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Diversity and density patterns of large old trees in China

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Abstract

Large old trees are keystone ecological structures that provide vital ecosystem services to humans. However, there are few large-scale empirical studies on patterns of diversity and density of large old trees in human-dominated landscapes. We present the results of the first nationwide study in China to investigate the patterns of diversity and density of large old trees in human-dominated landscapes. We collated data on 682,730 large trees ≥ 100 years old from 198 Chinese regions to quantify tree species diversity, tree density and maximum tree age patterns. We modelled the effects of natural environmental variables (e.g. climate and topography) and anthropogenic variables (e.g. human population density and city age) on these measures. We found a low density of large old trees across study regions (0.36 trees /km²), and large variation in species richness among regions (ranging from 1 to 232 species). More than 95% of trees were < 500 years old. The best fit models showed that: (1) Species diversity (species richness adjusted by region size) was positively associated with mean annual rainfall and city age; (2) Density of clustered trees, which are mostly remnants of ancient woods, was negatively influenced by human population density and rural population (% of total population). In contrast, the density of scattered trees, which are mostly managed by local people, was positively correlated with mean annual rainfall and human population density. To better protect large old trees in cities and other highly-populated areas, conservation policy should protect ancient wood remnants, mitigate the effects environmental change (e.g. habitat fragmentation), minimize the negative effects of human activities (e.g. logging), and mobilize citizens to participate in conservation activities (e.g. watering trees during droughts).

Keywords:

Ancient trees, biodiversity, conservation, density, human influences, scattered trees.

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1. Introduction

Large old trees are keystone ecological structures that play important roles in supporting natural community structure and dynamics (Lindenmayer et al., 2014; Stephenson et al., 2014), maintaining critical ecosystem functions (Lutz et al., 2018; Slik et al., 2013), and providing habitat for a wide range of native organisms (Van der Hoek et al., 2017). They have high conservation, cultural and aesthetic values (Blicharska and Mikusiński, 2014; Lindenmayer and Laurance, 2017). Many populations of large old trees worldwide are declining due to environmental change and human influences (Lindenmayer et al., 2012; Patrut et al., 2018). However, conservation of large old trees requires a basic understanding of the factors influencing their diversity and density (Lindenmayer and Laurance, 2016), especially in human-dominated landscapes (e.g. urban and rural areas) where they are threatened by land use practices (Stagoll et al., 2012).

Most current knowledge on the factors driving diversity and density patterns of large old trees comes from natural forests. At local scales, topography and landscape configuration can have significant effects on large trees (Ikin et al., 2015; Lindenmayer et al., 2016; Moga et al., 2016; Thomas et al., 2013). For example, areas around Mount Kilimanjaro, the highest mountain in Africa, support Africa's tallest trees (Hemp et al., 2017). At regional scales, the diversity and density of large old trees is influenced by climate variables (Larjavaara, 2014; Lutz et al., 2009; Slik et al., 2013), soil properties (Venter et al., 2017), and natural disturbances (Lindenmayer and Laurance, 2017). For example, large trees are more common in regions characterized by high water availability and moderate temperatures (Venter et al., 2017). Natural disturbances such as storms, fires and insect attack can badly damage large old trees (Jim and Liu, 1997; Lindenmayer et al., 2016; Lindenmayer and Laurance, 2017).

However, these studies have limited practical large-scale conservation implications. First, they use different definitions of large old trees that limit cross-study comparison. Authors have arbitrarily defined large old trees based on diameter-specific criteria (e.g. trunk diameter at breast height (DBH) >127 cm, Moga et al. 2016; DBH >100 cm, Stagoll et al. 2012; DBH > 60 cm, McIntyre et al. 2015), or age-specific criterion (Tree age ≥ 200 years; Chambers et al., 1998). Second, the factors influencing occurrence and diversity patterns of large old trees in human-dominated areas such as urban and rural areas remain poorly known, which has generated increasing research interest in recent years (Hartel et al., 2018; Moga et al., 2016).

Earlier studies have demonstrated negative human influences on large old trees. Many populations of large old trees are declining as a result of logging, human-induced climate change, habitat loss and fragmentation (Bennett et al., 2015; Laurance et al., 2000; Lindenmayer et al., 2012). For example, large trees DBH >45 cm have declined from 19 per ha to one per ha in the southern boreal zone of central Sweden as a result of intensive logging (Jönsson et al., 2009). There was a 20% decline in populations of large old trees in parts of agricultural landscapes of New South Wales, Australia between the 1960s and 1990s, with a higher rate of loss in cropping landscapes than in grazing landscapes (Ozolins et al., 2001). Conversely, some studies have found a positive human influence on large old tree populations through planting, watering and disease management (Hartel et al., 2018; Min and Wang, 1994). Numerous large old trees have, for instance, been deliberately protected in ancient woodlands near historical sites, temples and shrines (Chen, 2010; Frascaroli et al., 2016; Zhang et al., 2017). For example, 1250 large old trees occur in a 21.8 ha area surrounding the Confucius temple in China (Min and Wang, 1994). Similarly, a large number of introduced exotic trees have been cultivated

in cities for ornamental and religious reasons (Blicharska and Mikusiński, 2014; Zhang et al., 2017). Therefore, human activities can have either negative or positive effects on the species diversity and population density of large old trees.

China has a long history of management of large old trees particularly around religious, historical and cultural sites (Min and Wang, 1994; Salick et al., 2007; Yuan and Liu, 2009). For example, Beijing currently supports 39,408 large old trees (Chen, 2010). To protect large old trees, in 2001 China published the *Regulation on the Protection and Management of Ancient and Famous Trees*. In addition, local researchers have published thousands of datasets on large old trees (e.g. Chen, 2010; Min and Wang, 1994; Zhang et al., 2017). Here we collate an unprecedented array of datasets comprising 682,730 trees from 198 regions using information from published papers and reports predominantly written in Chinese (and thus not accessible to non-Chinese scientists). We present, to the best of our collective knowledge, the first large-scale analysis of large old trees in the human-dominated landscapes of China. Specifically, we ask the following two key questions. (a) What are the patterns of species diversity, density and age structure of large old trees in human-dominated areas? And, (b) What environmental variables and human-generated factors influence these patterns? Given that large old trees are vulnerable to extreme drought and heat-induced mortality (Bennett et al., 2015; Choat et al., 2018), and are commonly found in remote, high-elevation regions with less human accessibility (Piovesan et al., 2018; Yang et al., 2014b), we predicted that: (1) Regions with favourable environmental conditions for the growth of large old trees, such as abundant rainfall, is characterised by both a higher diversity and density of large old trees. (2) Long-settled regions support more old trees mainly due to positive effects of human management activities; (3) Anthropogenic variables, such as

human population density, have both negative and positive effects on populations of large old trees.

2. Methods

2.1 Defining large old trees

Defining a large old tree is challenging (Lindenmayer and Laurance, 2017). In this paper, and consistent with ‘*Technical Guidelines for Document Establishment of General Survey of National Ancient – Famous Trees*’ of 2001 in China, we defined large old trees as trees ≥ 100 years old. A large number of datasets in China contain information on tree species richness and abundance, which are mostly gathered using a standard protocol (The State Forestry Administration, 2016), although again published primarily in Chinese (Table S1). These studies have used trunk circumference as a proxy for large old trees given that old trees typically have large DBHs (Chambers et al., 1998). For example, 83.1% of large old trees in Hebei province are >10 meters in height with most having trunk circumferences of ~ 200 -600 cm (Lu, 2012). Each large old tree was identified to species level, and its age, height and girth recorded (e.g. Zhang et al., 2017). Tree age in these datasets was determined for each tree by experienced investigators from various forestry departments using information derived from local documents and local knowledge, or estimated from trunk DBH data. Some studies used C_{14} isotopic data and tree ring analyses for age estimation (Yuan et al., 2012). Each tree in these datasets was tagged with protection cards by the various research teams who completed the original surveys. Three protection categories were defined based on estimated tree ages: $100 \text{ years} < \text{tier 1} \leq 299 \text{ years}$; $300 \leq \text{tier 2} \leq 499 \text{ years}$; $\text{tier 3} \geq 500 \text{ years}$. However, data on tree age for most of the trees were gathered by local experts and were not dendrochronologically dated, thus estimations of tree age >100 years maybe not reliable. Tree age estimations based on species-specific and scientifically dated data

should be further conducted.

2.2 Online search and selection criteria

To ensure our datasets were comparable among regions, we conducted our search of available datasets at a similar spatial scale, that is: only region-level documents were included in our analyses. We defined a region as an administrative city-level political division (city or county). A region included not only urban areas, but also adjacent rural areas, hence there was a range of land uses within a typical human-dominated landscape. To search for reliable information, we conducted an online search of the Chinese website: www.cnki.net on July 30, 2017, which is the largest scholarly website used by researchers for academic publications written in Chinese. Keywords searched included: “ancient trees”, “large trees”, “giant trees”, “old trees”, “sacred trees”, “old and precious trees”, “large-diameter trees”, “heritage trees” and “old-valuable trees”. We conducted a similar search on Google Scholar, but found only one relevant paper written in English (Zhang et al., 2017). To ensure our inventory was not geographically biased, we used two search engines, including Baidu (www.baidu.com, widely used in China) and Google, with the specific keywords and provinces names if no record was found for a specific province through the previous search. Government reports and online databases (e.g. Guangdong province: <http://gsmm.gdf.gov.cn:8070/>), including detailed information of large old trees, were also included in our analysis.

To reduce sampling bias, we tried to ensure that most provinces examined a similar number of regions providing a balanced dataset for comparative analyses. To ensure the quality of our datasets, we selected papers used for analysis based on the following selection criteria: 1) studies with clear survey

methods, with associated reports written by technicians from a forestry department; and 2) the latest publication if surveys were conducted in the same region but in different years. In total, we found 180 Chinese journal papers, 17 online reports and one English language paper from 198 regions (Fig. 1).

2.3 Response variables

Species diversity: To explore the patterns of large old tree species diversity, we extracted the number of species for each examined region from 121 studies. As region size varied substantially, we used adjusted species richness to eliminate the influence of region size (Qian, 1998) using the equation $D=S/\ln(A)$, where D is the modified species diversity index, S is the number of total species for a given region, and A is the area of the region.

Tree density: We calculated tree density as the number of trees in a region divided by the region size (trees per km²). However, some studies included only scattered trees, while tree groups from ancient woods were not well investigated. Therefore, to ensure our datasets were comparable among regions, we completed a separate analysis for 63 studies comprising systematic surveys including two types of tree density datasets. These were: (1) scattered trees, which are individually distributed and managed by local people, occur as small patches of vegetation among urban areas (Stagoll et al., 2012), and rural landscapes, such as farmlands and country yards (Gibbons et al., 2008; Hartel et al., 2018; Lumsden and Bennett, 2005); and (2) clustered trees, which are more likely to be found in forest remnants with at least 10 living co-located large old trees, e.g. those of from religious forests with spiritual symbolic meanings (Yuan and Liu, 2009; Zheng, 2016).

Maximum tree age: Where data were available, we recorded maximum tree age, defined as the age of the oldest tree in each region. For those regions with missing information, we sent emails to the authors of relevant reports, and searched for such information online in Google and Baidu based on reliable data sources, preferably peer-reviewed papers. Datasets on maximum tree age were used only when a clear record of the year in which a tree was planted could be found. In total, we compiled information for 137 regions with available data.

2.4 Explanatory variables

To identify the best predictors of tree species diversity and population density at the regional level, we chose environmental variables that have been shown to be key determinants of plant diversity and density patterns at large spatial scales: latitude (Gaston and Spicer, 2004), mean annual temperature and mean annual rainfall (Liu et al., 2017; Yang et al., 2014a), elevation range (Aronson et al., 2014; Lindenmayer et al., 2016) and potential evapotranspiration (Yang et al., 2014a). To avoid multi-collinearity, we excluded mean annual temperature and latitude because mean annual temperature was significantly correlated with potential evapotranspiration (Pearson's $r=0.96$, $n=198$, $P<0.001$) and latitude was significantly correlated with mean annual rainfall ($r=-0.802$, $P<0.001$). Data on mean annual rainfall and potential evapotranspiration were extracted from the US Geological Survey database (1996) at a spatial resolution of 10 arc-minutes and we used spatial average values for each county (Yang et al., 2014a). Similarly, we obtained elevation range for each county from Yang et al. (2014), as a proxy of topographical complexity index.

We included four anthropogenic variables as potential predictors of species diversity and density of

large old trees: annual Gross Domestic Product (GDP) per capita, human population density, city age and rural population (% total human population). These variables were selected as they are important socioeconomic factors likely to influence populations of large old trees (Andersson and Östlund, 2004). Age since city establishment was estimated from historical documents. As the majority of the surveys were conducted around the year 2010, data on human population density (measured in persons per square kilometer), and GDP per capita, were extracted from the 2010 yearbook of each of the examined regions (National Bureau of Statistics of China, 2010). Human population density and GDP per capita were not normally distributed and were \log_{10} transformed before analysis.

2.5 Data analyses

To meet the assumptions of the analytical techniques employed, we \log_{10} -transformed the density of large old trees. We detected no spatial autocorrelation for the three response variables (Moran's $I < 0.05$). We tested multi-collinearity of the predictor variables using variance inflation factors (VIF), but substantial collinearity was not found. We calculated all possible combinations of predictor variables and response variables and ran a model selection procedure with ordinary least squares multiple regressions using the software 'Spatial Analysis in Macroecology' (SAM) version 4.0 (Rangel et al., 2010). To quantify the strength of the predictor variables, we used a model averaging approach based on the Akaike Information Criterion weights. We calculated an Importance value of a predictor variable, which represents the sum of the AIC-weights of the models in which the variable was present. A high importance value for a variable indicates a high probability of it being included in the most plausible model. To determine the relative contribution of environmental and anthropogenic variables, we performed partial regression with SAM software for predictor variables with importance value >0.6 .

We employed the “ggplot2” package (Wickham and Chang, 2012) to generate graphical outputs from R (R Core Team, 2015).

3 Results

3.1 Descriptions of large old trees

We compiled a dataset of 682,730 trees in a total area of 1.95 million km² across 198 regions. Species richness ranged from 1 species in Changji City to 232 species in Yongzhou City. Most regions supported less than 50 species (Fig. 2a). The density of large old trees was 0.35 trees /km² on average, and ranged from 0.002 trees /km² in Tongyu County to 24.18 trees /km² in Macao (Fig. 2b). Regions with high tree species richness tended to have a high density of large old trees (Pearson’s $r=0.55$, $p<0.001$). As expected, clustered trees in a given region had a higher tree density and abundance than that of scattered trees (Paired t test: $n=63$, $p=0.0015$; Fig. 2c). Most trees were < 500 years old (95.5%; Fig. 2d). However, 102 of the 137 regions supported old trees that were ≥ 1000 years old. The oldest trees were claimed to be 3500 years old found in Xiao County (*Pteroceltis tatarinowii*) and Dongkou County (*Ginkgo biloba*), although they were not scientifically dated (Table S1).

3.2 Factors influencing species diversity, tree density and maximum tree age patterns

Species diversity (adjusted by region size), was associated primarily with mean annual rainfall. There was also a weak effect of city age (Table 1). That is, older regions with abundant rainfall supported the most large old tree species (Fig. 3a). Partial regression analyses showed that the pattern of species diversity was influenced by a combination of environmental and anthropogenic variables, with mean annual rainfall being the most important factor (as shown by the importance value) (Table 2).

The density of clustered trees was significantly affected only by anthropogenic variables: being negatively influenced by human population density and rural population (% of total population) (Table 2; Fig. 3b). In contrast, the density of scattered trees was associated with both environmental and anthropogenic variables (Table 2), with mean annual rainfall being the most important determinant (Fig. 3c). Interestingly, human population density tended to have a negative effect on density of clustered trees, but a marginally positive effect on density of scattered trees (Table 1).

Our analyses also revealed an association between maximum tree age and city age, with older regions typically supporting older trees (Fig. 3d).

4. Discussion

An increasing number of studies have reported that the occurrence of large old trees in human dominated landscapes, such as those in cities (Jim, 2004; Zhang et al., 2017), agricultural landscapes (Gibbons et al., 2008; Orłowski and Nowak, 2007) and other non-forested areas (Hartel et al., 2018). We found that China supports a large number of large old trees. Highly urbanized regions, such as Macao (24 trees per km²; Zhang et al., 2017), can support a higher density of large old trees than other regions with large area of forests (Fig. 2b). In addition, our study showed that China supports some extremely old trees including individuals approximately 3500 years old. However, the records of very old trees in China were extracted mostly from historical archives and were not dendrochronologically dated. The oldest living tree in China with tree ring data is a *Juniperus przewalskii* which is about 2200 years old, although the age of the species can exceed 3000 years (Yang et al., 2014b). Indeed, these

trees are comparable in age to the oldest scientifically dated trees recorded in South America (3620 years; Lara and Villalba, 1993), Europe (~1300 years; Piovesan et al., 2018), North America (4844 years old; Currey, 1965) and Africa (2450 years; Patrut et al., 2018).

Consistent with predictions made at the outset of this study, regions in China characterized by favourable growth conditions (e.g. higher rainfall) for large old trees, tended to have both more species and a higher density of such trees. In addition, anthropogenic variables had both negative and positive effects on the recorded density of large old trees. Overall, the patterns of species diversity and density of large old trees were influenced by a combination of natural environments and human influences (Table 2).

4.1 Influences of natural environment variables on large old trees

Consistent with plant distribution patterns found in natural environments (Slik et al., 2013; Vandekerkhove et al., 2018), our study identified a significant effect of mean annual rainfall on tree species diversity and density patterns. Water deficiency is a key threat to the survival of large old trees (Choat et al., 2018) as they require abundant precipitation and intermediate temperatures to prevent desiccation and limit tree mortality (Venter et al., 2017). For example, the tallest trees in the world are found in regions associated with high precipitation and/or prolonged periods of fog (Larjavaara, 2014).

Large old trees are particularly vulnerable to elevated drought and heat-induced mortality (Bennett et al., 2015). For example, large trees in California with a DBH > 61 cm declined by up to 50% between the 1920s to the 2000s as a result of increased water stress (McIntyre et al., 2015). Similarly, canopy desiccation killed approximately half of the large trees DBH \geq 60cm after 30 years of habitat

fragmentation in central Amazonia (Laurance et al., 2000). Although previous studies have occasionally reported that the density of large old trees increased as a result of favourable climate and site conditions (Vandekerkhove et al., 2018), environmental change in human-dominated landscapes is threatening the diversity and density of large old trees. For example, 18 large old trees died as a result of drought between 1998 and 2005 in the Yanping district of Nanping City (Ge and Yu, 2005). Nine of the 13 oldest trees in Africa have died in the past 12 years, and their deaths have, at least in part, been attributed to significant changes in climatic conditions (Patrut et al., 2018). In addition, large trees had higher mortality rates than smaller trees during climate change induced drought in Beijing (Zhang et al., 2014).

4.2 Human influences on large old trees

Several studies have suggested that anthropogenic variables are important drivers of patterns of species diversity in large old trees (Lindenmayer and Laurance, 2017; Zhang et al., 2017). Our study included several anthropogenic variables. Inclusion of other factors such as the rate of local GDP growth and the rate of local population growth, might improve our model fit. Nevertheless, we found that older cities supported more species of large old trees, consistent with our prediction at the outset of this investigation. It is possible that this occurred because older cities are characterized by lower rates of extinction of plant species (Hahs et al., 2009) or more time has elapsed for species to colonize and become established in human-dominated landscapes (Zhang and Jim, 2014).

Our results confirm that ancient wooded remnants (clustered trees) are the primary areas supporting large old trees in the human-dominated landscapes of China (Fig. 2c). For example, Taian City supports

19,483 large old trees, of which 18,195 are found on Mountain Tai, one of China's most sacred places (Zheng, 2016). However, our study found negative relationships between the density of clustered trees and human population density and the proportion of rural population (Table 1). Clustered trees are mostly remnants of ancient woods that were previously logged for agricultural uses and timber production (Lindenmayer and Laurance, 2017), leaving only limited areas of intact forest supporting large old trees (Watson et al., 2018). Such activities may accelerate the decline of large old trees (Lindenmayer et al., 2012) and clustered large old trees in China have declined rapidly in recent decades. For example, over half of the intact forests with a high density of large old trees in northeast China were destroyed between 1896 and 1948 due to logging (Yu et al., 2011). In the 1960s, large old trees with high biomass were a primary source of timber, resulting in a substantial loss of these trees (Wang and Delang, 2011).

We also found a positive relationship between human population density and the density of scattered trees (Table 1). Several factors may explain this finding. First, people often protect large old trees for tangible benefits like the production of fruit, edible flowers and medicines (Hartel et al., 2018). Second, large old trees are sometimes protected for their cultural and aesthetic values. For example, *Ficus religiosa* is regarded as a sacred tree that has important religious and spiritual value to the followers of Buddhism, Hinduism, and Jainism. As such, local people respect and protect especially large old individuals of this species (Blicharska and Mikusiński, 2014). Third, large old trees are protected for their ecological values (Lindenmayer and Laurance, 2017), such as shade for livestock (Hartel et al., 2017), and habitat for animals (Van der Hoek et al., 2017). Management activities including pest control and watering can help better protect large old trees, as has occurred in Asian countries such as

in Japan (Ishii et al., 2010) and India (Thaiutsa et al., 2008).

5. Conclusions: Implications for conservation and management

Loss of large old trees may have far-reaching ecological consequences that threaten critical habitats for a range of taxa that rely on large old trees (Ishii et al., 2018; Jones et al., 2018), and influence ecosystem adaptability to climate change (Bennett et al., 2015). Unfortunately, few ecologists have recognized the ecological consequences of the loss of large old trees in China and in particular in human-dominated landscapes. Therefore, conservation of large old trees, especially those set aside for religious and cultural reasons in cities and other highly populated areas (Chen, 2010; Yuan and Liu, 2009), should receive more attention from policy makers and resource managers (Lindenmayer et al., 2014).

Our study has important implications for conservation management. First, conservation projects often receive limited interest from the public (Balding and Williams, 2016). However, large old trees have received worldwide interest due to their high conservation, cultural and aesthetic values (Blicharska and Mikusiński, 2014; Lindenmayer and Laurance, 2017). Indeed, they should be considered as a conservation icon for plant conservation (Lindenmayer, 2017). Our study is based on a major set of databases on large old trees in China, and should be used to promote better conservation outcomes and environmental education. Second, our study shows dominant effects of natural environmental variables on tree species diversity and density patterns of large old trees in human-dominated landscapes. This can help identify hotspots for the conservation of large old trees. As an example from this study,

Yongzhou City supports many large old trees most likely because of high water availability and moderate temperatures, low level of human disturbances, and a traditional culture of tree protection. In particular, large old trees are vulnerable to drought. As such, to protect large old trees from climate change, fine scale conservation planning should consider environmental changes and approaches to combat extreme climate events (such as watering individual trees). Third, human influence is a double-edged sword for the conservation of large old trees. Logging has resulted in a dramatic decline of large old trees in natural forests (Lindenmayer et al., 2012) and in human-dominated landscapes. Conversely, the oldest trees can be maintained for thousands of years due to traditional tree protection measures. Hence, conservation policies (e.g. logging bans) should minimize negative human effects, but at the same time better mobilize citizens to save present large old trees in human-dominated landscapes (e.g. by advocating against their removal as part of urban development), and care for the future generations of large old trees that are adaptable to local environments.

Data Accessibility

The datasets supporting this article has also been uploaded as supporting materials.

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Fig. 1. Locations of the 198 studied regions in China. Red dots represent the studied regions mentioned in the paper.

Fig. 2. Information on large old trees across the study region. (a) Frequency distribution of species richness based on 121 studies; (b) Tree density data of 198 regions (not significant, but with a decreasing trend); (c) Comparisons between clustered trees (e.g. religious forests with >10 trees living together) and scattered trees (e.g. individually distributed trees) based on 63 studies with both datasets; (d) Age categories based on 145 studies with available datasets.

Fig. 3. Key determinants for the (a) Species diversity; (b) Density of clustered trees; (c) Density of scattered trees and (d) Estimated maximum tree age (without dendrochronological evidence) patterns of large old trees.

Tables

Table 1. The averaged model for the estimation of species diversity, maximum tree age and density of large old trees. Predictor variables with average importance value > 0.6 were given in the table. Importance value represents the sum of the AIC-weights of the models in which the variable was present, ranged from 0 to 1 (1 stands for the best predictor). SRC: Standardized regression coefficients from AIC-wi weighted averaged models. MAR: mean annual rainfall; LogPD: Log₁₀ transformed human population density.

Response variables	n	Key predictors	Importance value	SRC	R ²
Species diversity	121	MAR	1	0.495 ***	0.273
		City age	0.618	0.143	
Maximum tree age	137	City age	1	0.554***	0.369
		Proportion of rural population	0.902	0.209	
Tree density (Clustered trees)	62 [§]	LogPD	0.927	-0.404**	0.225
		Proportion of rural population	0.901	-0.406**	
Tree density (Scattered trees)	63	MAR	1	0.754***	0.629
		LogPD	0.951	0.3***	

[§] One study was removed for analyses as tree density is extremely low and influenced the distributional properties of the response variable.

Table 2. Relative contribution of environmental and anthropogenic variables to the total variance of response variables.

Response variable	Environmental	Anthropogenic	Joint effect	All
Species diversity	0.238	0.019	0.014	0.243
Maximum tree age	0	0.364		0.364
Tree density				
Clustered trees	0	0.183	0	0.183
Scattered trees	0.448	0.098	0.058	0.604

Highlights:

1. We collated data on 682,730 large trees ≥ 100 years old from 198 Chinese cities.
2. Regions with high water availability tend to be hotspots of large old tree species
3. Large old trees have declined as a result of human disturbance.
4. Cities/rural areas can support substantial numbers of large old trees.

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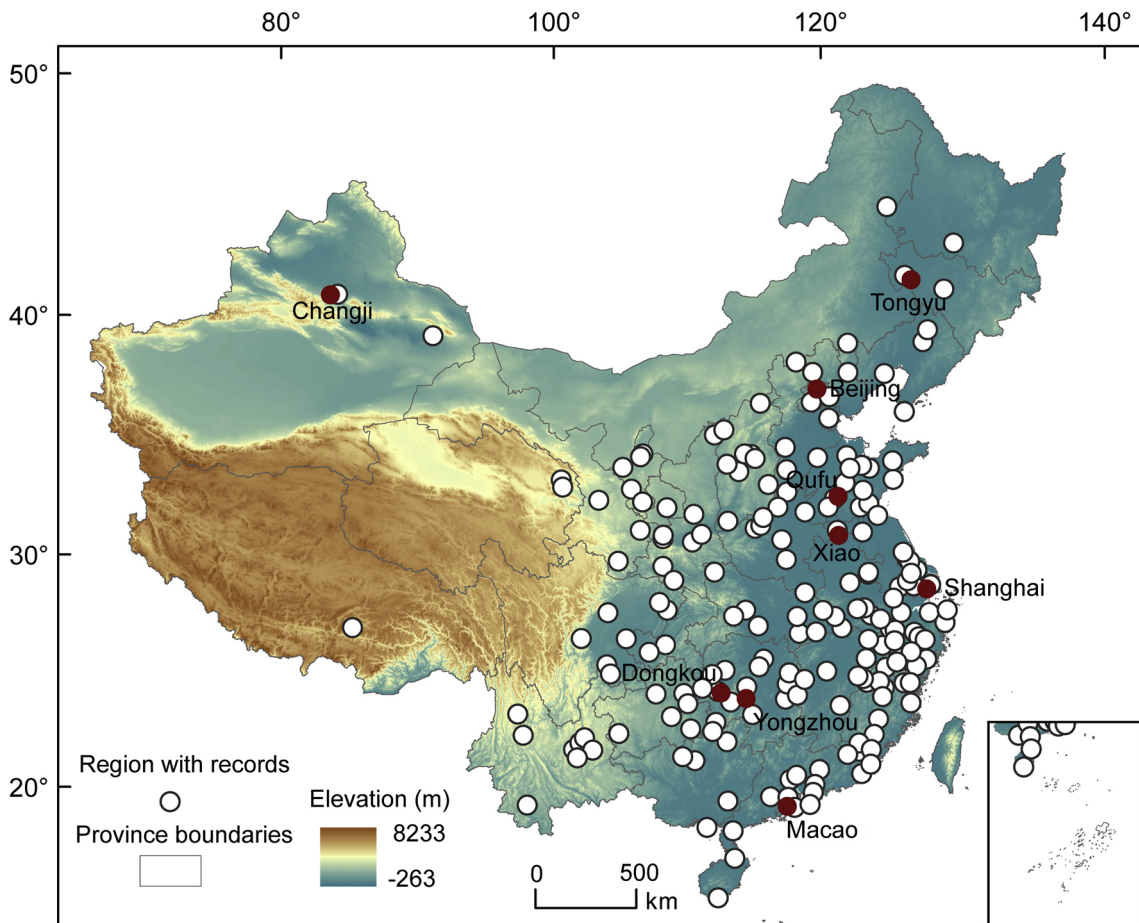
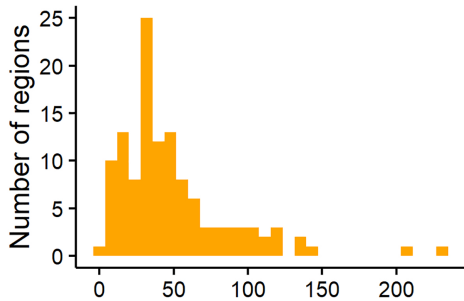
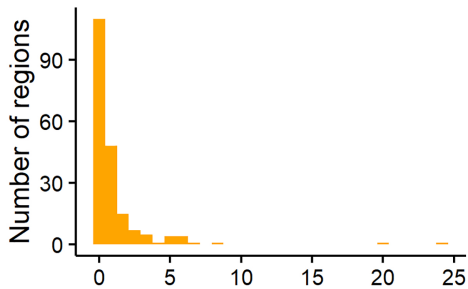


Figure 1

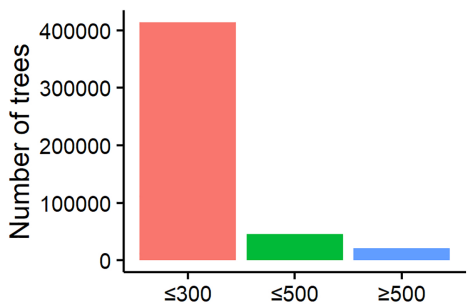
(a) Species richness



Tree density (n/km^2)



(c) Tree types



(d) Age categories

Figure 2

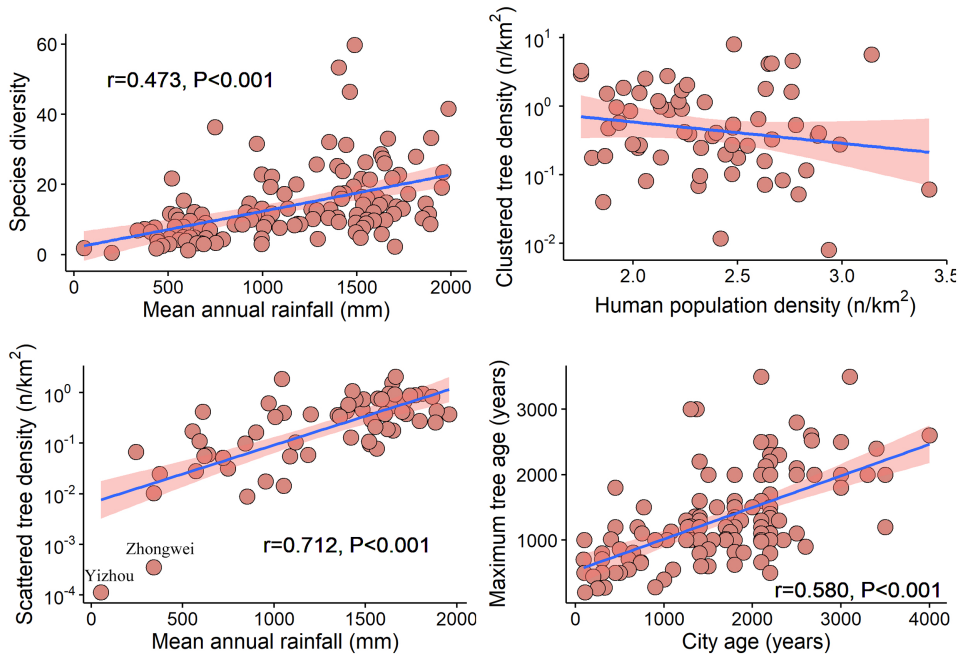


Figure 3