



Modelling chestnut biogeography for American chestnut restoration

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ABSTRACT

Aim Chestnuts (*Castanea* spp.) are ecologically and economically important species. We studied the general biology, distribution and climatic limits of seven chestnut species from around the world. We provided climatic matching of Asiatic species to North America to assist the range-wide restoration of American chestnut [*C. dentata* (Marsh.) Borkh.] by incorporating blight-resistant genes from Asiatic species.

Location North America, Europe and East Asia.

Methods General chestnut biology was reviewed on the basis of published literature and field observations. Chestnut distributions were established using published range maps and literature. Climatic constraints were analysed for the northern and southern distribution limits and the entire range for each species using principal component analysis (PCA) of fourteen bioclimatic variables. Climatic envelope matching was performed for three Chinese species using Maxent modelling to predict corresponding suitable climate zones for those species in North America.

Results Chestnuts are primarily distributed in the warm-temperate and subtropical zones in the northern hemisphere. PCA results revealed that thermal gradient was the primary control of chestnut distribution. Climatic spaces of different species overlap with one another to different degrees, but strong similarities are shown especially between Chinese species and American species. Climatic envelope matching suggested that large areas in eastern North America have a favourable climate for Chinese species.

Main conclusions The general biological traits and climatic limits of the seven chestnut species are very similar. The predictions of Chinese species climatic range corresponded with most of the historical American chestnut range. Thus, a regionally adapted, blight-resistant, introgressed hybrid American chestnut appears feasible if a sufficiently diverse array of Chinese chestnut germplasm is used as a source of blight resistance. Our study provided a between-continent climate matching approach to facilitate the range-wide species restoration, which can be readily applied in planning the restoration of other threatened or endangered species.

Keywords

American chestnut, climatic envelope matching, conservation biogeography, Fagaceae, restoration, species distribution modelling.

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INTRODUCTION

Managed reintroduction and relocation have been recognized as viable options to assist the restoration and recovery of

endangered or locally extinct species (Seddon *et al.*, 2007; Richardson *et al.*, 2009). Successful zoological stories include some charismatic species such as the gray wolf (*Canis lupus* L.) in the western Great Lakes region in North America

(Mladenoff *et al.*, 1995) and golden lion tamarins (*Leontopithecus rosalia* L.) in Brazil (Kleiman & Mallinson, 1998). While reintroduction and relocation have also been applied to plants, most efforts have focused on population, community and ecosystem levels (Young, 2000). Range-wide species-level-managed reintroductions of plants are rare, and literature on the special problems of restoring plant species to their former habitat is scant (Falk *et al.*, 1996). As pointed out by Seddon *et al.* (2007), successful reintroduction often involves the use of habitat simulation modelling and requires a well-designed reintroduction plan. In this study, we demonstrate the use of ordination and climate matching techniques to understand the biogeography of chestnut (*Castanea*, Fagaceae) to assist in the range-wide ecological restoration of American chestnut [*C. dentata* (Marsh.) Borkh.] through the incorporation of regionally adapted and blight-resistant genetic materials from Chinese chestnut species.

Castanea is a genus of forest trees with rather exceptional ecological, economic and even cultural importance, primarily because species of this genus regularly bear abundant mast crops of sweet nuts. The chestnut genus includes seven species with their native ranges widely distributed in the northern hemisphere. Four species occur in Asia [*C. mollissima* Bl., *C. henryi* (Skan) Rehder & Wilson, and *C. seguinii* Dode. in China and *C. crenata* Sieb. & Zucc. in Japan] (Wu & Raven, 1999), and one species occurs in Europe (*C. sativa* Mill.) (Conedera *et al.*, 2004). At least two native chestnut species are found in North America (*C. dentata* and *C. pumila* Mill.) (Johnson, 1988). Some studies have separated *C. pumila* into eight or more poorly defined taxa according to growth form, leaf morphology, bur characteristics, habitat and blight susceptibility (Payne *et al.*, 1991). In this study, only *C. pumila sensu stricto* was included in the analysis. The biology and ecology of chestnuts were well studied for species such as *C. mollissima* and *C. sativa* (e.g. Zhang & He, 1999; Conedera *et al.*, 2004), but for other species in the genus, fragmented and sometime anecdotal information was available.

In North America, American chestnut was historically one of the most ecologically and economically important trees in the eastern forests (Lutts, 2004; Davis, 2006), a dominant timber species over much of its range (Paillet, 2002) and the most common tree in portions of its range such as Pennsylvania (Illick, 1919). Chestnut-dominated forests covered 80 million ha of the land from Maine all the way to Mississippi (MacDonald, 1978). During the early 20th century, the non-native chestnut blight fungus [*Cryphonectria parasitica* (Murr.) Barr, formerly *Endothia parasitica*] completely eliminated American chestnut trees from the overstorey (McCormick & Platt, 1980), and by the early 1970s not a hectare of the original forest remained blight-free (Hepting, 1974). All that remains of this once prominent species are root-collar sprouts that grow into small trees between recurrent cycles of blight infection. The loss of this historically dominant and important forest species is one of the most important events in the history of the eastern North American forests.

To begin the process of restoring American chestnut to its former habitats, efforts are currently underway to introduce blight-resistance alleles by hybridizing the species with *C. mollissima* and recovering the American type by backcrossing and recurrent selection (Hebard, 2006). Because the blight fungus is native to Asia, all Asiatic chestnut species carry natural levels of resistance, although the number of genes involved, whether they differ among species, and how they are distributed among linkage groups is largely unknown. It is possible that the other Asiatic species (*C. crenata*, *C. seguinii* and *C. henryi*) carry resistance genes that are not present in *C. mollissima*. If that is the case, intercrosses with those species would be highly useful in backstopping and potentially strengthening the resistance levels achieved in the initial stages of breeding using *C. mollissima* alone. Although the backcross and recurrent selection process is intended to dilute the Asiatic portion of the hybrid genome in favour of the American portion (except for resistance alleles, of course, which are retained through strong selection pressure), some non-American traits will remain depending upon how tightly linked they are to resistance loci. Furthermore, it is unknown to what extent resistance alleles may influence other fitness characteristics (and vice versa) through pleiotropy and epistasis. Unlike other highly bred plants that are intended for propagation under cultivation, a version of American chestnut will ultimately be restored to the wild state to face decades or centuries of unmitigated competition in the natural forest environment. For these reasons, it is very important that the species donating resistance alleles be reasonably well adapted to the environment of American chestnut lest some element of unfitness be inadvertently retained through the breeding process. A particular concern for potential blight-resistant backcross trees is whether they possess sufficient biogeographical adaptability to enable restoration throughout the historical American chestnut range. Hence, a climatic matching of Asiatic species to North America will provide quantitative assessment of the potential climatic fitness of the backcross trees for restoring American chestnut forests. Unlike many reintroduction projects that attempt to re-establish species within their historical ranges through the release of wild or captive-bred individuals following extirpation or extinction in the wild (IUCN, 1998), the restoration of American chestnut involves the incorporation of blight-resistant genetic materials from Asiatic species of the same genus. Therefore, unlike most current reintroduction research that gains its inference mainly from post hoc interpretation of monitoring results (Seddon *et al.*, 2007), a spatially explicit climatic modelling approach is needed to plan for the reintroduction of blight-resistant American chestnut.

The geographic distribution of a species is a function of biotic factors (limits of genetic and physiological adaptation, competitive interactions, etc.), abiotic factors and movement factors (movement and dispersal opportunities and events) (Peterson, 2011). Climatic variables, which constitute a major portion of abiotic factors, are first-order constraints of

species distribution, as evidenced in many range equilibrium studies (e.g. Geber & Eckhart, 2005; Griffith & Watson, 2006). The three continental regions where chestnut species naturally occur, North America, southern and central Europe, and East Asia, are affected by different air masses and have various topographic settings (Fang & Lechowicz, 2006). It is yet to be understood how the resultant climatic gradients in these regions influence the distribution of chestnut species. What are the similarities and dissimilarities of climate variables in forming different distribution patterns for the various chestnut species? Answering these questions will not only fill the knowledge gap in chestnut biogeography, but also provide important references for species conservation and restoration.

In this study, we investigated the general biogeography of seven chestnut species, reconstructed their respective geographic ranges and analysed the corresponding climatic constraints. Through bioclimatic analysis and simulation, we specifically intended to provide a comprehensive study of chestnut species distribution and their association with bioclimatic factors and to further predict the climatic suitability of Chinese species in North America to facilitate the efforts in American chestnut restoration. In addition, we will show that the bioclimatic limits of the modern genus *Castanea* are consistent with our knowledge of the origins and biogeography of the genus in the early Cenozoic and later, indicating that although the genus has migrated extensively, its bioclimatic envelope appears to have remained relatively unchanged for the past tens of millions of years.

METHODS

Chestnut biology and distribution

We reviewed the general biology and biogeography of all seven chestnut species based on published literature and field observations. Spatial distributions of the two American species were based on Little's (1977) maps. The distribution of *C. sativa* was based on the natural and naturalized range composed by members of the EUFORGEN Noble Hardwoods Network (Fernández-López & Alía, 2003). The distribution of *C. crenata* was digitized from a map in *Atlas of the Japanese Flora* (Horikawa, 1972). Distribution maps of the three Chinese species were taken from the *Database of China Woody Plants* (<http://www.ecology.pku.edu.cn/plants/woody/index.asp>), which contains the distribution of all 11,405 woody plants in China. In the database, these county-level resolution distribution maps were compiled using information from all published flora records in China, including *Flora of China* (Wu & Raven, 1999), additional national-level and provincial floras, as well as a great number of regional flora and local checklists of woody species. Distributions of the American species are putative pre-Columbian distributions (Little, 1977). Modern distributions of European and Asian species are presumed to have been influenced by cultivation.

Climatic parameters

Studies have demonstrated that regional-level distributions of plant species are highly correlated with climatic factors (e.g. Fang & Lechowicz, 2006; Rehfeldt *et al.*, 2006). In this study, we adopted a suite of fourteen climatic and bioclimatic variables that likely affect the distribution of chestnut species, akin to an approach used in delineating climatic limits of world-wide beeches (*Fagus* spp.) (Fang & Lechowicz, 2006). These variables offer a comprehensive characterization of climatic factors that impose potential physiological constraints on tree growth and regeneration. Monthly mean temperature, monthly precipitation and geographic location data are major inputs for deriving these biologically related variables. For convenience in the analysis, these variables are grouped into the following three categories: thermal variables, moisture variables and variability indices.

Thermal variables

Temperature plays a fundamental role in controlling the natural range of a tree species (Woodward, 1987). In particular, growing season warmth and winter coldness are two direct limiting factors for plant growth (Fang & Lechowicz, 2006). Here, the accumulation of growing season warmth is represented with the Kira's warmth index (Kira, 1991) and Holdridge's annual biotemperature (Holdridge, 1947):

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

$$ABT = \frac{\sum T}{12} \text{ (for months in which } T > 0^{\circ}\text{C),} \\ \text{in units of degree months}$$

where WI is the warmth index, ABT is the annual biotemperature, and T is the monthly mean temperature over the year. Winter coldness, which mainly affects the northern boundaries of the distribution of tree species, is described with the mean temperature for the coldest month (MTCM) and Kira's coldness index (Kira, 1991):

$$CI = \sum (T - 5) \text{ (for months in which } T < 5^{\circ}\text{C),} \\ \text{in units of degree months}$$

where CI is the coldness index. In addition, annual mean temperature (AMT) and mean temperature for the warmest month (MTWM) were included as general thermal variables.

Moisture variables

Moisture availability, another primary limiting factor for species distribution, was also represented with several variables. Annual precipitation (AP) is a first overall measure of moisture availability. In addition, potential evapotranspiration (PET),

which is primarily a function of temperature, was produced to quantify potential moisture loss to the atmosphere. PET was estimated using the Thornthwaite (1948) method:

$$PET = \sum 16 \times (10 \times T/I_h)^a \text{ (for months in which } T > 0^\circ\text{C)}$$

where I_h is the monthly heat index and a is an empirical exponent based on I_h as defined below

$$I_h = \sum (T/5)^{1.514} \text{ (for months in which } T > 0^\circ\text{C)}$$

$$a = 6.75 \times 10^{-7} \times I_h^3 - 7.71 \times 10^{-5} \times I_h^2 + 1.79 \times 10^{-2} \times I_h + 0.49$$

With both precipitation and PET data available, one additional variable, moisture index (Im), can be calculated by accounting for the surplus and deficit conditions in water budget:

$$\text{Surplus} = \sum (P - PET) \text{ (for months in which } P \geq PET)$$

$$\text{Deficit} = \sum (P - PET) \text{ (for months in which } P < PET)$$

$$Im = (100 \times \text{Surplus} + 60 \times \text{Deficit})/PET$$

where P is the monthly precipitation. The sums are given for 12 months. Another combined index of temperature and moisture availability, the Ellenberg quotient (EQ) (Ellenberg, 1978), was useful for temperate tree climate delineation (Jahn, 1991) and was computed as:

$$EQ = \frac{MTWM}{AP} \times 1000$$

Finally, precipitation for the wettest month (PWM) and precipitation for the driest month (PDM) were included as general indicators of precipitation regimes.

Variability indices

First, annual climatic variability is directly represented with the annual range of monthly mean temperatures (ART), which is the difference of maximum and minimum temperatures over the year. Further, the degree of continentality is quantified with Gorczynski's continentality index (Gorczynski, 1922):

$$K = (1.7 \times \frac{ART}{\sin(Lat)}) - 20.4$$

where K is the continentality index, and Lat is the latitude in decimal degree.

Analysing climatic limits and spaces

Meteorological records since 1950 provided reliable data for characterizing Earth's climate. To derive the climatic variables described earlier, a global climate dataset based on observations during a period of 1950–2000 was used (WorldClim:

<http://www.worldclim.org/>). In this dataset, monthly temperature and precipitation data were compiled and interpolated for all land regions across the world (Hijmans *et al.*, 2005). The resultant continuous climate data layers were available in raster format with a spatial resolution as fine as 30 arc-seconds (*c.* 1 km). The dataset also provides a suite of additional derived variables, including AMT, MTWM, MTCM, ART, AP, PWM and PDM. We calculated the additional bioclimatic variables (WI, CI, ABT, K, PET, Im and EQ) needed for the analysis.

The climatic information was extracted for the southern and northern limits, as well as the entire distribution range for each chestnut species. In geoprocessing, range polygons of chestnut distribution were superimposed on climatic data layers. We manually placed 100 sample points along each range boundary (either south or north). Climatic data were then extracted for the sample points representing limiting climatic conditions on the range boundaries of chestnut species. In addition, a comprehensive sampling was conducted within the entire distribution range for each chestnut species. For sampling an entire range, a systematic grid scheme with an interval of 15 arc-min between points along both latitudinal and longitudinal dimensions was employed. Layer manipulation and sampling were performed using ArcGIS (ESRI, Redlands, CA, USA) and XTools Pro (Data East, LLC, Novosibirsk, Russia).

Data analysis including the derivation of additional variables from the existing extracted variables was carried out using R (R Development Core Team). For the northern and southern limits, averaged values with standard errors were computed for all climatic variables by species. Further, a principal component analysis (PCA) was applied to the suite of climatic variables to generate integrated climatic gradients. All variable values were first standardized using the formula: (value – mean)/standard deviation. This was performed for each species individually, and for the entire genus combined, with respect to the northern distribution limits, southern distribution limits and complete ranges of species (yielding a total of 24 datasets). Each dataset was tested for multivariate normality and linearity using R commands 'mvnorm.etest' (R library 'energy') and 'raintest' (R library 'lmtest'), respectively. Two-thirds of our datasets (16/24) were normally distributed ($\alpha = 0.01$), and one-third (8/24) passed the linearity test ($\alpha = 0.10$). These assumptions are not critical for interpreting results for descriptive purposes (Jolliffe, 1986), which is the case here. The PCA analysis was performed using R command 'pca' (R library 'labdsv'), and the first two principal components (PC1-2) were employed to generate two-dimensional ordination plots showing climatic spaces of chestnut species. When generating ellipses for data distribution, we employed 'dataEllipse' command in R library 'car'.

Climatic matching

Climatic envelope matching was performed using Maxent modelling (Phillips *et al.*, 2006; Phillips & Dudik, 2008). The potential distributions of three Chinese chestnut species

(*C. mollissima*, *C. seguinii* and *C. henryi*) in North America were predicted by that method. Through iterative testing of different variable combinations for model inputs, climatic

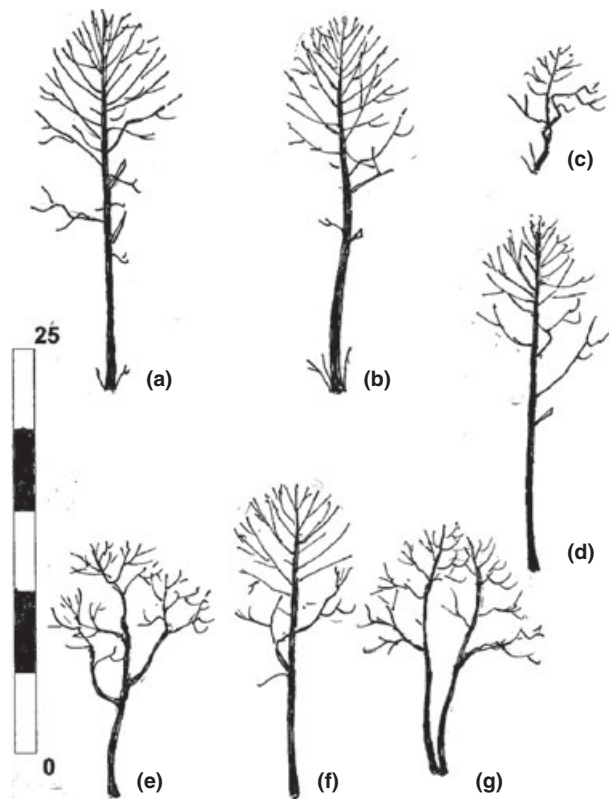


Figure 1 Chestnut (*Castanea* spp.) tree form and size based on field specimens: (a) *C. dentata*, West Salem naturalized stand, Wisconsin, USA (60 cm diameter and 25 m height); (b) *C. sativa*, Caucasus Biosphere Preserve, Russia (70 cm diameter and 25 m height); (c) *C. pumila*, Oconee National Forest, Georgia, USA (12 cm diameter and 7 m height); (d) *C. henryi*, Dalaoling Forest Preserve, Hubei, China (40 cm diameter and 25 m height); (e) *C. crenata*, out-planting in forest setting, Connecticut, USA (40 cm diameter and 18 m height); (f) *C. seguinii*, Dalaoling Forest Preserve, Hubei, China (40 cm diameter and 25 m height); (g) *C. mollissima*, Dalaoling Forest Preserve, Hubei, China (25 cm diameter and 15 m height).

variables that had the largest loadings on the first two principal components in PCA for southern/northern limits and complete range were selected as predictors in models. The Maxent model generates threshold-independent, continuous output for climatic suitability range (0–1). We then evaluated the model performance using the receiver operating characteristic (ROC) analysis (Zweig & Campbell, 1993) with the area under ROC curve (AUC) index (Fielding & Bell, 1997).

To estimate thresholds for thematic approximation of different climatic suitability zones, we employed a multi-threshold method utilizing the sum of sensitivity and specificity (SSS) index. Sensitivity indicates the portion of correctly predicted presence, and the specificity indicates the portion of correctly predicted absence (Jimenez-Valverde & Lobo, 2007). The sum of these two portions provides an index to evaluate the overall accuracy of model predictions. We experimented with categorizing continuous Maxent outputs (0–1) using a sequence of testing thresholds with 0.01 intervals. A particular threshold that yields maximum SSS value is considered the central threshold that provides an optimum dichotomous presentation of the prediction. Further, we calculated moving standard deviations (window size 3 – standard deviation of SSS values at a given threshold and its neighbouring thresholds at each side) to quantify the changes of SSS values over the spectrum of testing thresholds. We then visually identified points where apparent increases of standard deviation occurred on both sides of the central threshold. These points were used as boundary thresholds that allowed further stratification of the results into the following categories: unsuitable (below lower boundary threshold), low suitability (from lower boundary threshold to the central threshold), medium suitability (from central threshold to upper boundary threshold) and high suitability (above the upper boundary threshold).

RESULTS

Chestnut general biology and geographic distribution

The growth habit of chestnut species varies from shrub-like to large, forest canopy-dominant trees (Fig. 1, Table 1). Specifically, *C. dentata* reached 30–35 m in height and several metres

Table 1 General biological traits of chestnuts (*Castanea* spp.).

<i>Castanea</i> species	Flower	Nut size (cm)	Nut/burr	Max height (m)	Blight resistance	References
<i>C. dentata</i> (Marsh.) Borkh.	June–July	1.8–2.5	1–3	30–35	No	FNA (2011)*
<i>C. pumila</i> var. <i>pumila</i> Mill.	May–June	0.7–2.1	1	5–8	Low	FNA (2011), Payne <i>et al.</i> (1991)
<i>C. sativa</i> Mill.	May–July	2.5–3.5	1–3	30–40	Low	Fernández-López & Alía (2003) Groom (1907)
<i>C. crenata</i> Sieb. & Zucc.	April–June	2–3	2–3	15–20	Yes	Wu & Raven (1999) Sumida <i>et al.</i> (2002)
<i>C. mollissima</i> Bl.	April–June	2–3	2–3	20–25	Yes	Wu & Raven (1999), Field observations
<i>C. henryi</i> (Skan.) Rehder & Wilson	May–July	1.5–2	1	30–35	Yes	Wu & Raven (1999), Field observations
<i>C. seguinii</i> Dode.	May–July	1.5–2	2–3	20–30	Yes	Wu & Raven (1999), Field observations

*Flora of North America.

in diameter before the invasion of chestnut blight, but survives mainly as understory sprouts from the base of blight-killed trunks (Paillet, 2002). *Castanea pumila* var. *pumila* is a large, spreading, multi-stemmed shrub, 2–5 m tall, but occasionally single-stemmed and as tall as 15 m (Johnson, 1988). *Castanea sativa* can reach a height of 30–40 m in forest conditions (Pridnya *et al.*, 1996) but rarely exceeds 18 m when grown for nuts (Fernández-López & Alía, 2003). *Castanea seguinii* is often described in the literature as a shrubby, small-sized tree (Wu & Raven, 1999). Yet in our field observation in forests in central China, *C. seguinii* was observed reaching 30 m in height (Fig. 1f). In addition, we have observed *C. mollissima* reaching 20–25 m in forest conditions (Fig. 1g), although it is typically much shorter and round-topped when observed in the usual orchard environment. Similar to *C. mollissima*, *C. crenata* is often observed as a dwarf rarely reaching 15 m in height (Wu & Raven, 1999), but can grow up to 20 m in forest conditions (Sumida *et al.*, 2002). As the tallest one among the four Asian species, *C. henryi* can grow up to 30–35 m in height based on field observations.

All seven chestnut species are deciduous and produce both male and female flowers on the same tree, although cross-

pollination is required to set seed (Bounous & Marinoni, 2004). They blossom in late spring to early summer, later than almost all of their forest associates (Table 1). All chestnuts produce edible nuts which is one of the major reasons that they are economically and culturally important. Both *C. pumila* var. *pumila* and *C. henryi* only bear one nut per cupule, and their nuts are smaller in comparison with the other species. The other three Asian species all bear 2–3 nuts per cupule, with *C. seguinii* having smaller nuts compared with others. Both *C. dentata* and *C. sativa* bear 1–3 nuts per cupule, and the latter has the largest nuts on average compared with those of other species. To different degrees, all American and European chestnut species are susceptible to chestnut blight, while all Asian species are resistant (but not immune) to the blight (Bounous & Marinoni, 2004).

All seven chestnut species are broadly distributed in a geographic sense, with *C. mollissima* having the widest latitudinal distribution and *C. sativa* the widest longitudinal distribution (Fig. 2). Both of these species have a long history of cultivation, and their ranges and local genotypes may have been influenced by a long history of human manipulation. Before the blight epidemic, *C. dentata* was distributed from 31

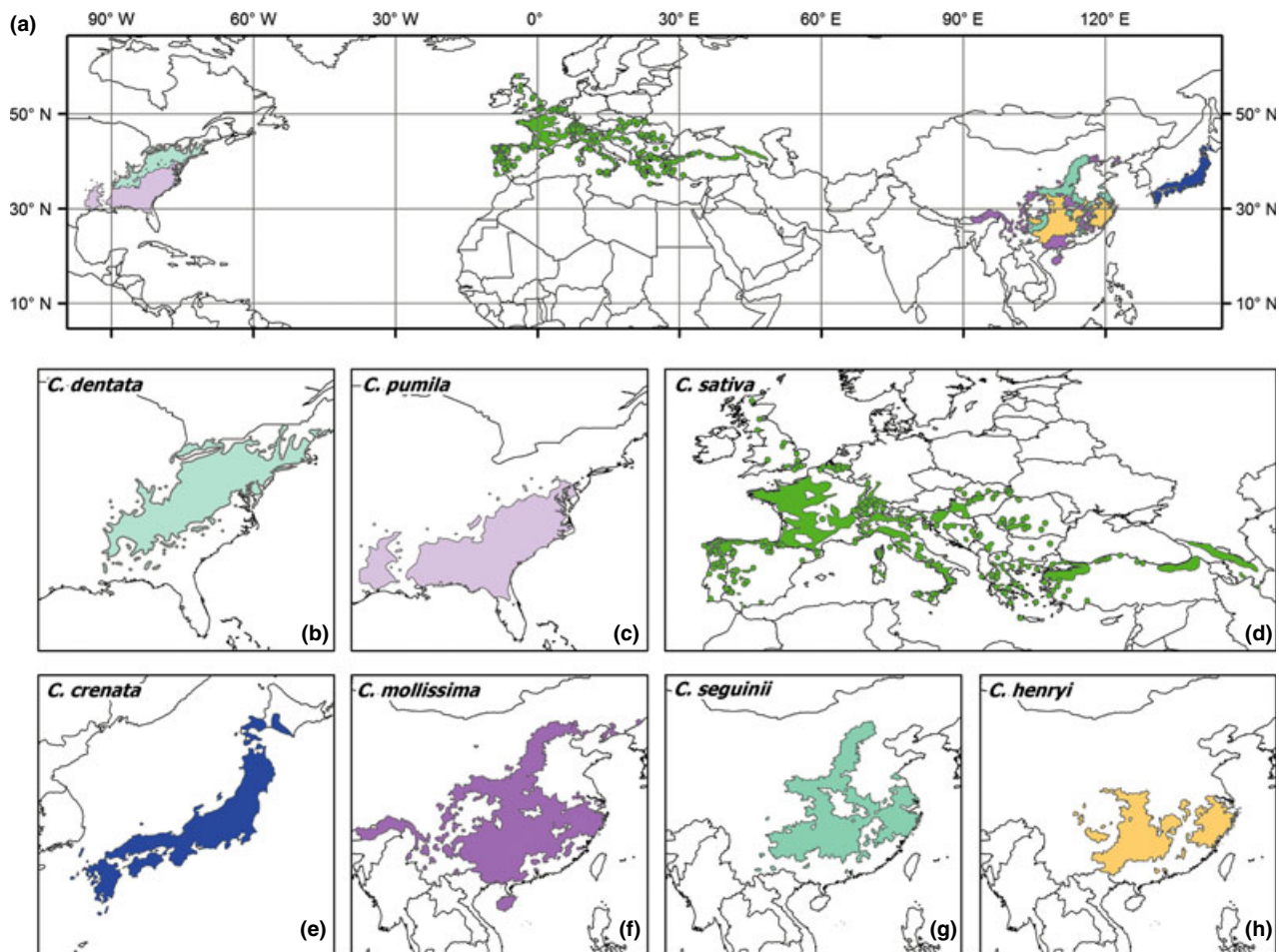


Figure 2 Distribution of major chestnuts (*Castanea* spp.) across the world. The distribution of *C. dentata* (b) is the pre-blight natural range based on Little (1971); distribution of *C. sativa* (d) is a combination of natural and naturalized range (Fernández-López & Alía, 2003); distributions of the four Asian species (e–h) reflect the anthropogenically influenced natural and naturalized ranges.

to 45° N in the forests of the Appalachian Mountains, Allegheny Plateau and southern New England (Fig. 2b) (Little, 1977; Smith, 2000). *Castanea pumila* var. *pumila* is mainly distributed in the south-eastern USA from southern New Jersey and Pennsylvania to Florida and Texas (Fig. 2c) (Little, 1977). The European chestnut currently has a wide range of distribution from England and Belgium south to the Greek island of Crete and from the Atlantic Ocean east to the Caspian Sea (Fernández-López & Alía, 2003), a latitudinal expansion of 58° (9° W to 49° E) (Fig. 2d). The current natural and naturalized distribution is believed to be the result of natural dispersion from six macro refugium areas (Krebs *et al.*, 2004) and active human cultivation (Conedera *et al.*, 2004). The distribution of *C. sativa* was likely influenced by the presence of an east–west mountain range migration barrier (Alps and Caucasus), whereas American and Chinese species could respond to the climatic extremes of the Pleistocene by migration along mountains orientated in a north–south direction. Distribution of *C. crenata* is confined by the archipelago of Japan (Fig. 2e). Its northern limit reaches to the southern portion of the Hokkaido region (44° N). Among the three Chinese species, *C. mollissima* has the widest distribution and *C. henryi* the narrowest (Figs. 2f–g). The northern range for *C. mollissima* reaches 41° N following the mountain ranges of Yanshan, Taihangshan and Qinling mountains. Its southern range extends to 18° N in the Wuzhi Mountains of Hainan Island (Fig. 2f). Because this species is widely cultivated, it is likely that the current distribution reflects anthropogenic influences. *Castanea seguinii* has a northern distribution similar to *C. mollissima* but with higher latitude for its southern limit (23° N) (Fig. 2g). Its southern range is confined by the Wuyi and Nanling Mountain ranges and its western range by the Sichuan Basin. The distribution of *C. henryi* ranges from 22° N in the south to 33° N in the north, reaching the southern aspect of the Qinling Mountains (Fig. 2h).

Overall climatic limits of chestnut distribution

We calculated climatic limits for chestnut species at their southern and northern distribution boundaries. The statistics of climatic parameters provided explicit windows in which favourable conditions for chestnut growth are found (Table S1). From north to south, the overall thermal range for all chestnut species is from 5.9 to 19.7 °C for averaged AMT, and from 17.5 to 27.4 °C for MTWM. Growing season warmth requirements are from 56.6 to 176.8 degree months for WI, and from 7.7 to 19.7 °C for ABT. Cold hardiness limits for all species are from –45.8 to –5.2 degree months for Kira's Coldness Index (CI) and from –7.7 to 2.2 °C for MTCM. The limits of moisture availability are between 516.5 and 1305.1 mm for AP, and from –1.2 to 183.6 for moisture index (Im).

Distributions of different chestnut species fall into warm-temperate and subtropical regions in the northern hemisphere, as defined by the Köppen-Geiger climate classification system

(Kottek *et al.*, 2006). Both *C. pumila* var. *pumila* and *C. henryi* occur in areas that have hot summers with MTWM above 22 °C and AMT above 10 °C. These criteria match those that specify a mesothermal humid subtropical climate. The southern climatic limits of *C. dentata*, *C. mollissima* and *C. seguinii* also meet these criteria. As influenced by altitudinal effects in the Appalachian Mountains, the range of *C. dentata* also covers a cooler marine coast climate (Rohli & Vega, 2008). For the northern limits of these three species, MTWM are all above 10 °C (and above 22 °C for *C. mollissima* and *C. seguinii*) and their MTCM are below –3 °C, hence representing a microthermal hot summer continental climate for *C. mollissima* and *C. seguinii*, and both hot summer and warm summer continental climates for *C. dentata*. *Castanea dentata*'s climate extends further into colder regions in the north. *Castanea crenata* found on the Japanese archipelago spans the humid subtropical climate in the south, and warm summer (mixed with hot summer) continental climate in the north, with the most ample annual rainfall (AP: from 1305.1 to 2461.6 mm, from south to north) of all the chestnut-growing regions. European chestnut generally falls within the temperate/mesothermal climate group with MTWM above 10 °C and MTCM between –3 and 18 °C for both southern and northern limits. According to the Köppen-Geiger climate map (Kottek *et al.*, 2006), distribution of *C. sativa* encompasses a unique assemblage of Mediterranean, humid subtropical and maritime temperate climates, which are difficult to demarcate from the climatic parameter statistics alone. Besides, for both *C. sativa* and *C. crenata*, averaged continentality index (*K*) values are relatively small (49.9 and 65.0, respectively), indicating strong maritime climate influences.

Climatic factors influencing chestnut distribution

The aggregated effects of 14 climatic variables in controlling chestnut species distribution were summarized from PCA results (Tables 2 and 3). For the combined distribution limits and ranges of all chestnut species, the first two principal components accounting for the largest amount of variability in the dataset show strong loadings on temperature-based (PC1) and moisture-based (PC2) variables (Table 2). The first principal component (PC1) was highly correlated with thermal variables, especially AMT, WI and ABT. The second principal component (PC2) was primarily correlated with moisture variables, especially AP, Im and EQ. Therefore, PC1 and PC2 strongly represented the thermal gradient and the moisture gradient, respectively. The third principal component (PC3) was highly correlated with the climatic variability indices (ART and *K*). For all PCA cases, PC1 and PC2 cumulatively accounted for at least 70% of the total variance (Table 3). With PC3 included, the first three principal components explained over 84% of total variance.

Principal component analysis for each chestnut species revealed more detailed patterns of climatic controls (Table S2). Across the different species, PC1 was predominantly driven by thermal variables, for both southern and northern limits, as

Table 2 Correlations of climatic variables with the first three principal components (PC1-3) from a principal component analysis of the distribution limits and complete ranges for world chestnuts (*Castanea* spp.)

Climate variable	Southern limit			Northern limit			Complete range		
	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3
AMT	0.98	-0.19	0.03	0.98	0.20	-0.02	0.98	-0.18	0.07
WI	0.97	-0.20	0.04	0.97	-0.01	0.21	0.96	-0.24	-0.02
CI	0.54	0.00	-0.08	0.82	0.45	-0.30	0.80	0.06	0.39
ABT	0.98	-0.20	0.03	0.99	0.08	0.11	0.97	-0.21	0.03
MTWM	0.88	0.02	0.36	0.87	-0.17	0.40	0.82	-0.36	-0.33
MTCM	0.88	-0.32	-0.28	0.78	0.53	-0.31	0.90	0.06	0.41
ART	-0.27	0.17	0.92	-0.18	-0.73	0.57	-0.36	-0.42	-0.77
K	0.55	0.02	0.55	0.27	-0.67	0.65	0.37	-0.41	-0.75
AP	0.46	0.87	-0.11	-0.11	0.82	0.55	0.70	0.61	-0.35
PET	0.94	-0.25	0.00	0.99	0.08	0.10	0.95	-0.23	0.01
Im	-0.01	0.97	-0.13	-0.57	0.65	0.45	0.04	0.88	-0.41
EQ	-0.39	-0.78	0.09	0.31	-0.87	-0.23	-0.35	-0.87	-0.01
PWM	0.49	0.69	-0.39	0.16	0.15	0.78	0.66	0.28	-0.31
PDM	0.15	0.55	0.56	-0.31	0.77	0.19	0.14	0.53	-0.25

AMT, annual mean temperature; WI, warmth index; CI, coldness index; ABT, annual biotemperature; MTWM, mean temperature for the warmest month; MTCM, mean temperature for the coldest month; ART, annual range of mean temperature; K, continentality index; AP, annual precipitation; PET, annual potential evapotranspiration; Im, moisture index; EQ, Ellenberg quotient; PWM, precipitation for the wettest month; PDM, precipitation for the driest month.

Table 3 Proportion (%) of cumulative variance explained by the first three principal components (PC1-3) in a principal components analysis of the distribution limits and complete ranges for world chestnuts (*Castanea* spp.).

<i>Castanea</i> species	Southern limit			Northern limit			Complete range		
	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3
<i>C. crenata</i>	44.2	77.5	91.3	69.4	91.4	97.6	50.8	75.5	93.1
<i>C. dentata</i>	58.7	82.6	91.9	75.2	87.7	97.3	61.4	84.1	95.8
<i>C. henryi</i>	62.4	79.5	88.9	60.0	87.7	96.8	48.4	74.2	91.6
<i>C. mollissima</i>	44.8	71.0	91.2	50.3	76.5	94.4	58.8	80.2	91.6
<i>C. pumila</i> var. <i>pumila</i>	64.0	82.6	93.6	57.9	92.7	96.4	54.5	76.6	92.9
<i>C. sativa</i>	53.9	84.0	92.9	58.7	86.0	95.4	54.0	79.4	91.9
<i>C. seguinii</i>	44.5	84.1	96.1	57.7	87.7	93.7	65.1	85.2	95.0
All species	47.0	71.2	84.6	46.8	75.6	92.4	51.2	72.1	86.7

well as for the complete range. However, while PC2 was strongly influenced by moisture variables in most cases, exceptions existed to imply additional climatic factors controlling distribution of different chestnut species. For example, at the northern limit of the *C. crenata* distribution, climatic variability indices (ART and K) had the largest loadings on PC2. This was also the case for the *C. henryi* southern limit, the *C. seguinii* complete range and the *C. mollissima* complete range. For *C. sativa*, PC2 loadings at the southern and northern limits, as well as for the complete range, all had largest loadings on ART and K, but with relatively large loadings on moisture-based variables as well.

Interspecific climatic space analysis

The variation and resemblance of climatic limits for different chestnut species were investigated further using two-dimen-

sional climatic spaces specified by the first two principal components (Figs 3–5). Depicted in this way, climatic spaces represent the dual influences of thermal and moisture gradients on the distribution of chestnut species and facilitate species comparisons with respect to climatic requirements. At the southern limits of chestnut distribution (Fig. 3), *C. mollissima*, *C. henryi*, *C. pumila* var. *pumila* and *C. seguinii* are more situated towards warmer climates than other species, with the latter three completely encompassed by that of *C. mollissima*. *Castanea dentata* has a relatively small climatic space that overlaps with that of *C. mollissima*; yet is centered more towards the colder and wetter domain. *Castanea crenata* occupied a distinct space characterized by higher precipitation as indicated by the climatic parameter statistics. The climatic space of the southern limit for *C. sativa* appeared to be distributed within a colder and drier climate than other species.

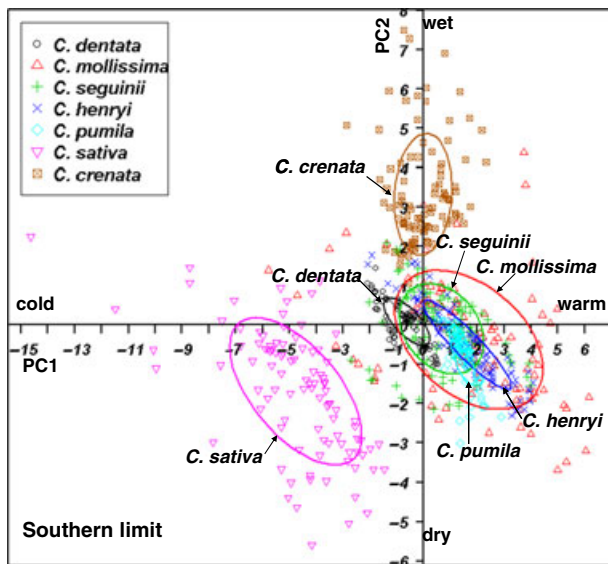


Figure 3 Climatic spaces for chestnuts (*Castanea* spp.) at their southern distribution limits. The first two principal components (PC1-2) are plotted. The first axis indicates a gradient in thermal climate and the second a moisture gradient in the overall distribution of world chestnut species. The 95% ellipse is drawn for major chestnut species to show primary ranges of their southern limits.

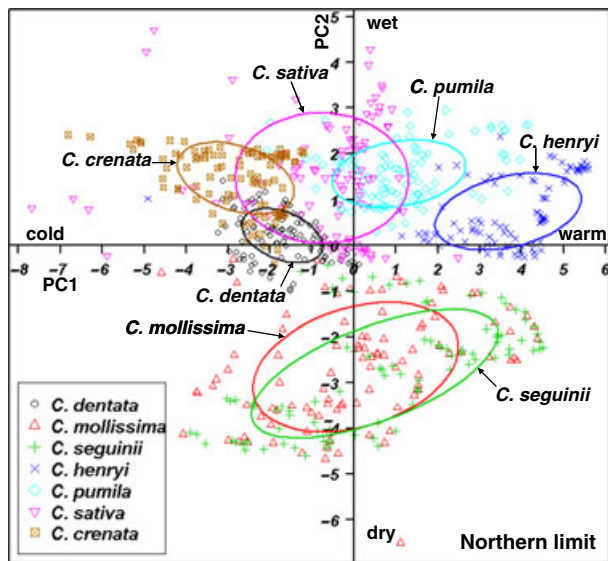


Figure 4 Climatic spaces for chestnuts (*Castanea* spp.) at their northern distribution limits. The first two principal components (PC1-2) are plotted. The first axis indicates a gradient in thermal climate and the second a moisture gradient in the overall distribution of world chestnut species. The 50% ellipse is drawn for major chestnut species to show primary ranges of their northern limits.

The northern limits of the chestnut species exhibited quite different distribution patterns than the southern limits. *Castanea dentata*, *C. crenata* and *C. pumila* var. *pumila* all overlap with *C. sativa* that occupies a relatively larger climatic

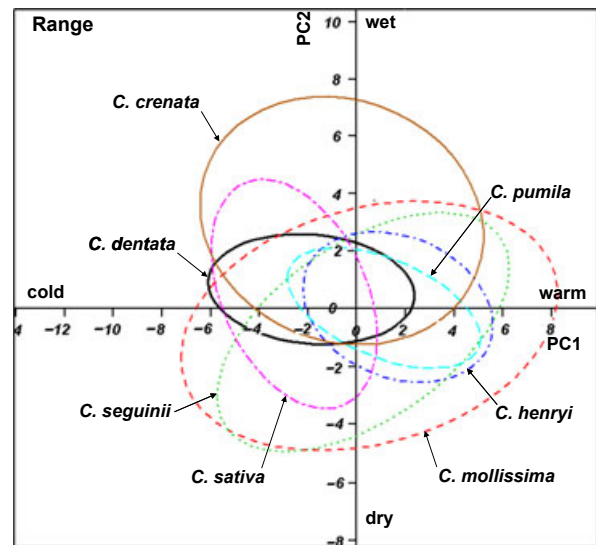


Figure 5 Climatic spaces for chestnuts (*Castanea* spp.) across their full global distribution. The first two principal components (PC1-2) are plotted. The first axis indicates a gradient in thermal climate and the second a moisture gradient in the overall distribution of world chestnut species. The 95% ellipse is drawn for major chestnut species to show their primary overall distribution ranges.

space. While *C. sativa*'s northern limit is mostly located in wetter and colder climate, *C. dentata* is primarily in a colder climate, *C. crenata* in the even colder and wetter domain, and *C. pumila* var. *pumila* in relatively warmer climate. The northern limit of *C. henryi* appears to have the warmest climatic space setting. *Castanea mollissima* and *C. seguinii* both appear to have relatively large climatic space with broader thermal gradient span and are located within much drier climates than those inhabited by the other species.

Climatic spaces for the complete geographic ranges of all chestnut species better reveal the overall similarities and differences among species (Fig. 5, Table 4). *Castanea mollissima* has the largest climatic space, which completely encompasses the climatic spaces of *C. henryi* and *C. pumila* var. *pumila* and also overlaps with the majority (99%) of *C. seguinii*'s space. *Castanea sativa* largely overlaps (79%) with the climatic space of *C. mollissima*, but extends farther into colder and wetter climate. *Castanea dentata* also extends into a colder and wetter domain, but one that is drier than that of *C. sativa*. *Castanea crenata* also has fairly large climatic space but overlaps the least (50%) with *C. mollissima*'s climatic space among all the other species. The distribution of *C. crenata*'s climatic space is significantly towards wetter and colder climatic domains in comparison with the climatic spaces of all the other *Castanea* species.

Intercontinental climatic matching

We predicted the distributions of three Chinese chestnut species in North America using Maxent models driven by the

Table 4 Percentage of climatic space overlap among world chestnuts (*Castanea* spp.) (also see Fig. 5); percentages were calculated based on overlapping areas between each pair of species divided by the area occupied by the climatic space area occupied by each species listed in the species column (e.g. the overlapping area between *C. crenata* and *C. dentata* occupies 88% of *C. dentata*'s climatic space and 29% of *C. crenata*'s climatic space).

<i>Castanea</i> species	Climatic space overlap (%)						
	<i>C. crenata</i>	<i>C. dentata</i>	<i>C. henryi</i>	<i>C. mollissima</i>	<i>C. pumila</i> var. <i>pumila</i>	<i>C. sativa</i>	<i>C. seguinii</i>
<i>C. crenata</i>		29	27	50	22	34	37
<i>C. dentata</i>	88		50	96	52	82	67
<i>C. henryi</i>	68	40		100	68	31	97
<i>C. mollissima</i>	38	24	31		22	31	65
<i>C. pumila</i> var. <i>Pumila</i>	75	58	95	100		42	97
<i>C. sativa</i>	68	53	25	79	24		58
<i>C. seguinii</i>	44	26	46	99	33	35	

Table 5 Summary of Maxent models for environmental matching of three Chinese chestnut (*Castanea*) species from East Asia to North America.

<i>Castanea</i> species	Model contribution of environmental predictors (%)						
	AMT	WI	ABT	AP	Im	EQ	Model AUC
<i>C. mollissima</i>	70.3	5.0	0.0	15.0	1.9	7.8	0.883
<i>C. seguinii</i>	68.2	10.2	0.1	12.3	2.7	6.4	0.921
<i>C. henryi</i>	40.9	0.9	0.1	50.5	0.6	7.1	0.947

AMT, annual mean temperature; WI, warmth index; ABT, annual biotemperature; AP, annual precipitation; Im, moisture index; EQ, Ellenberg quotient; AUC, area under curve.

climatic variables that most strongly contributed to the thermal and moisture gradients (Tables 2 and 5). As discussed earlier, these variables included AMT, WI and ABT for the thermal gradient, and AP, Im and EQ for the moisture gradient. Maxent model outputs showed that these predictors contributed quite differently to the predictions. Distributions of *C. mollissima* and *C. seguinii* were most responsive to AMT and AP, with AMT contributing approximately 70% to the models. *Castanea henryi* was more responsive to precipitation than to temperature, with over 50% contribution from AP, and only about 40% from AMT. The rest of the variables used had relatively small contribution to the models. In all cases, ABT appeared to have the least impact on models. All three models had AUC measures over 0.88, suggesting fairly good performance (Table 5).

Predictions in continuous data format from Maxent models were further classified into climatic suitability levels as delineated using the sum of SSS index threshold approach (Fig. 1s). Corresponding to the maximum values of SSS index, central thresholds were determined to be 0.25, 0.18 and 0.17 for *C. seguinii*, *C. henryi* and *C. mollissima*, respectively. For all three species, fluctuations of SSS index curves demonstrated identifiable 'plateaus' around the central thresholds, implying that the threshold could well be a value range rather than a single point. Accordingly, boundary thresholds where significant changes occurred were determined using the moving standard deviation analysis. This approach allowed us to minimize uncertainties by using a single, clear-cut threshold

for climatic suitability estimation. Based on this classification system, we delineated zones of 'unsuitable', 'low', 'medium' and 'high' climatic suitability for the three Chinese chestnut species with respect to the climate of eastern North America (Fig. 6). The predicted *C. mollissima* range covered a large part of eastern North America, and 93% of the historical range of *C. dentata* is predicted to have medium and high climate suitability for *C. mollissima* (Fig. 6a). Our prediction for *C. seguinii* demonstrated similar patterns, but its geographic coverage was somewhat less extensive than *C. mollissima*, and 83% of the historical range of *C. dentata* is predicted to have medium and high climate suitability for *C. seguinii* (Fig. 6b). The predicted habitat for *C. henryi* in North America is mostly restricted to the South and Southeast and falls short of covering the northern third or so of the historical range of *C. dentata*'s (Fig. 6c).

DISCUSSION

The general biological traits of the seven chestnut species are mostly very similar. In forest conditions, *C. dentata* (historically), *C. henryi*, *C. seguinii*, *C. sativa* and *C. mollissima* have similar growth forms and occupy upper canopy positions in tall, closed forests. All chestnut species appear to bloom unusually late (typically from late spring to early summer) compared with their forest associates, which is presumably a strategy to circumvent spring frost and probably contributes to the absence of pronounced extremes in annual seed

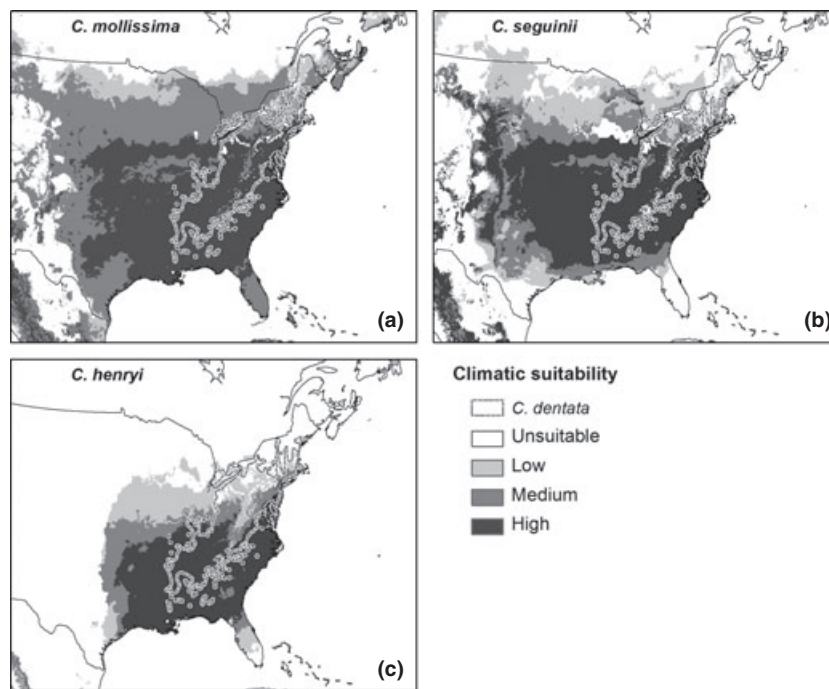


Figure 6 Predicted distribution (climatic suitability zones) of Chinese chestnut species: (a) *Castanea mollissima*, (b) *C. seguinii* and (c) *C. henryi* in eastern North America. The historical range of *C. dentata* is shown on all panels.

production, as tend to characterize other members of the Fagaceae (Bounous & Marinoni, 2004). Most chestnut species yield multiple nuts per cupule, except for *C. henryi* and *C. pumila* var. *pumila*, which produce single-nut cupules. In terms of general biological traits, *C. pumila* var. *pumila* is the least similar to other species in this genus, as represented by its prevalent shrub-like growth form (Payne *et al.*, 1991).

Chestnut species are also similar in terms of their geographic distributions and climatic limits. The latitudinal spans and land-ocean configurations are comparable for the chestnut ranges in East Asia, eastern North America and Europe. In general, chestnut trees grow in relatively mild and moist regions where temperate forests are found. As reflected by the overlapping patterns in the climatic space, chestnut distributions respond to climate-imposed thermal and moisture gradients regardless of species. At its southern limit, the climatic space of *C. sativa* lies in a colder and drier domain, which is likely a result of higher latitude (as restricted by the Mediterranean Sea) and subtropical high pressure cells (which usually reduce rainfall in the summer). Also, the southern limit of *C. crenata* has a distinctly wetter climate than that of other species, reflecting the uniquely abundant precipitation on Japanese islands. The rest of the chestnut species in East Asia and North America have significantly overlapping climatic spaces. At the northern limit, two Chinese species (*C. mollissima* and *C. seguinii*) appear to be adapted to a much drier climate than the others. All species spread over a relatively wide thermal gradient, with *C. crenata* showing the greatest cold hardiness and *C. henryi* adapting to the warmest climate.

Climatic spaces for the complete chestnut species ranges revealed great overlap among all species. *Castanea mollissima* possesses the most extensive coverage of climatic gradients, which encompasses virtually all of the climatic space of every other species except *C. sativa* and *C. crenata*. The less continental climates of Japan and Europe were reflected in the large coverage of *C. crenata* and *C. sativa* in the wetter and colder domains beyond those of other species. The strong similarities in climatic space between Chinese species and American species permitted us to successfully project the climatic envelopes of all three Chinese species onto potential distributions within eastern North America.

The similarities observed among the seven chestnut species are not surprising. Chestnut is consistently and unambiguously present in the fossil record in America, Europe and Asia starting in the Eocene (ca. 50 Ma) and may extend even farther back in time according to a few fragmentary and ambiguous references (Graham, 1999; Lang *et al.*, 2007). North America, Europe and Asia were connected by land in the early Tertiary, and early studies (e.g. Gardner & Ettingshausen, 1879) suggested that there was a continuous, temperate Arcto-Tertiary Flora across this landscape in the higher latitudes. Land connections between Asia and North America continued until about 3 Ma (and were renewed during the Pleistocene), but the plant migration route between North America and Europe via a North Atlantic land bridge (NALB) was effectively severed by the Miocene as a result of continued northward rifting and colder temperatures (Graham, 1999; Manchester, 1999). It is now recognized that orbital insolation cycles have always been forcing climate change and that post-Eocene

temperate forests were probably subjected to a continuing sequence of disruptions. The Arcto-Tertiary Flora concept is now interpreted as an over-simplification (Wolfe, 1994; Graham, 1999). Phylogenetic analysis of chloroplast DNA sequence data indicates an origin for chestnut in eastern Asia and migration to North America from Europe via the NALB (Lang *et al.*, 2007). Molecular evidence (Lang *et al.*, 2007) places the earliest phylogenetic divergence of extant taxa in the early Eocene and a split between European and American chestnut in the late Eocene (39.14 Ma). This estimate of the timing of the European-American split is consistent with our current understanding of the availability of the NALB for the exchange of warm- and cool-temperate floristic elements (Graham, 1999; Lang *et al.*, 2007).

The Eocene climate was much warmer than today's, but the fossil occurrence of chestnut in mid- to high latitudes suggests climatic space for the genus similar to that of today. For example, chestnut pollen in Eocene sediments from Ellesmere Island (latitude 81°30') is found with an assemblage of conifer and hardwood genera suggestive of a modern Lake States (USA) or Appalachian highlands forest (Graham, 1999). Basinger *et al.* (1994) estimated the AMT in this ancient environment to be 12–15 °C, which is within the range of all modern species, though near the apparent cold limit for *C. henryi* and the warm limit for *C. sativa* (Table S1). In the somewhat cooler, middle Eocene (ca. 45 Ma) climate of central Idaho, chestnut occurred in a flora dominated by conifers under an AMT estimated at 8.5 °C (Axelrod, 1998). This would have been near the 'northern' limits of distribution for most modern species and clearly outside the range of *C. henryi* (Table S1).

To provide a complete account of biogeography for all seven chestnut species world-wide, the distributions of three Chinese species are covered for the first time in our study. This provides a comprehensive record of the geographic ranges the *Castanea* genus and forms an essential reference in support of future research, conservation planning and forest management. However, given the data limitation, caution is needed in utilizing these continental-scale distribution maps for applications at finer spatial scales. Such data limitations first include the coarse resolution for generated distribution maps. For instance, range maps for the Chinese species were county based. Therefore, the included areas are affected by political boundaries and do not necessarily match the exact range limits at fine spatial scales. Second, although we focused our study on natural distributions of chestnut species, we omit those populations introduced into many other parts of the world (such as those in the southern hemispheric countries) (Avanzato, 2009). The long history of human cultivation of *C. sativa*, *C. mollissima* and *C. crenata* makes it difficult or impossible to distinguish the boundaries between natural and naturalized distributions. Cultivation of sweet chestnut (*C. sativa*) in Europe has occurred for as many as four thousand years, and 19.3% of the current 2.5 million ha chestnut-growing area is managed for fruit production (Conedera *et al.*, 2004; Conedera & Krebs, 2007). Similarly, cultivation of

C. mollissima and *C. crenata* has a long history (Bounous & Marinoni, 2004; Avanzato, 2009). Hence, our ability to delineate pre-anthropogenic distributions for these species is very limited. Nonetheless, this does not substantially affect our ability to investigate the bioclimatology of chestnut species because human-related range dynamics played most likely within the general climatic limits, as well as other ecological niche restraints. Also, it is possible that a lack of botanical records may have caused underestimation of natural distributions even within historical times, such as is probably the case with *C. dentata* in the coastal piedmont area of eastern North America (Fei, 2007).

In addition to providing a better and more complete understanding of chestnut species distribution world-wide, we evaluated the potential climatic fitness of three Chinese species in North America. This was intended to provide a biogeographic basis for the conservation and restoration of *C. dentata* through incorporating blight-resistant genetic materials from Chinese species, especially *C. mollissima*. The predictions of Chinese species range covered the majority of the historical American chestnut range, strongly suggesting a favourable climatic and regional adaptability to North America. Thus, a regionally adapted, blight-resistant, introgressed hybrid American chestnut appears feasible if a sufficiently diverse array of Chinese chestnut germplasm is used as a source of blight resistance. The prediction accuracy for our models could be improved by incorporating additional non-climatic environmental variables, such as properties of soil and associated bedrock that are known to influence the survival and growth of chestnut (Fei *et al.*, 2007). Unfortunately, data for environmental variables such as these are very difficult, if not impossible, to obtain for all geographic areas included in the present study. Moreover, caution is needed in applying our modelling results because the geographic distribution of a given species is constrained not only by abiotic factors such as climatic variables modelled here, but also by biotic factors such as biotic interaction among associated species and by limitations of species movement (Peterson, 2011). Additional uncertainties may arise from limitations of the modelling techniques employed, such as potential over-fitting of the MaxEnt technique (Elith *et al.*, 2011) and possible dimension dependence of the predicted climatic space because of the number of environmental variables included (Peterson, 2011). Nevertheless, the overall similarity and comparability of American chestnut and Chinese chestnut in their continental-scale biogeography are evident and supported by their spatial distribution in climatic space. Finally, it should be noted that further testing in field experiments and long-term observations is still needed to ascertain to what degree the climatic adaptability traits from parent trees are carried over to the hybrid generations.

In conclusion, we surveyed and described in a comprehensive manner the general biology, geographic distribution and climatic limits of world chestnut species in this paper. It is vital to comprehend *Castanea*'s biogeography to conserve

economically and ecologically important genus. We expect that the information provided in this paper will be an essential reference for scientific research and conservation management of chestnut species. Such biogeographic and bioclimatic studies are especially needed to facilitate backcrossing programmes and to guide planning of pilot restoration projects in the ongoing effort to reclaim American chestnut forests by introducing blight-resistance genes from related species growing on a different continent. In addition, our study enriches the field of conservation biogeography by providing a between-continent climate matching approach to facilitate the range-wide restoration of an ecologically and economically important species, which can be readily applied for the planning of the restoration of other threatened or endangered species.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Threshold determination using sum of sensitivity and specificity (SSS) index for *Castanea mollissima*, *C. seguinii*, and *C. henryi*.

Table S1 Mean and standard error of climatic variables at southern and northern distribution limits of chestnuts worldwide (*Castanea* spp.)

Table S2 Correlations of climatic variables with the first three principal components (PC1-3) from a principal component analysis of the distribution limits and complete ranges for each chestnut (*Castanea*) species. Symbol '-' indicates no estimation due to the coldness index (CI) being a constant (0)

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