 mm the predicted probabilities of moso bamboo occurrence were extremely high. We initially assumed that the unusual values obtained for probabilities of 0.4–0.5 might have been associated with some specific region(s), but after checking this we found that probability values of 0.4–0.5 did not cluster in any particular region (Fig. S2). The outlier in the 0.4 to 0.5 probability class with a large confidence interval might have been caused by a small sample size because the number of sites with predicted probabilities falling in this range was only 9. For all other predicted probability classes except 0–0.1 and 0.9–1.0, the numbers of sites ranged from 20 to 30 per class.

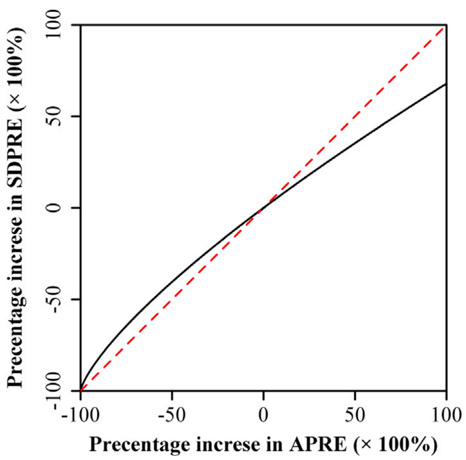

Fig. 8. Effects of the percent change in APRE on the percent change in SDPRE. The solid curve represents the predicted results, and the red dashed line is the expected 45° (1:1) straight line. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article).

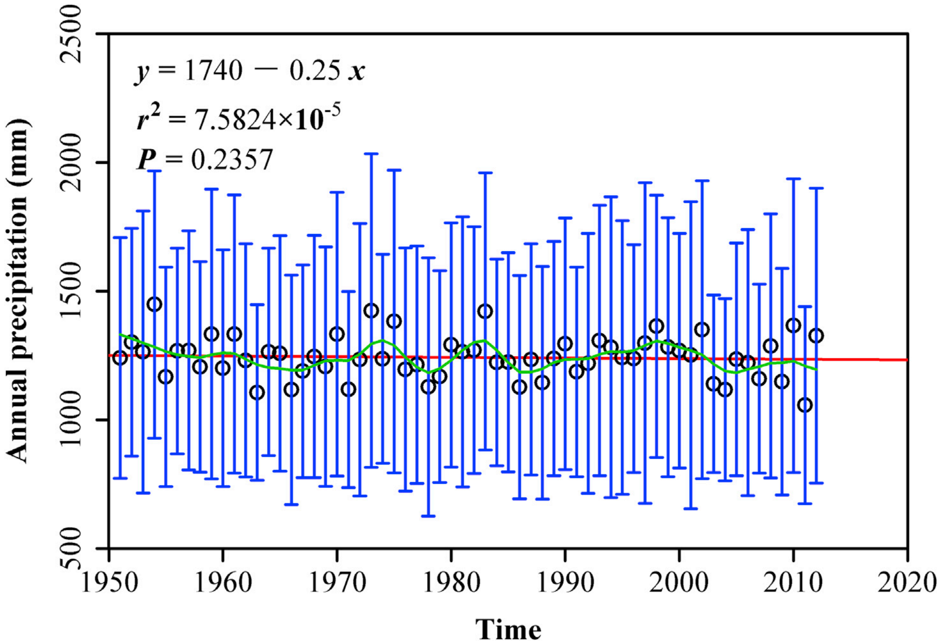

Fig. 9. Linear fit of the pooled annual rainfall data of 327 climate sites in central and southern China (with longitude $\geq$ 97.5°E and latitude $\leq$ 35°N) from 1951 to 2012. The open circles represent the mean annual rainfall values for each year, while the error bars are their corresponding standard deviations; the red straight line is the regression line; the green curve is the fitted trend obtained using Friedman's super smoother. The *P*-value of the regression is $P > 0.05$, which indicates that the slope is not significantly different from zero. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article).

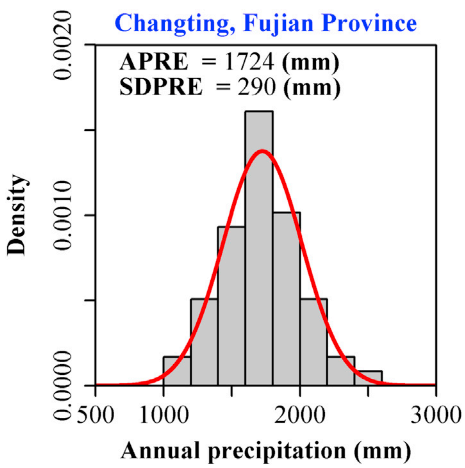

Fig. 10. Frequency distribution of annual rainfall values in Changting County, Fujian Province, China, from 1951 to 2012.

5. Conclusions

The distribution of moso bamboo is strongly affected by climate. Although there is evidence that temperature can significantly impact the developmental progress and average individual biomass of this plant, our study showed that, on a large regional scale, precipitation is the key factor impacting this species' distribution. The average and variability of annual precipitation were demonstrated to be the most important factors determining moso bamboo presence, and could account for approximately half of the deviance in moso occurrence data explained in the best generalized additive model we tested. Although location variables, including longitude, latitude, and altitude, also significantly affected the distribution of moso bamboo and accounted for a further half of the explained deviance in these data, it is not necessary to consider their influence under climate change scenarios due to the fact that climate change does not lead to large changes in terrain on a centenary scale. We hypothesized six climate scenarios representing how the APRE could change, and found that increases in the APRE could cause the potential and core distributions of this plant to expand considerably, while deceases in this variable could cause these areas to greatly shrink. The core distribution of moso bamboo could be shrunk to a small area (less than 35000 km^2) lying along the junction of Anhui, Jiangxi Zhejiang, and Fujian Provinces with a decrease in the APRE by 75%. Conversely, an increase in the APRE by 75% could lead the core distribution of moso bamboo to expand, and further extend to cover Chongqing, eastern Guizhou, and northern Guangxi Provinces. It should be pointed out that, even under the 75% increase scenario, the northern limits of moso bamboo could not reach to northern Shandong and Henan or southern Shaanxi Provinces because of the persistent issues with drought in these northern provinces. Our study showed which places in Mainland China are suitable for this plant to survive, and can help local governments avoid blindly introducing this plant without knowing the link between the species' distribution and precipitation. In addition, our results might also apply to other similar plants that have obvious geographical distributional limits. Our study implies that the variability in precipitation should be included in predictive models used in future climate change studies on species' distributions.

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2020.e00924.

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