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Decadal changes in population structures of rare oak species Quercus chungii

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Abstract

Quercus chungii is an endemic tree species in China, rare and endangered in subtropical areas of China. Understanding its population structure and temporal dynamics is crucial for conserving and restoring Q. chungii population and its associated ecosystems. However, large knowledge gaps remain about its population structure and temporal change, and its key demographic rates across size classes. In this study, we investigated the population structures of Q. chungii in 2013 and 2023 in a nature reserve specifically established to better conserve Q. chungii and its associated ecosystems. We found that Q. chungii increased in its overall abundance, frequency and tree size in the past decade, suggesting active regeneration and fast growth rate of this species and the effectiveness of past conservation efforts. The age structure in 2023 shows a pyramid shape, with a sharp decline in the numbers of individuals from germinated seeds to seedlings and from seedlings to saplings. These lead to the low numbers of seedlings and saplings and high age-specific death probabilities at the early developmental stages. These results indicate potential risks of future population decline. These risks may have already manifested over the past decade, as a high mortality rate during the seedling-to-sapling transition could be one of the primary reasons contributing to the decreased proportion of saplings in 2023 compared to 2013. We propose that future studies may benefit from in-depth studies on the regeneration processes of Q. chungii by considering seed predation and germination under changing climate. This study improves the prediction of population development of Q. chungii and provide theoretical guidance for the conservation of Q. chungii.

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Abstract

Quercus chungii is an endemic tree species in China, rare and endangered in subtropical areas of China. Understanding its population structure and temporal dynamics is crucial for conserving and restoring *Q. chungii* population and its associated ecosystems. However, large knowledge gaps remain about its population structure and temporal change, and its key demographic rates across size classes. In this study, we

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investigated the population structures of *Q. chungii* in 2013 and 2023 in a nature reserve specifically established to better conserve *Q. chungii* and its associated ecosystems. **We found** that *Q. chungii* increased in its overall abundance, frequency and tree size in the past decade, suggesting active regeneration and fast growth rate of this species and the effectiveness of past conservation efforts. The age structure in 2023 shows a pyramid shape, with a sharp decline in the numbers of individuals from germinated seeds to seedlings and from seedlings to saplings. These lead to the low numbers of seedlings and saplings and high**age-specific death probabilities at the early developmental stages.** These results indicate potential risks of future population decline. These risks may have already manifested over the past decade, as a high mortality rate during the seedling-to-sapling transition could be one of the primary reasons contributing to the decreased proportion of saplings in 2023 compared to 2013. We propose that future studies may benefit from in-depth studies on the regeneration processes of *Q. chungii* by considering seed predation and germination under changing climate. This study improves the prediction of population development of*Q. chungii* and provide theoretical guidance for the conservation of *Q. chungii* .

KEYWORDS: life table, population structure, *Quercus chungii*, secondary forest, temporal change

1. INTRODUCTION

Population structure and its dynamics are fundamental to understand and predict population development and critical for the conservation of rare and endangered species (Harcombe 1987, Ezard et al. 2010, Salguero-Gomez and Gamelon 2021). *Quercus chungii* is a tree species of Fagaceae, endemic to China, and rare and endangered in Fujian Province (Wang et al. 2011, Jiang et al. 2019, Sun et al. 2021). The distribution area and population size of *Q. chungii* drastically reduced in the last century due to extensive logging for its high-quality timber (Wang et al. 2011). Previous work has focused on the community structures of*Q. chungii* forest communities, and spatial genetic pattern and distribution, seed production and germination of *Q. chungii* population (Chen 2004, Huang et al. 2010, Li et al. 2010, Wang et al. 2011, Huang et al. 2017, Jiang et al. 2019, Sun et al. 2021). However, large knowledge gaps remain about its age or size structures and temporal change, and its key demographic rates across age classes. Understanding the population structure and its temporal dynamics of*Q. chungii* is crucial for conserving and restoring *Q. chungii* population and its associated communities and ecosystems.

Age structure and life table are important tools to study population demographics (Harcombe 1987, Ezard et al. 2010, Jones 2021). We can infer reproductive strategy and predict population development from age structure by presenting the number of individuals in different developmental stages of a population. The information of age structure can be further used to construct a life table by calculating the key population parameters, such as age-specific survival and mortality probabilities. Thus, **life table is a fundamental tool to explore the heterogeneity of demographic processes across population developmental stages and predict population dynamics and structures** (Harcombe 1987, Jones 2021)**. Static or period life table is often used for long-lived species as it is difficult to track individuals from birth to death for such species (Jones 2021). It focuses on the fate of a population with mixed age classes during a particular time period.** ***We can derive survivorship and mortality curves (Harcombe 1987) from life tables to assess mortality risks across age classes. There are usually three types of survivorship curves. Type I is a convex curve, indicating an increasing risk of death with age. Type II is a declining line, indicating a constant risk of death over all ages. Type III is a concave curve, indicating a decreasing risk of death with age. Survivorship curves of long-lived, slowing-growing tree populations may not exactly fall into the three above types, but show a mix of them (Harcombe 1987).***

Seeds are essential for population survival and development, as they determine seed plant reproduction and represent the start of any seed plants (Willson al. 2014). Although seed data are crucial for population analyses of plant species (Adams et al. 2005, Salguero-Gomez and Gamelon 2021), they are rarely incorporated into life table analyses of tree populations. Since seed data are usually difficult to obtain, most previous studies on tree population life tables set seedlings or sapling as the starting stage (Farahat 2020,

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Wei et al. 2020, Ta et al. 2021, Wu et al. 2021, Zhang et al. 2023). Ignoring seed stage may result in inaccurate assessment and prediction of population demographics.

This study focuses on the population structure and its temporal change of *Q. chungii* in the Fujian Minqing Huangchulin National Nature Reserve, which was established in 1985 to better conserve *Q. chungii* and its associated communities and ecosystems (Li et al. 2010). We aim to study the following questions: (1) What is the current population structure of *Q. chungii* ? (2) How do the population structures change from 2013 to 2023? (3) How does the mortality risk change across size classes? We surveyed population of *Q. chungii* in both 2013 and 2023, and compared their temporal changes in population structures. We estimated the number of germinated seeds from a previous study on seed rain of *Q. chungii* . We assessed the mortality risks across size classes by deriving survivorship and mortality curves from the static life table. This study would improve the understanding of current status and the prediction of the future development of *Q. chungii* population, thus providing important guidance for the conservation of *Q. chungii* .

2. MATERIALS AND METHODS

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2.1. Study site

We surveyed the population structures and dynamics of *Q. chungii* in Minqing Huangchulin National Nature Reserve located in Fujian Province, China (26°15’29”N ˜ 26deg22’41”N, 118deg39’38Ë ˜ 118deg51’19Ë, with an elevation range of 100 ˜ 595 m). This area has the most intense distribution of *Q. chungii* in the world (Li et al. 2010). The reserve was specifically established to conserve *Q. chungii* and its associated communities and ecosystems (Li et al. 2010). The reserve has a mid-subtropical maritime monsoon climate, with an average annual temperature of 17.5degC, an average annual sunshine duration of 1,871.4 hours, a frost-free period of 294 days, and an average annual precipitation of 1,400 to 1,900 mm. The forest soil is predominantly mountainous red soil (Li et al. 2010).

2.2. Population survey

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We established two permanent plots in the nature reserve to survey the population of *Q. chungii* in 2013. One plot is 40 m x 40 m located near Tangxia village, and the other is 20 m x 30 m located at Fengshiling. We measured every tree with a DBH (diameter at breast height) [?] 2.5 cm within the plots in 2013.

To assess the temporal changes in population structures, we re-surveyed the population in the two permanent plots in 2023. To obtain a more complete structure of population, we measured all individuals, including seedlings with a DBH $<$ 2.5 cm, within the permanent plots. We established four additional 20 m x 20 m plots near Tangxia village in the nature reserve to measure all individuals of*Q. chungii.* Thus, in 2023, we surveyed the population structure of *Q. chungii* in a total area of 3800 m^2 with dense distribution of the focal species.

2.3. Population age structure

We used the size structure of *Q. chungii* to represent its age structure, as it is difficult to directly measure age from such a rare and endangered tree species and size structures are commonly used to infer population age structures of tree species (Harcombe 1987, Wei et al. 2020, Ta et al. 2021, Wu et al. 2021, Zhang et al. 2023). We separated the population into seven age classes based on the estimated relationship between tree age and size from logged *Q. chungii* in this nature reserve (Yang 2005) and previous studies on the growth (Liu 2005) and population structures

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(Wang et al. 2011) of this species. The seven age classes are (1) germinated seeds, (2) seedlings with DBH < 2.5 cm, (3) saplings with 2.5 cm [?] DBH < 12.5 cm,(4) medium trees with 12.5 cm [?] DBH < 22.5 cm, (5) medium trees with 22.5 cm [?] DBH < 32.5 cm, (6) large trees with 32.5 cm [?] DBH < 42.5 cm, and (7) large trees with DBH [?] 42.5 cm. Germinated seeds were estimated from a previous study on seed rain and germination of *Q. chungii* (see below), while data of age classes 2–7 were from field survey of this study. We obtained all the age classes in 2023, while only age classes 3–7 were available in 2013.

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We estimated the number of germinated seeds by assuming that a tree population with a larger total basal area will produce more germinated seeds, and this proportional relationship remains constant through time:

$$\frac{\text{Number of germinated seeds in 2007}}{\text{Species basal area in 2007}}=\frac{\text{Number of germinated seeds in 2023}}{\text{Species basal area in 2023}}(1).$$

The number of germinated seeds in 2007 was from a previous study (Huang et al. 2010). This study set up sixty 1 m^2

seed traps in three 20 m x 20 m plots in the same nature reserve in 2007 and counted the number of germinated seeds. Species basal area in 2023 were from this study. If the total basal area of the community did not change from 2007 to 2023, we can estimate the number of germinated seeds in 2023 from the following equation:

$$\frac{\text{Number of germinated seeds in 2007}}{\text{Relative species basal area in 2007}}=\frac{\text{Number of germinated seeds in 2023}}{\text{Relative species basal area in 2023}}(2).$$

The relative species basal area of *Q. chungii* in 2007 was from a previous study on *Q. chungii* communities in the same nature reserve (Wang et al. 2011); the relative species basal area in 2023 was from this study. We also estimated the number of germinated seeds in 2023 by assuming a constant proportional relationship between the number of germinated seeds and the average of relative species basal area and abundance, or the number of germinated seeds did not change through time. These two alternative analyses produced qualitatively similar results, thus we did not present them in the paper.

2.4. Temporal change in population structures

We selected the age classes 3–7 (DBH $\geq$ 2.5 cm) with available data both in 2013 and 2023 to compare the temporal changes in population numbers in each age class. We also compared the overall difference in basal areas, abundances, and frequencies by aggregating data from these age classes. Frequency was calculated as the proportion of 10 m x 10 m plots with *Q. chungii* presence.

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2.5. Construction and analysis of static life table

We constructed the static life table of *Q. chungii*population by following the definition in Jones (2021) (Table 1). *Survivorship and mortality curves were derived from the life table to assess mortality risks across age classes.* We applied smoothing approach (Wratten and Fry 1980) to deal with the issue of negative number of individuals died during the observational period ($_{n}\boldsymbol{D_x}$). For example, the observed number of individuals alive in age class 3 ($_{n}N_3 = 21$) is smaller than that in age class 4 ($_{n}\boldsymbol{N_4} = 34$), then the estimated $_{n}\boldsymbol{D_3} = {}_{n}\boldsymbol{N_3} - {}_{n}N_4$ would be a negative value. The smoothing approach assumes an equal proportional change in$_{n}N_x$ **in an interval centered at such age class (2–4 in this case). We calculated the average value (μ) and the difference between the maximum and**

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minimum values ([?]) of$_n\boldsymbol{N}_x$ **from the three age classes. The estimated** of $_n\boldsymbol{N}_x$ after smoothing are$_n\boldsymbol{N}_2* = \mu - \frac{[?]}{3}, {}_n\boldsymbol{N}_3* = \mu,\ and_n\boldsymbol{N}_4* = \mu + \frac{[?]}{3}$.

All the above analyses were performed in R 4.3.1 (R Development Core Team 2023), and the graphs were created using the "*ggplot2*" package in R (Wickham 2016).

3. RESULTS

3.1. Population structure and its temporal change

We found 144 individuals of *Q. chungii* with DBH $\geq$1 cm and 37 individuals with DBH $<$ 1 cm within 3800 m^2 **in 2023. Only one of the seedlings with DBH $<$ 1 cm was produced from seed, while the others were sprouted from roots of established trees. The overall population density was about 4.76 individuals per** $100\ \text{m}^2$.

The population structure in 2023 showed a pyramidal structure (Fig. 1). The focal species could produce a large number of germinated seeds (age class 1), but the number of seedlings (age class 2) dramatically decreased, suggesting high risks of death from stages of seed to seedling. The pattern is similar from stages of seedling to sapling (age class 3). The numbers of medium trees at age classes 4–5 were larger than those of saplings and large trees (age classes 6–7).

In the past decade of 2013–2023, both the abundance and frequency of*Q. chungii* increased, suggesting active regeneration processes (Fig. 2). The basal area also increased in this decade (Fig. 2). For individuals with DBH $\geq$ **2.5 cm** (age classes 3–7) surveyed in both years, the proportion of saplings decreased from 2013 to 2023, while the proportions of trees with larger sizes (age classes 5–7) increased through time (Fig. 3), suggesting substantial growth in the past decade.

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3.2. Life table and survivorship curve

Based on the static life table in 2023 (Table 2), we found that the number of individuals died from germinated seeds to seedlings ($_nD_1$) was the highest, which leads the corresponding highest age-specific mortality rate ($_nm_1$) and age-specific death probability ($_nq_1$). The smallest coefficients associated with these mortality risks occurred in small-medium trees at age class 4.

The survivorship curve showed a reverse sigmoid pattern (Fig. 4a). That is, the decreasing rate of age-specific survival probability (l_x) slowed down in smaller age classes (1–4; i.e., shown as Type III concave curve), but speeded up in larger age classes (4–6; i.e., show as Type I convex curve). This pattern of survivorship trend is the result of a U-shape mortality curve (Fig. 4b). That is, the age-specific death probability (q_x) first decreased then increased with age classes. The transition of the temporal direction of death probability occurred in small-medium trees at age class 4.

4. DISCUSSION

In this study, we found that *Q. chungii* increased in its overall abundance, frequency and tree size in the last decade, suggesting active regeneration and fast growth rate of*Q. chungii* . These results indicate the effectiveness of conservation efforts from establishing the nature reserve. However, the in-depth analyses of population structures warn potential risks of the future population development of *Q. chungii* .

The age structure of *Q. chungii* population in 2023 shows a pyramidal shape, with a sharp decline in the numbers of individuals from germinated seeds to seedlings and from seedlings to saplings. Saplings, a key stage for determining the future population, had a low number of individuals. These lead to the high **age-specific death probabilities at the early developmental stages.** These results indicate potential risks of population decline in the future. The observed decline in sapling proportion from 2013 to 2023 may signify a population decline trend within the species. This decrease could be attributed to either

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accelerated ontogenetic progression of saplings into larger size classes or elevated mortality rates during early developmental stages and within the sapling cohort. If mortality factors predominate, it underscores a potential population decline over the past decade.

The seed-to-seedling stage may be the most important period limiting the regeneration of *Q. chungii* population, because the highest mortality probabilities occurred from germinated seeds to seedlings. This is also consistent with our observation in the field. We found a very low density of seedlings with **DBH <1cm** in 2023. Only one of them may be produced from seed, while the others were evidently sprouted from roots of established trees. The scarcity of seedlings produced from seeds were already spotted in more than a decade ago (Wang et al. 2011), which may be one of the reasons driving the decadal decline of sapling proportion observed in this study. The dependence of clonal reproduction can be one of the most important reasons driving the highly aggregated spatial distribution of*Q. chungii* in natural forests (Wang et al. 2011). The aggregated distribution may increase the risk from pests and diseases. The reduced genetic diversity due to clonal reproduction may further increase these risks (Gilbert and Webb 2007, Bagchi et al. 2014, Liu et al. 2015, Liang et al. 2016), thus threatening the health and development of *Q. chungii* population in the future.

We estimated the number of germinated seeds from historical data of seeds. We assumed that trees with larger basal area will produce more germinated seeds, because larger trees can obtain more resources and produce more seeds (Visser et al. 2016). We acknowledge that the production and germination of seeds are complex processes determined by multiple factors, such as climate, soil, animal predation, plant physiology and human disturbance (Donohue et al. 2010, Baskin and Baskin 2014). The accuracy of our estimation approach thus relies on how these biotic and abiotic factors change in the past decade within the nature reserve. We thought that these changes should be slow due to the relative short temporal duration and the prevention from human activities by administrative office of the nature reserve. The findings of a high number of germinated seeds were also confirmed from the recent field observation by the officers of the nature reserve. But most of the seeds were found to be eaten by boars and rodents.

Despite the high predation risks from mammals, the structural and physiological traits of *Q. chungii* may also drive the severe decline in population numbers from seeds to seedlings. The germination pore of *Q. chungii* seed locates at a key place for water transportation, which may make it vulnerable to rapid water deficits (Sun et al. 2021). *Q. chungii* has a substantially delayed shoot emergence following a fast root emergence. The breakage of this shoot dormancy often needs 3–5 months with warm temperature (Sun et al. 2021). These seed traits can make*Q. chungii* very sensitive to precipitation and temperature abnormality, thus reducing the probability of transition from seeds to seedlings.

The age-specific death probability of *Q. chungii***first decreased then increased with age classes, resulting in a U-shape pattern. Large and tall trees are more vulnerable to disease, wind, and other causes of death (Lu et al. 2021, Fernandez-de-Una et al. 2023), which may drive the increasing mortality probability from medium to large trees.**

5. CONCLUSIONS

In this study, we found significant increases in tree density and size of the rare and endanger oak species *Q. chungii* . However, the high mortality probabilities from seeds to seedlings and saplings suggest a potential risk of regeneration failure and population decline in the future. The low transition probability from seeds to seedlings could be the reasons of high predation pressure of seedlings from mammals, sensitivities of seed germination to precipitation and temperature. These highlight the importance to study the impacts of multitrophic interactions and climate change on *Q. chungii* population dynamics in the future. This study improves the prediction of population development of *Q. chungii* and provide theoretical guidance for the conservation of *Q. chungii* .

AUTHOR CONTRIBUTIONS

Xueer Zhong: Writing – original draft (lead); writing – review and editing (equal); methodology (equal);

investigation (equal); data curation (lead); formal analysis (lead); visualization (lead); conceptualization (equal). **Wenbin Li:** Writing – original draft (lead); writing – review & editing (lead); methodology (equal); investigation (equal); supervision (lead); conceptualization (lead); project administration (equal). **Zhenji Li:** Writing – review & editing (equal); methodology (supporting); investigation (equal); funding acquisition (lead); conceptualization (equal); project administration (equal). **Yonghui Huang:** Writing – review & editing (equal); methodology (equal); investigation (supporting); project administration (supporting). **Xinfeng Chen:** Writing – review & editing (supporting); investigation (equal); project administration (supporting). **Lihan Huang:** Writing – review & editing (supporting); investigation (equal); project administration (supporting). **Ya Wang:** Writing – review & editing (supporting); Investigation (equal). **Yuxin Chen** : Writing – original draft (supporting); Writing – review & editing (supporting); Investigation (equal); Funding acquisition (lead); Conceptualization (equal).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

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DATA AVAILABILITY STATEMENT

The datasets that supporting the findings of this study are available in the figshare at https://figshare.com/s/d9adcf4b14c940891840.

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Tables and Figures:

TABLE 1 Definition and calculation of coefficients in static life table.

Coefficient	**Definition and calculation**
x	Age at the start of each age class. We assume xs are 1–7 for age classes 1–7.
n	Interval length between age classes, which is assumed to be one in this study.
${}_n\boldsymbol{N_x}$	Observed number of individuals alive in the middle of an age interval. ${}_nN_x$ **in the first age class was calc**
${}_n\boldsymbol{N_x}$*****	Estimate of ${}_n\boldsymbol{N_x}$ by smoothing **(see Materials and Methods)**.
${}_n\boldsymbol{D_x}$	Number of individuals died during the observational period: ${}_n\boldsymbol{D_x} = {}_n\boldsymbol{N_x}\boldsymbol{*} - {}_n\boldsymbol{N_{x+n}}\boldsymbol{*}$. All individuals are ass

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Coefficient	Definition and calculation
${}_n\boldsymbol{m_x}$	Age-specific mortality rate: ${}_nm_x = {}_nD_x \,/\, {}_nN_x$.
${}_n\boldsymbol{a_x}$	Average length of survival time in each age range, which is assumed to be 0.5.
${}_n\boldsymbol{q_x}$	Probability of death from ages x to x+n: ${}_nq_x = (n\cdot{}_nm_x) \,/\, (1+(n-{}_na_x)\cdot{}_nm_x)$. ${}_nq_x$ of the last age class is assu
${}_n\boldsymbol{p_x}$	Probability of survival from ages x to x+n: ${}_np_x = 1-{}_nq_x$.
l_x	Relative number of individuals entering the interval at age x. $l_{x+n} = l_x{}^*{}_np_x$. The initial population size enter
${}_n\boldsymbol{d_x}$	Relative number of individuals died from ages x to x+n: ${}_nd_x = l_x - l_{x+1}$.

TABLE 2 Static life table of *Quercus chungii* population in 2023.

Age classes (cm)	x	${}_nN_x$	${}_nN_x{}^*$	${}_nD_x$	${}_na_x$	${}_nm_x$	${}_nq_x$	${}_np_x$	l_x	${}_nd_x$
Germinated seeds	1	5506	5506	5464	0.500	0.992	0.663	0.337	1.000	0.663
DBH < 2.5	2	46	42	8	0.500	0.190	0.174	0.826	0.337	0.059
2.5 [?] DBH < 12.5	3	21	34	9	0.500	0.265	0.234	0.766	0.278	0.065
12.5 [?] DBH < 22.5	4	34	25	1	0.500	0.040	0.039	0.961	0.213	0.008
22.5 [?] DBH < 32.5	5	33	24	10	0.500	0.417	0.345	0.655	0.205	0.071
32.5 [?] DBH < 42.5	6	6	14	9	0.500	0.643	0.487	0.513	0.134	0.065
DBH [?] 42.5	7	4	5	5	0.000	1.000	1.000	0.000	0.069	0.069

Note: The calculation of static life table is based on population survey in total area of 3800 m^2.

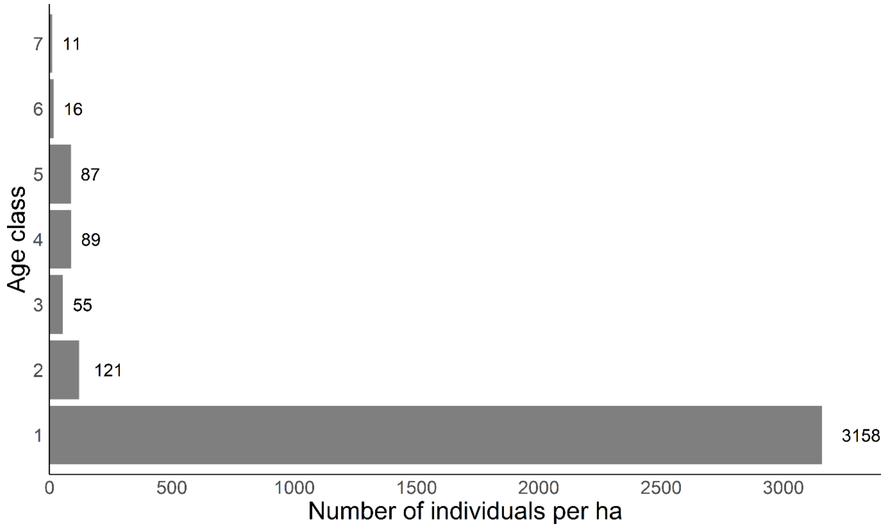

FIGURE 1 Age structure of *Quercus chungii* population in 2023. Numbers besides bars indicate the numbers of individuals per ha within each age class. The population number in the first age class was calculated by assuming a proportional relationship between the number of germinated seeds and overall basal area of the population; the population numbers of other age classes (2–7) are from field survey. Detailed information about the age structures is shown in Table 2.

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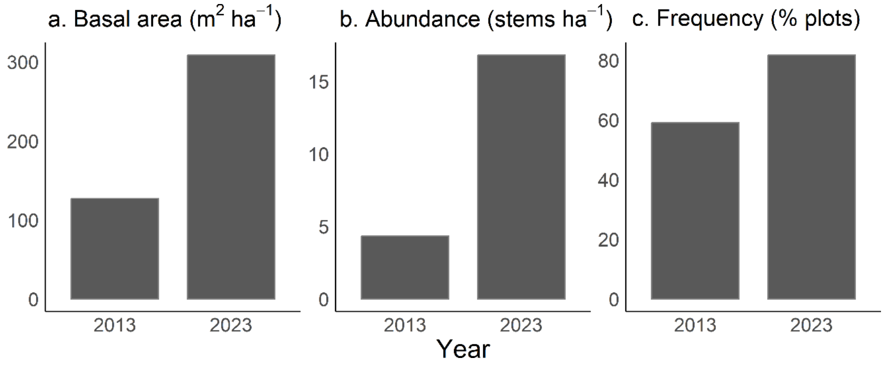

FIGURE 2 ***Quercus chungii*** **increases in basal area (a), abundance (b) and frequency (c) from 2013 to 2023. Frequency was calculated as the percentage of 10 m × 10 m plots of** ***Quercus chungii*** **presence.**

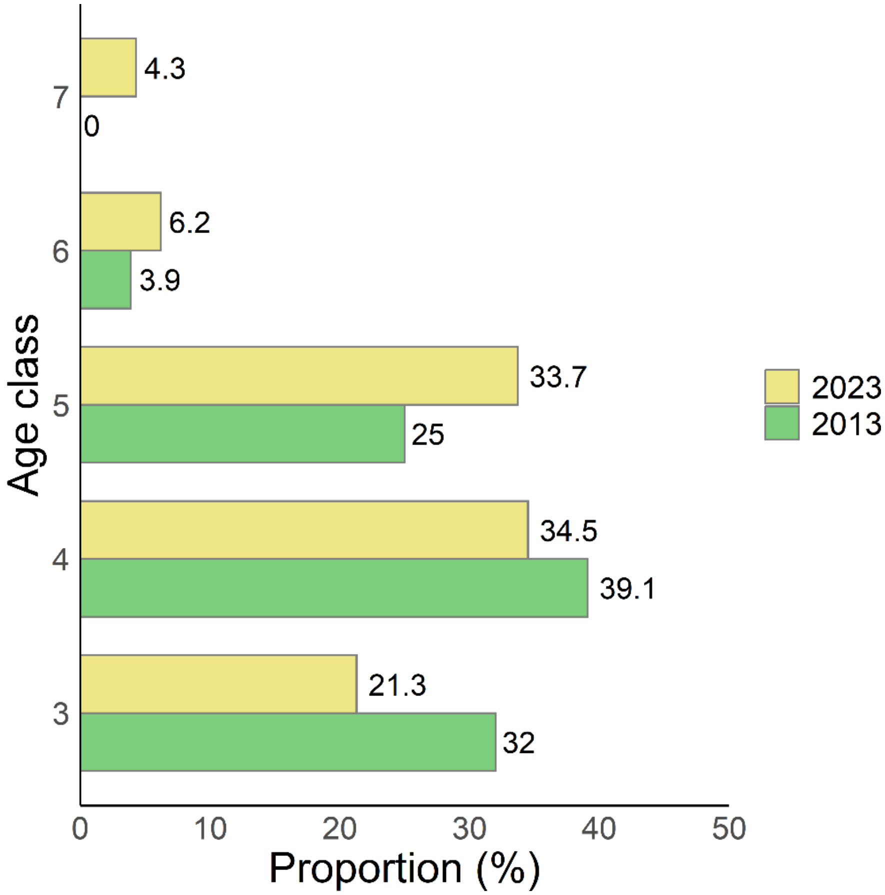

FIGURE 3 Difference in age structures of ***Quercus chungii*****population between 2013 and 2023. Proportions of individuals were calculated for age classes 3–7 surveyed in both years. Numbers besides bars represent the proportions within each age class in each year. Detailed information about the age structures is shown in Table 2.**

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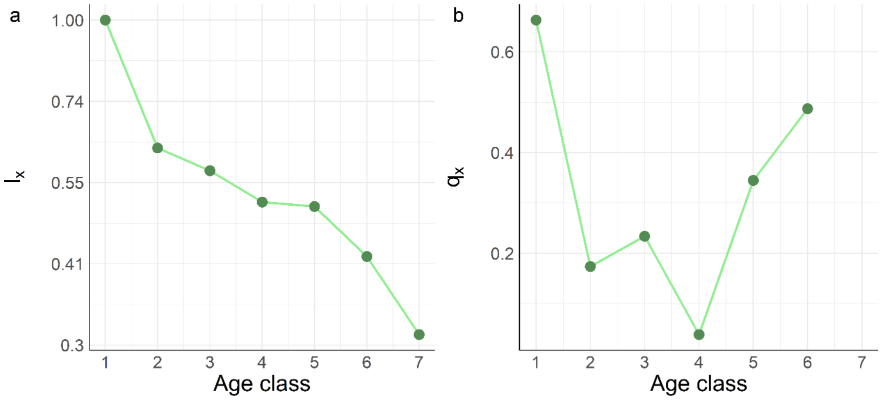

FIGURE 4 Survivorship (a) and mortality (b) curves of*Quercus chungii* population in 2023. Probability of survival to age class x (l_x) was plotted in log-transformed scale but shown with its original values, as proportional changes inl_x can be better compared with the changes in age specific probabilities of death (q_x). **Detailed information about the age structures is shown in Table 2.**