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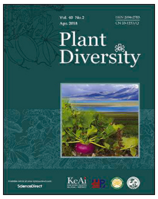

Research paper

Evolution of fruit functional traits provides insights into the drivers of cycle-cup oaks (*Quercus* section *Cyclobalanopsis*) diversification in evergreen broadleaf forests

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ABSTRACT

The impact of key traits on lineage diversity remains a central focus in macroevolutionary research. Seeds, encapsulated within fruits, carry the complete genetic blueprint of their species, and the capacity of their adaptive evolution to diverse environmental conditions shapes species origination and extinction dynamics. However, the role of specific traits in driving species diversification under changing environmental conditions remains poorly understood, particularly among taxa that produce desiccation-sensitive seeds. In this study, we reconstructed the phylogenetic relationships of *Quercus* section *Cyclobalanopsis* based on whole-genome resequencing data from 52 species, covering approximately 50% of the section. We investigated six fruit traits—fruit volume, shape, maturation period, cotyledonary petiole, embryonic axis position and dormancy type—through experimental observations and data collection. The influence of these traits, climatic variables, and phylogenetic signal on diversification rates, along with the effects of climatic variables on these traits were analysed. Our findings reveal substantial diversity in fruit trait states within the section *Cyclobalanopsis*. Climates characterized by hot summers and wet-cold winters provide favorable habitat conditions that promote speciation. Furthermore, ancestral fruit traits, such as small acorns, oblong ellipsoid shapes, normal cotyledonary petioles, and embryonic axes near the apex, along with the derived trait of annual fruit maturation, were associated with increased net diversification rates. These ancestral fruit traits, adapted to the subtropical evergreen broad-leaved forests of East Asia, facilitated rapid evolutionary radiation during the Miocene through climatic niche innovation. In contrast, species inhabiting tropical landscapes appear to adapt to local environmental changes through fruit trait innovations, such as larger fruits and rapid germination.

1. Introduction

In the context of global climate change, plant lineages are undergoing spatial redistributions, with those exhibiting adaptive functional traits and enhanced survival abilities more capable of persisting across environmental gradients (Wiens and Donoghue, 2004; Donoghue, 2008; Crisp et al., 2009; You et al., 2024). Functional trait diversity varies among environments and closely

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related taxa, influenced by abiotic factors and evolutionary history, balancing environmental adaptation and phylogenetic conservatism in shaping biodiversity (Peres-Neto et al., 2012; Sternberg and Kennard, 2014). Understanding how functional traits affect community assembly, ecosystem processes, and biodiversity across broad spatial and temporal scales is a key focus in community ecology and evolutionary biology (Ackerly, 2009; Mitchell et al., 2015; Alcantara et al., 2018; Xue et al., 2020; Liu et al., 2024a). Quantifying community assemblage through multidimensional diversity indices has become central to functional ecology (Cadotte et al., 2013; Han et al., 2020; Xue et al., 2020; You et al., 2024). Although functional and phylogenetic diversity represent distinct biodiversity dimensions, they remain interconnected through selection-driven trait emergence-where functional traits are shaped by natural selection on genetic variation, while phylogenetic reconstructions decode evolutionary trajectories by mapping trait conservatism to shared ancestry through comparative analyses (Cadotte et al., 2013; Tucker et al., 2018). Thus, integrating trait-based approaches with phylogenetic and environmental contexts enhances our understanding of biodiversity patterns and the mechanisms driving them (Coelho et al., 2023; Liu et al., 2024a; Zhong et al., 2025).

Many functional traits play a critical role in species adaptation to environmental pressures, facilitating successful recruitment and persistence within complex ecological niches (Kempel et al., 2013; Read et al., 2014; Xia et al., 2025). In particular, seed regeneration traits, encompassing diverse dispersal mechanisms (Poschlod et al., 2013), variable energy and nutrient storage capacities (Welch, 2024), and complex germination and dormancy regulation (Donohue et al., 2010; Willis et al., 2014; Saatkamp et al., 2019), are fundamental to plant evolutionary success, conferring adaptive advantages that have facilitated remarkable diversification and optimized reproductive strategies across heterogeneous environments (Liu et al., 2024b; Ma et al., 2024; Zhang et al., 2024a; Wang et al., 2025). Understanding how these key functional traits shape diversification is central to uncovering the mechanisms driving lineage radiation and expansion in plants.

Existing research has primarily concentrated on drought-tolerant seeds or orthodox species (sensu Roberts, 1973), such as exploring ecological trade-offs between seed size and quality and their potential influence on diversification processes (Díaz et al., 2016). Such orthodox seeds can withstand desiccation to remarkably low moisture content (MC) levels (approximately 3–7% on a fresh weight basis) and are commonly found in seasonal climates (Wyse and Dickie, 2017). However, research on desiccation-sensitive or recalcitrant seeds remains notably insufficient, even though global estimates suggest that up to 15% of species produce seeds that are sensitive to desiccation (Wyse and Dickie, 2017). These seeds lose viability when moisture content reaches below approximately 20% (fresh weight basis) and are restricted to humid environments or stable climatic zones with water availability such as tropical rainforests (Wyse and Dickie, 2017). Against the backdrop of global climate change, decreasing rainfall and frequent droughts have placed recalcitrant seeds at higher risk of extinction. This not only threatens species survival but could also substantially alter the long-term diversification trajectories of associated lineages. Therefore, it is necessary to urgently investigate their evolutionary adaptation mechanisms and ecological vulnerability (Pritchard et al., 2022; Jaganathan et al., 2024). Although they may represent ancient reproductive strategies, their adaptive evolutionary pathways that either promote or constrain diversification, climate response thresholds, and synergistic relationships with dormancy traits remain systematically unresolved (Dickie and Pritchard, 2002; Berjak and Pammenter, 2008; Jaganathan, 2021). In particular, whether recalcitrant seeds represent an ancestral state or a derived adaptation involving diverse dormancy strategies remains unclear. The extent to which various forms of dormancy contribute to reproductive stability and influence species richness across plant lineages remains an open question that requires further investigation.

Quercus provides an ideal system to explore these questions, as it comprises approximately 450 species-making it the most species-rich and geographically widespread genus within the Fagaceae family. It is widely distributed across various ecosystems in the Northern Hemisphere and holds significant ecological, economic, and cultural value (Gugger and Cavender-Bares, 2013; Carrero et al., 2020; Fazan et al., 2020; Wang et al., 2025). Notably, the fruits of nearly all *Quercus* species—commonly known as acorns—are highly sensitive to desiccation and are classified as recalcitrant (Jaganathan and Phartyal, 2024). Across Fagaceae, most genera (with the exception of *Fagus* and *Chrysolepis*) produce recalcitrant seeds (Jaganathan, 2021; Li et al., 2024). This pattern suggests that recalcitrance may represent a phylogenetically conserved trait at the family level, offering important insights into its evolutionary origins and potential contribution to the remarkable species diversity observed in Fagaceae—particularly within the *Quercus*.

Beyond their desiccation sensitivity, *Quercus* seeds are also remarkable for their frequent co-occurrence of recalcitrance and dormancy—a combination that is relatively uncommon in the plant kingdom. Typically, recalcitrant seeds germinate rapidly after dispersal to escape drought stress and enhance seedling establishment (Farnsworth, 2000; Dalling et al., 2011). However, many *Quercus* species exhibit physiological dormancy (PD), due to delay in shoot emergence, i.e., epicotyl dormancy, suggesting a more complex germination strategy than previously assumed (Sun et al., 2021; Jaganathan and Phartyal, 2024). In PD, germination is delayed because embryo lacks sufficient growth potential to protrude the seed coat, whereas dormancy associated with epicotyl allows radicle to emerge but halts the shoot emergence until suitable environmental cues alleviate the block (Baskin and Baskin, 2014, 2021). These dormancy mechanisms, despite their differences, both functions to postpone complete seedling establishment—potentially providing a fitness advantage in seasonally moist environments. In the revised dormancy classification system, Baskin and Baskin (2021) included epicotyl dormancy to be a subclass of PD.

Adding to this complexity, the position of the embryonic axis within *Quercus* seeds has been shown to vary from proximal (near the scar) to distal (near the apex), reflecting significant morphological diversity among species (Jaganathan and Phartyal, 2024). This structural difference strongly influences the germination mode and prompted these authors to propose a classification system across Fagaceae: Type I (embryonic axis near the fruit base, sitting immediately above the apex) and Type II (embryonic axis positioned away from the base, close to the scar tissue). Such variation could influence desiccation sensitivity, germination strategies and possibly dormancy, with axes near the apex generally better protected against moisture loss due to the protection offered by the pericarp (Xia et al., 2012; Kang et al., 2023). Indeed, diversity in embryonic axis placement is considered an adaptive trait, enabling *Quercus* species to thrive across different environmental conditions. However, the position of the embryonic axis remains far less studied, even though this morphological divergence reflects developmental plasticity and may be linked to ecological niche differentiation and adaptation. A particularly illustrative group within *Quercus* is the section *Cyclobalanopsis*, which exemplifies the complexity and diversity described above. Phylogenetic evidence places the section *Cyclobalanopsis* within subgenus *Cerris* as a monophyletic group of evergreen oaks, comprising roughly 90 to 120 species (Denk et al., 2017; Deng et al., 2018; Carrero et al., 2020). These species are widely distributed across the subtropical evergreen broad-leaved forests of East and Southeast Asia. Importantly, the group has evolved under prolonged exposure to highly heterogeneous climatic conditions, resulting in pronounced morphological and physiological variation in fruit traits (Farnsworth, 2000; Jansen et al., 2006; Xia et al., 2012; Yi et al., 2013; Song et al., 2019; Xu et al., 2020; Jin et al., 2024). As such, the section *Cyclobalanopsis* provides a promising model for exploring the evolutionary pathways of recalcitrant seeds, the ecological function of dormancy, and the interplay between seed traits and environmental adaptation.

Here, we constructed the most up-to-date phylogenetic framework for *Quercus* section *Cyclobalanopsis* and investigated the evolutionary significance of fruit functional traits within its phylogenetic patterns. Our central goal was to understand the coevolution of fruit morphological characteristics (volume and shape) and seed physiological attributes (germination pattern and dormancy type) in relation to key climatic variables, specifically temperature and precipitation regimes. Based on this phylogenetic framework, we compiled a comprehensive dataset of fruit functional traits across representative species. This approach illuminates the evolutionary trajectory of these traits and their influence on diversification patterns and species vulnerability. By integrating climatic data and functional trait information within a phylogenetic context, we aim to uncover signatures of adaptive evolution manifested in trait-climate niche associations. More specifically, this study examines 52 species within *Quercus* section *Cyclobalanopsis* to: (1) elucidate the evolutionary history of fruit functional traits; (2) investigate potential adaptive evolution through fruit trait-climate niche correlations; and (3) explore the role of fruit functional traits in species diversification. Our findings provide crucial insights into the drivers of species diversification in subtropical evergreen broadleaf forests.

2. Materials and methods

2.1. Phylogeny

To elucidate the evolutionary history of fruit functional traits, we collected leaf samples and specimens from 52 species of *Quercus* section *Cyclobalanopsis* between 2011 and 2023 from various locations across China. The relevant collection site information is presented in Table S1. All voucher specimens are deposited at the Herbarium of Shanghai Chenshan Botanical Garden (CSH), Shanghai, China. Total genomic DNA was extracted from silica-dried leaves using a modified cetyl trimethyl ammonium bromide (CTAB) protocol (Doyle and Doyle, 1987). Sequencing (150 bp pair-end) for all the samples was performed on the DNBSEQ platforms with a sequencing depth of 20× . These data are part of our unpublished study focusing on the phylogenomics of Eurasian oaks which is unpublished with the project number of PRJCA041903.

We got the single nucleotide polymorphisms (SNPs) after data filtered (Fastp v.0.20.0), data mapping (BWA v.0.7.17), and SNPs calling (VCFtools v.0.1.16) (Li and Durbin, 2009; Danecek et al., 2011; Chen, 2023). Consensus genomes for each sample were constructed based on the reference genome of *Quercus lobata* by BCFtools v.1.19 (Danecek et al., 2021). Finally, we used ASTRAL-III (Zhang et al., 2018) to construct the phylogenomic tree of *Quercus* section *Cyclobalanopsis*. Divergence times were estimated using a relaxed molecular clock model in the Phylogenetic Analysis by Maximum Likelihood (PAML) software (Yang, 2007), employing the approximate likelihood method. For time calibrations, we applied crown calibration points for the genus *Quercus* and section *Cyclobalanopsis*, using 95% highest posterior density (HPD) intervals of 55.18–60.52 million years ago (Mya) and 47.7–48.98 Mya, respectively (Hipp et al., 2020). The MCMC chain was run for 50 million generations, with samples taken every 1000 generations. The first 10% of samples discarded as burn-in. Convergence was assessed using TRACER v.1.7 (Rambaut et al., 2018).

2.2. Branch-specific diversification rates

We used the Bayesian method implemented in RevBayes v.1.2.5 (Höhna et al., 2016) to estimate the diversification rate of each branch on the phylogenetic tree. This method assumes that the evolutionary rates of individual branches are sampled from a continuous distribution, which is discretized into several rate categories. A Markov process is subsequently employed to model the transition of rate categories throughout the tree. Following the tutorial provided at "https://revbayes.github.io/tutorials/", we performed Bayesian MCMC sampling to obtain the posterior distribution of diversification rates for each branch. Subsequently, we applied the Episodic Diversification Rate Estimation model to infer changes in speciation and extinction rates over time. We set NUM_INTERVALS to 100 to allow for high-resolution detection of rate shifts throughout evolutionary history. Finally, visualized the rate variation and lineage heterogeneity using the R package "*RevGadgets*" (Tribble et al., 2022).

2.3. Fruit collection

Fruits/acorns of *Quercus* section *Cyclobalanopsis* were collected during their natural dispersal period. Only healthy-looking fruits were selected by visual inspection, collected from the ground within a few days of falling, and gently pressed between fingers to assess freshness before, being transported to the laboratory at the Shanghai Chenshan Botanical Garden, Shanghai, China, by air freight. The fruits arrived within a week of collection were inspected and any debris, soil matter, or cupules were carefully removed. We conducted a flotation test to eliminate fruits that were empty or infested by insects. The full, intact fruits were then disinfected using a 1% potassium permanganate solution for 30 min, followed by three times rinse with distilled water to ensure cleanliness. Finally, the fruits were sealed in zip-lock bags and stored in a cryogenic storage cabinet at 4 °C until used in the experiments. Unless otherwise indicated, all experiments were conducted within three months to ensure that the physiological maturity of the fruits remained unchanged, as they would naturally experience such a low temperature if they had persisted in the soil.

2.4. Germination and dormancy tests

Germination and dormancy tests were conducted in illuminated incubators under a consistent 12/12-h light/dark cycle, with the photoperiod aligning with the 12-h high-temperature phase of the diurnal cycle. When sufficient fruits were available, we employed five temperature regimes (15/5 °C, 20/10 °C, 25/15 °C, 30/20 °C, and 35/25 °C) to assess root and shoot germination. In cases of limited fruit availability, germination was tested at 20/10 °C, 25/15 °C, and 30/20 °C, or fewer temperatures. Each treatment included three replicates with either 20 or 10 fruits per replicate. Fruits were planted in seedling bags (25× 20 cm) filled with vermiculite and were monitored and watered every two days over a period of 28 days. Shoot germination was recorded for 28 days starting from the date of root germination. Radicle and shoot germination were defined by the emergence of at least 0.5 cm. The experiment spanned four months, after which final germination rates were used to determine dormancy class. Based on our observations and classification of dormancy in Baskin and Baskin (2014), we classified species whose seeds completed both root and shoot germination within 30 days as non-dormant (ND). If seed required more than 30 days for radicle emergence, they were categorized as PD (PD subclass 1). In species where the radicle emerged within 30 days but shoot emergence was delayed by more than 30 days, the seeds were classified as epicotyl physiological dormancy ePD (PD subclass 2). During the process, we also observed cotyledonary petiole morphology (normal or elongated). Cotyledonary petiole morphology and dormancy type traits for 14 *Quercus* section *Cyclobalanopsis* species are provided in Table S2. In cases where fruits were extremely limited, we conducted germination experiments primarily to observe the embryonic axis position (apex or scar) and the cotyledonary petiole morphology. Additionally, we compiled available information on seed dormancy classes of the section *Cyclobalanopsis* species from previously published studies (Soumoy et al., 1996; Xia et al., 2015, 2016; Xu et al., 2020; Choi et al., 2022), as summarized in Table S2.

2.5. Morphometric measurement

We examined fruit characteristics of 52 *Quercus* section *Cyclobalanopsis* species, analyzing one continuous trait (fruit volume), four binary traits (fruit shape, maturation period, cotyledonary petiole morphology, and embryonic axis position), and one categorical trait (dormancy class). The dormancy class of the species was assigned as ND, PD, and ePD. For all species, we defined the distance from the fruit scar to the apex as the height. Species with a height greater than the cross-sectional diameter were classified as prolate spheroid, while those with a height smaller than the cross-sectional diameter were classified as oblate spheroid. Fruit shape (oblong ellipsoid and oblate spheroid) was determined based on size data and confirmed with the information available on the Flora of China, and related literature (Huang et al., 1999). We measured their morphological data of fresh fruits to calculate fruit volume using the ellipsoid volume formula: 4/3* π* length* width* height. For each species, 5 to 30 fruits were measured, and the average value was used for analysis. For species without available fresh fruit samples, data were obtained from the *Flora of China* and other publications (Serit et al., 1991; Li et al., 2016; Kim et al., 2018; Hirayama et al., 2019). Information on fruit maturation period (annual or biennial) was obtained from literatures (Huang et al., 1999; Denk et al., 2017). Detailed information is provided in Table 1.

2.6. Ancestral state reconstruction

Based on the established phylogenetic framework, we employed the stochastic character mapping (SIMMAP) method implemented in the "*phytools*" package in R (Bollback, 2006; Revell, 2012) to reconstruct ancestral states for four categorical traits. This method first fits a continuous-time reversible Markov model, and then uses the fitted model along with the observed tip states on the tree to simulate random character histories. We evaluated three continuous-time Markov models—Equal Rates (ER), Symmetrical Rates (SYM), and All Rates Different (ARD)—based on their AICc scores. Ancestral state reconstructions for each trait were generated from 100 simulations, and the posterior probabilities of each character state at each node were summarized accordingly. For continuous character data on fruit volume, the fastAnc algorithm within the "*phytools*" package was used to estimate ancestral states with maximum likelihood.

2.7. Phylogenetic signals of traits

To assess the strength of phylogenetic signal in fruit traits, we calculated Blomberg's K (Blomberg et al., 2003) and Pagel's λ (Pagel, 1999) using the "*phylosig*" function from the R package "*phytools*" (Revell, 2012). Blomberg's K quantifies the degree of trait conservatism across a phylogenetic tree; higher K values indicate greater similarity among closely related species and thus a stronger phylogenetic signal. Conversely, K values less than 1 suggest that closely related species exhibit greater trait divergence than expected under a Brownian motion model. Pagel's λ estimates the phylogenetic dependence of trait variation via maximum likelihood; a λ value of 1 indicates that trait variation fully conforms to the phylogenetic structure, whereas a λ value of 0 suggests complete phylogenetic independence. All analyses were conducted using phylogenetic tree of 52 *Cyclobalanopsis* species. Statistical significance was evaluated by comparing observed values to a null distribution generated through 1,000 random permutations of trait data across the tree tips.

2.8. Relationship of climate on trait variation

To investigate the correlation between fruit traits and climatic niches of *Quercus* section *Cyclobalanopsis*, as well as the climatic drivers of species diversification within this section, we gathered distribution data (the coordinates of latitude and longitude) of each species from multiple sources, including the Global Biodiversity Information Facility (GBIF, 2024) , Chinese Virtual Herbarium (CVH, 2024), Chinese Field Herbarium (CFH, 2024), and our field survey data. We reviewed data for all species, removing points located in botanical gardens and those with erroneous coordinates. To reduce sampling bias, we retained only one occurrence per 2.5× 2.5 arc-minute grid cell. All records were cross-verified to ensure alignment with species distribution records, resulting in 3,214 unique occurrence points (Table S3). We extracted 19 bioclimatic variables from WorldClim v.2.1 (Fick and Hijmans, 2017) for the period from 1970 to 2000, which describe the primary temperature and precipitation dimensions for each species. Based on previous research (Onstein et al., 2016; Xia et al., 2022), we applied a square root transformation to eight precipitation-related variables to approximate normality. We computed the median meteorological data for each species across different locations generating 19 climate variable values per species. We performed a Principal Component Analysis (PCA) of climate variables across 52 species with "*FactoMineR*" package (Lê et al., 2008). The results of first two principal components (PC1 and PC2) and 19 climate variable values were plotted by function "*fviz_pca_biplot*" in "*factoextra*" package (Kassambara and Mundt, 2016). Heat map of Pearson correlation coefficients between climate variables and principal components were explored by "*pheatmap*" package (Kolde, 2010).

The relationship between fruit traits and climate variables was evaluated using Phylogenetic Generalized Least Squares (PGLS) regression, implemented in R via the "*pgls*" function from the "*caper*" package (Orme et al., 2018). The PGLS approach concurrently estimates both phylogenetic signal and regression parameters while accounting for the phylogenetic structure in model residuals.

2.9. Diversification rates associated with climate and traits

We applied the Quantitative State Speciation and Extinction (QuaSSE) model to investigate the influence of climate drivers on

Table 1

Summary of fruit traits and dormancy characteristics for 52 species of *Quercus* section *Cyclobalanopsis*. Fruit volume is measured in cm^3, while fruit shape is classified as oblong ellipsoid (OE) or oblate spheroid (OS). Fruit maturation period is categorized as annual or biennial, cotyledonary petiole morphology as normal or elongated, or embryonic axis position as apex or scar. Dormancy type is assigned as non-dormant (ND), physiological dormancy (PD), or epicotyl physiological dormancy (ePD).

Species	Fruit volume (cm^3)	Fruit shape	Fruit maturation period	Cotyledonary petiole morphology	Embryonic axis position	Dormancy type
Quercus arbutifolia	1.24	OE	Biennial	Normal	Apex	PD
Q. argyrotricha	0.57	OE	Annual	Normal	Apex	PD
Q. augustinii	0.71	OE	Biennial	Normal	Apex	ND
Q. austrocochinchinensis	9.40	OS	Biennial	Elongated	Scar	ePD
Q. austroglauca	4.85	OE	Biennial	Normal	Apex	PD
Q. bella	7.18	OS	Annual	Normal	Apex	ND
Q. blakei	7.95	OE	Annual	Normal	Apex	ND
Q. camusiae	2.57	OE	Biennial	Normal	Apex	PD
Q. championii	2.06	OE	Biennial	Normal	Apex	PD
Q. chapensis	3.69	OS	Biennial	Normal	Apex	ND
Q. chungii	1.89	OE	Biennial	Elongated	Scar	ePD
Q. daimingshanensis	1.86	OE	Biennial	Normal	Apex	PD
Q. delavayi	0.74	OS	Biennial	Elongated	Scar	ePD
Q. disciformis	3.67	OS	Biennial	Normal	Apex	PD
Q. edithiae	12.27	OE	Biennial	Normal	Apex	PD
Q. eumorpha	2.68	OE	Annual	Normal	Apex	ND
Q. fleuryi	12.27	OE	Annual	Normal	Apex	ND
Q. gambleana	2.36	OE	Annual	Normal	Apex	PD
Q. gilva	1.21	OE	Biennial	Normal	Apex	PD
Q. glabricupula	2.05	OS	Biennial	Normal	Apex	ND
Q. glauca	0.90	OE	Annual	Normal	Apex	PD
Q. helferiana	1.82	OS	Annual	Elongated	Scar	ePD
Q. hypophaea	2.55	OE	Biennial	Elongated	Scar	ePD
Q. kerrii	5.46	OS	Biennial	Elongated	Scar	ePD
Q. kiukiangensis	2.01	OE	Biennial	Normal	Apex	ND
Q. kouangsiensis	16.36	OE	Biennial	Normal	Apex	PD
Q. lamellosa	16.04	OS	Biennial	Normal	Apex	PD
Q. langbianensis	5.95	OE	Biennial	Normal	Apex	ND
Q. litseoides	0.86	OE	Biennial	Normal	Apex	ND
Q. lobbii	1.13	OE	Biennial	Normal	Apex	ND
Q. longinux	0.51	OE	Annual	Normal	Apex	PD
Q. morii	2.05	OE	Biennial	Normal	Apex	PD
Q. multinervis	0.94	OE	Biennial	Normal	Apex	PD
Q. myrsinifolia	3.13	OE	Biennial	Normal	Apex	PD
Q. neglecta	1.77	OE	Biennial	Normal	Apex	PD
Q. oxyodon	2.39	OE	Biennial	Normal	Apex	PD
Q. pachyloma	2.31	OE	Biennial	Normal	Apex	PD
Q. patelliformis	8.27	OS	Biennial	Normal	Apex	ND
Q. phanera	9.28	OE	Biennial	Normal	Apex	PD
Q. platycalyx	0.84	OE	Biennial	Normal	Apex	PD
Q. poilanei	1.95	OE	Biennial	Normal	Apex	PD
Q. rex	28.37	OS	Biennial	Elongated	Scar	ePD
Q. saravanensis	2.36	OE	Biennial	Normal	Apex	PD
Q. schottkyana	0.45	OE	Biennial	Normal	Apex	PD
Q. semiserrata	9.50	OE	Biennial	Normal	Apex	PD
Q. sessilifolia	1.42	OE	Biennial	Normal	Apex	PD
Q. shennongii	0.92	OE	Biennial	Normal	Apex	PD
Q. sichourensis	6.41	OS	Annual	Normal	Apex	PD
Q. stewardiana	0.80	OE	Biennial	Normal	Apex	PD
Q. tiaoloshanica	2.47	OE	Biennial	Normal	Apex	ND
Q. yingjiangensis	9.42	OS	Biennial	Normal	Apex	ND
Q. yonganensis	2.14	OE	Biennial	Normal	Apex	PD

species diversification. Five QuaSSE models of increasing complexity were constructed using the “*diversitytree*” package (FitzJohn, 2012): (1) constant λ; (2) linear λ; (3) sigmoidal λ; (4) linear λ with drift; and (5) sigmoidal λ with drift. The optimal model was selected based on the lowest corrected Akaike’s information criterion (AICc) value. To streamline the analysis, only morphological functions were fitted, utilizing scripts adapted from Zhang et al. (2021).

In addition, we employed the Binary State Speciation and Extinction (BiSSE; Maddison et al., 2007) and Hidden State Speciation and Extinction (HiSSE; Beaulieu and O’Meara, 2016) models to investigate how binary trait changes influence the diversification rates within *Quercus* section *Cyclobalanopsis*. The BiSSE analysis was conducted using the Maximum Clade Credibility (MCC) tree and implemented in R via the “*diversitytree*” package (FitzJohn, 2012). For each binary trait, we evaluated four diversification models using maximum likelihood (ML) estimation. Each model included three parameters: speciation rate (λ), extinction rate (μ), and transition rate (q). The parameter configurations were as follows: (1) λ free, μ free, q free; (2) λ equal, μ free, q free; (3) λ free, μ equal, q free; and (4) λ free, μ free, q equal. Model selection was performed using AICc scores. Additionally, MCMC simulations with 10,000 iterations were employed to estimate speciation, extinction, and net diversification rates.

While the BiSSE model is a widely used framework in large-scale phylogenetics (Gamisch, 2016), its underlying assumptions are often overly simplistic, potentially leading to Type I errors (Maddison et al., 2007; Maddison and FitzJohn, 2015; Rabosky and Goldberg, 2015). To address these limitations, the HiSSE model extends BiSSE by incorporating unmeasured, hidden factors that may influence the estimation of diversification rates for observed traits (Zhao et al., 2023). HiSSE enables the comparison of complex null models that account for feature-independent diversification. Following Beaulieu and O'Meara (2016) methodology, we constructed 25 HiSSE models using the "*hisse*" package in R. These included four models analogous to binary state speciation and extinction, four null HiSSE models based on character-independent diversification (CID), and 17 models incorporating hidden state-dependent diversification. AICc scores were again used for model selection, and model-averaged marginal ancestral state reconstructions were utilized to calculate speciation, extinction, and net diversification rates.

To further explore diversification drivers, we applied the Multiple States Speciation and Extinction (MuSSE; FitzJohn, 2012) model, focusing specifically on seed dormancy types. This analysis was also conducted in R using the "*diversitytree*" package. For the multi-state seed dormancy trait, six MuSSE models were fitted with varying parameter constraints: (1) all parameters free; (2) λ free, with μ and q equal; (3) μ free, with λ and q equal; (4) λ equal, with μ and q free; (5) μ equal, with λ and q free; and (6) q equal, with λ and μ free. AICc scores were used to evaluate model performance, and posterior probability distributions were presented to illustrate results. Additionally, we employed QuaSSE models to estimate speciation, extinction, and net diversification rates, as well as to assess their association with the continuous trait of fruit volume.

3. Results

3.1. Phylogenetic and diversification rates

Using whole-genome resequencing data from 52 species, we reconstructed the phylogenetic relationships of the section *Cyclobalanopsis*, representing approximately 50% of the species in this group (Fig. 1a). The inferred phylogenetic structure and divergence times are broadly consistent with previous studies (Deng et al., 2018; Hipp et al., 2020; Jin et al., 2024). The 52 sampled species were resolved into two major lineages encompassing six clades: (1) the compound trichome base lineage (CTB lineage), comprising the Gilva and Helferiana clades; (2) the single-celled trichome base lineage (STB lineage), including the Semiserrata, Acuta, Glauca, and Cyclobalanoides clades. Estimates of branch-specific diversification rates revealed a pronounced increase around the Oligocene–Miocene boundary, during which both major lineages underwent rapid diversification, giving rise to multiple distinct evolutionary clades (Fig. 1b and S1).

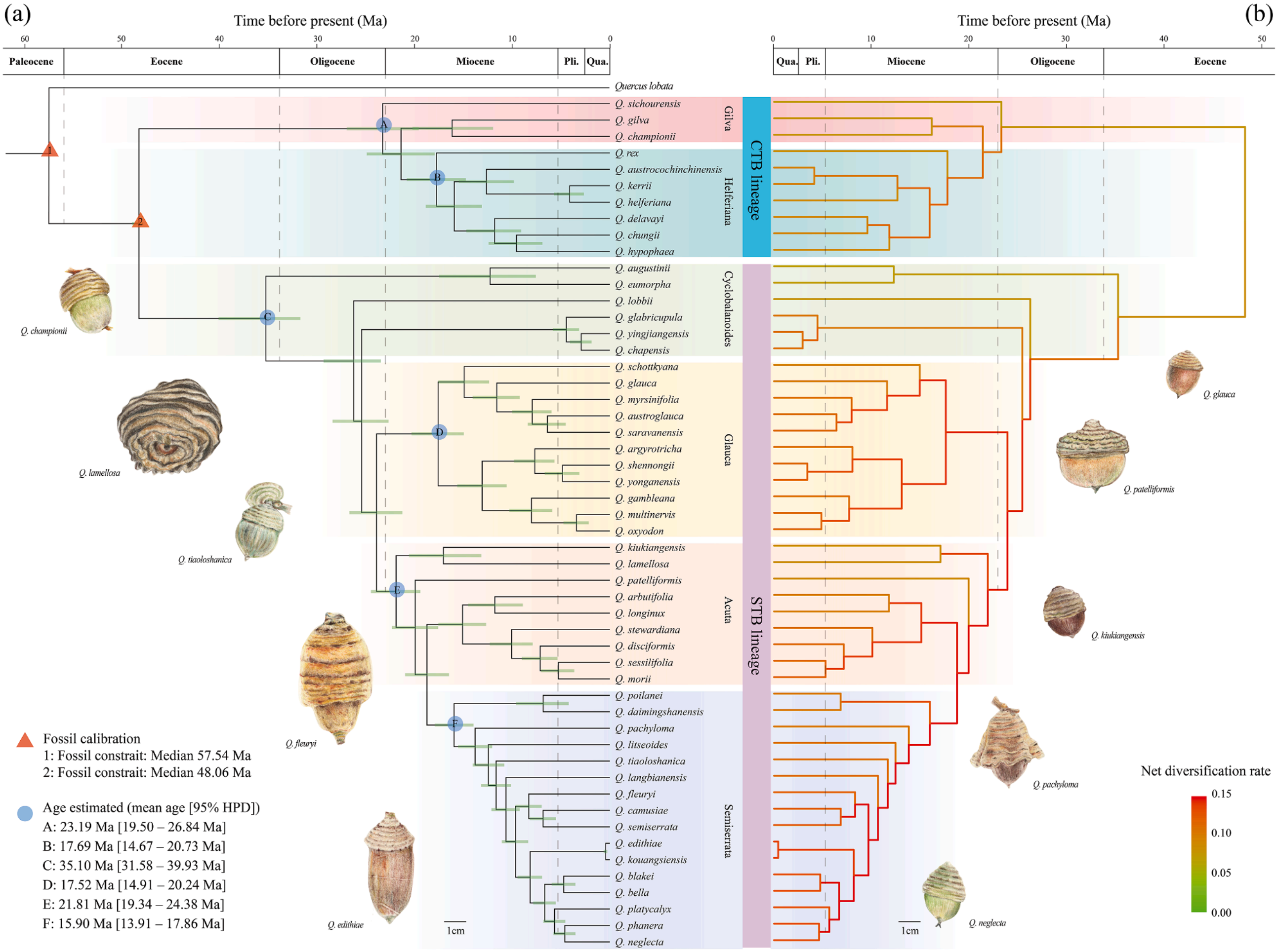

Fig. 1. Based on the fossil-calibrated phylogeny of *Quercus* section *Cyclobalanopsis*, green bars on the nodes indicate the 95% confidence intervals for divergence time estimates. Geological time abbreviation: Qua. = Quaternary; Pli. = Pliocene (a); Diversification rate of the section *Cyclobalanopsis* inferred using the Branch-Specific Diversification Rate Estimation (BDS) model (b).

3.2. Fruit morphometry and germination

Fruit size varied significantly among the species examined, with *Quercus rex* producing exceptionally large fruits, averaging 28 cm^3 in volume, whereas *Q. augustinii* and *Q. multinervis* yielded much smaller fruits, each with a volume of less than 1 cm^3 (Table 1). Morphologically, oblong ellipsoid fruits were the most common, representing 75% of the sample (39 out of 52 species). Additionally, a biennial fruit maturation period was observed in 80.77% of the species (42 out of 52 species; Table 1).

Notably, only seven species (*Quercus rex*, *Q. austrocochinchinensis*, *Q. kerri*, *Q. helferiana*, *Q. delavayi*, *Q. chungii*, and *Q. hypophaea*), which formed a single clade, exhibited an embryonic axis positioned near the scar and elongated cotyledonary petioles. These traits facilitated shoot emergence at a distance from the fruits or acorns, forming a distinct "tuber-like" structure (Type-IIS remote tubular). Furthermore, these seven species exhibited immediate root emergence but delayed shoot growth (Tables 1 and S2). In contrast, the remaining species had an embryonic axis located just beneath the apex. PD was prevalent, occurring in 59.62% of the species (31 out of 52), while 26.92% of the species (14 out of 52) produced ND seeds (Tables 1 and S2).

3.3. Ancestral state and evolution of fruit traits

In the ancestral state reconstruction analysis, different traits were best explained by different evolutionary models. The SYM model was identified as the best-fitting model for fruit shape, dormancy class, and cotyledonary petiole morphology/embryonic axis position, with AICc scores of 49.352, 15.878, and 67.181, respectively (Table S4). In contrast, the fruit maturation period was best explained by the ARD model, which had an AICc score of 54.272.

Based on ancestral state reconstructions, small fruit size was the most likely ancestral state for the section *Cyclobalanopsis*, a trait retained by most extant species across various clades (Fig. 2a). The oblate spheroid fruit shape was likely ancestral in the CTB lineage, with multiple transitions occurring within the Helferiana and Gliva clades. In contrast, the oblong ellipsoid fruit shape was reconstructed as the ancestral condition in the STB lineage, with a few transitions to oblate spheroid forms within the Cyclobalanoides, Acuta, and Semiserrata clades (Fig. 2b). The ancestral state of fruit maturation period was less clear; however, biennial maturation was more frequently inferred as the ancestral condition in both CTB and STB lineages (Fig. 2c).

The ancestral state of the section *Cyclobalanopsis* includes a normal (short) cotyledonary petiole and embryonic axis positioned near the scar. A single transition to an elongated cotyledonary petiole and embryonic axis positioned near the apex occurred during the Helferiana-Gliva split (Fig. 2d). Regarding dormancy types, PD is reconstructed as the ancestral state. A transition to ePD is observed within the CTB lineage, coinciding with the emergence of the Helferiana clade. In the STB lineage, multiple independent transitions from PD to ND occurred, and all six species within the Cyclobalanoides clade exhibit the ND state (Fig. 2e).

3.4. Effect of phylogenetic on fruit traits

Strong phylogenetic signals were detected for fruit shape, embryonic axis position/cotyledonary petiole morphology, and seed dormancy type ($K = 0.619$, $p < 0.01$; $K = 2.744$, $p < 0.01$; $K = 1.061$, $p < 0.01$, respectively; Table S5), indicating that these traits exhibit high phylogenetic conservatism. In contrast, fruit volume and fruit maturation period showed little to no phylogenetic signal, tending to evolve independently of phylogenetic history.

3.5. Relationship of climate on trait variation

The first two principal components (PCs) collectively explained 75.9% of the total variation in climatic variables among 52 oak species of the section *Cyclobalanopsis* (41.5% and 34.5% for PC1 and PC2, respectively; Fig. 3a). Correlation analysis indicated that climatic PC1 was strongly associated with temperature variables, whereas PC2 was primarily correlated with precipitation variables (Fig. 3b). *Q. morii*, *Q. longinux*, and *Q. hypophaea* showed significant separation along PC2, demonstrating strong positive correlations with high precipitation during both the coldest quarter (bio19) and driest periods (bio14, bio17). The 16 species of the Semiserrate clade were predominantly clustered in the upper-right quadrant of the PCA space, showing shared associations with both principal components. In contrast, the 11 species of the Glauca clade were separated along PC1, positioned on the left side of the PC1 axis and displaying strong correlations with Temperature Seasonality (bio4) and Temperature Annual Range (bio7). The majority of species from both the Cyclobalanoides and Helferiana clades were distributed on the lower side of PC2 axis, showing significant associations with Mean Diurnal Range (bio2), Isothermality (bio3), and Precipitation Seasonality (bio15) (Fig. 3a and Table S6).

The distribution of six fruit traits along the principal components of climatic variation showed that fruit shape was primarily separated along climate PC2, while cotyledonary petiole morphology/embryonic axis position and fruit volume were more distinctly differentiated along PC1 (Fig. S2). Further analysis using Phylogenetic Generalized Least Squares (PGLS), which accounts for phylogenetic relatedness, revealed a significant positive association between climate PC1 and fruit volume, and a significant negative association between PC2 and fruit shape, whereas no significant relationships were found between either PC axis and cotyledonary petiole morphology or embryonic axis position (Table 2). These results were further supported by PGLS analyses based on all 19 individual bioclimatic variables (Table S7).

3.6. Diversification rates associated with climate and traits

The QuaSSE analysis results for climate clearly showed that the sigmoidal λ with drift model provided the best fit for both climate PC1 and PC2, with AICc values of 629.561 and 615.019, respectively (Table S8). According to the best-fitting models, the diversification rate of the section *Cyclobalanopsis* increases approximately linearly with rising values of climate PC1. In contrast, for climate PC2, a marked increase in diversification rate occurs when PC2 exceeds a threshold value of 0.59 (Fig. 4).

For various functional traits, distinct species origination and extinction models were applied, each incorporating specific parameter subdivisions. Based on AICc scores, summaries of the best-fit models for QuaSSE (Table S8), BiSSE (Table S9), MuSSE (Table S10), and HiSSE (Table S11) are provided in the supplementary material.

The optimal QuaSSE model for fruit volume (Table S8, $AICc = 687.289$) assumes a constant extinction rate. According to this model, species of the section *Cyclobalanopsis* with fruit volume below 4.275 cm^3, exhibit consistently high and stable rates of speciation and net diversification rate. However, both rates drop sharply as fruit volume increases beyond this threshold (Fig. 5a–c). For the four discrete traits—fruit shape, fruit maturation period, cotyledonary petiole morphology, and embryonic axis position—the best-fitting BiSSE model in all cases was the equal μ model (Table S9, with AICc scores of 422.4, 419.93, 386.92, and 386.92,

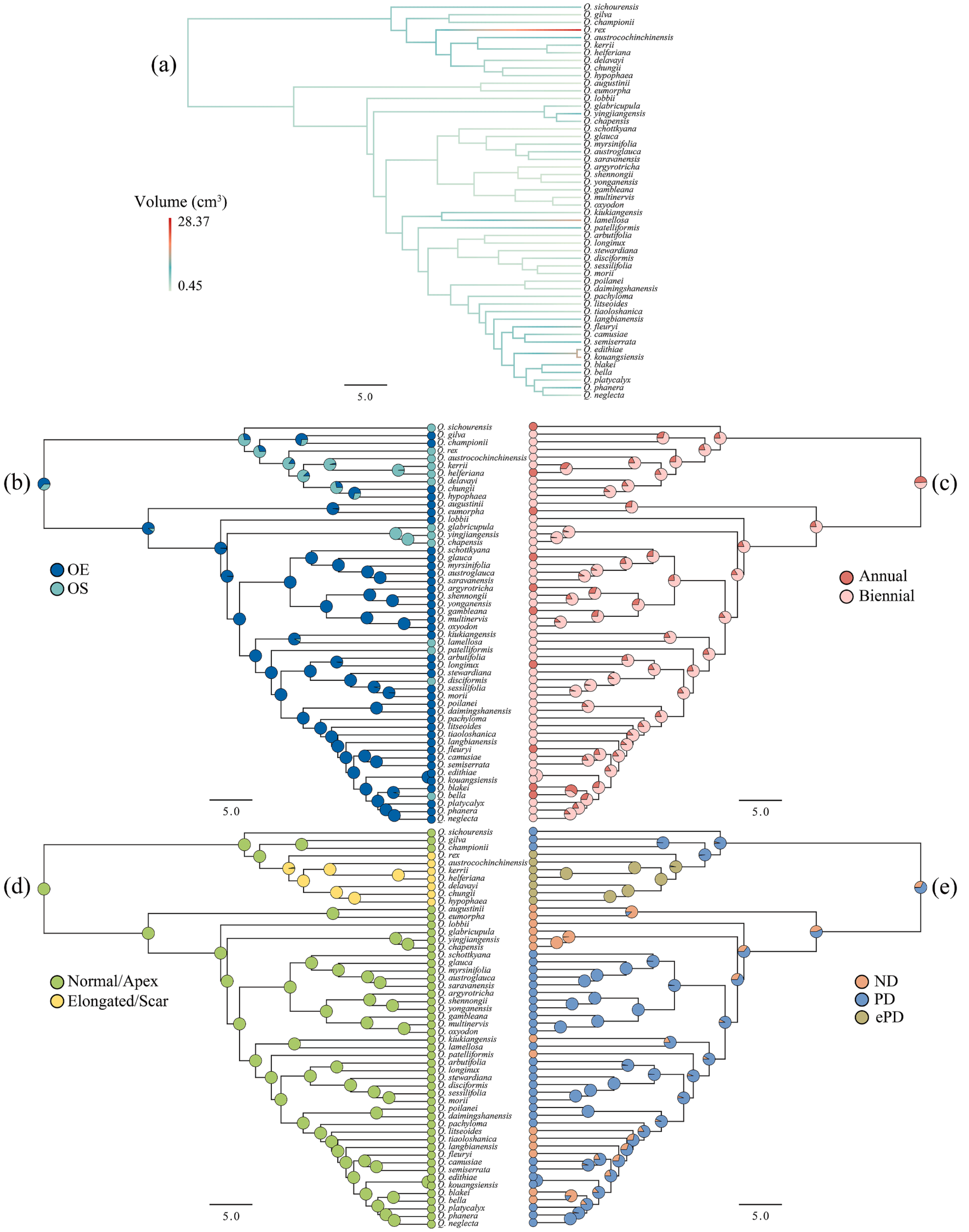

Fig. 2. Ancestral states of six fruit traits of the section *Cyclobalanopsis*: fruit volume (a), fruit shape (b), fruit maturation (c), cotyledonary petiole morphology or embryonic axis position (d), dormancy type (e). Fruit volume is used fastAnc function, while other traits use the SIMMAP method. Trait abbreviations are shown in Table 1.

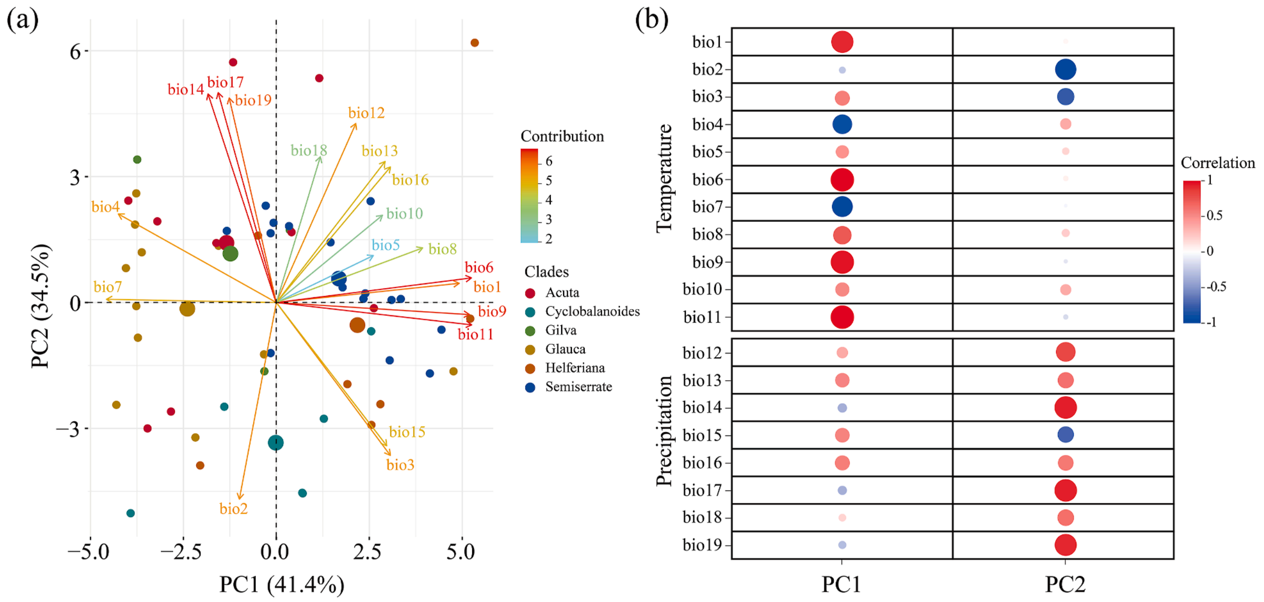

Fig. 3. Dimensionality reduction of climate variables. Principal component analysis (PCA) for climate variables (a); Heat map of Pearson correlation coefficients of climate variables and their principal components (b). Abbreviations: bio1 (Annual Mean Temperature), bio2 (Mean Diurnal Range), bio3 (Isothermality), bio4 (Temperature Seasonality), bio5 (Max Temperature of Warmest Month), bio6 (Min Temperature of Coldest Month), bio7 (Temperature Annual Range), bio8 (Mean Temperature of Wettest Quarter), bio9 (Mean Temperature of Driest Quarter), bio10 (Mean Temperature of Warmest Quarter), bio11 (Mean Temperature of Coldest Quarter), bio12 (Annual Precipitation), bio13 (Precipitation of Wettest Month), bio14 (Precipitation of Driest Month), bio15 (Precipitation Seasonality), bio16 (Precipitation of Wettest Quarter), bio17 (Precipitation of Driest Quarter), bio18 (Precipitation of Warmest Quarter), and bio19 (Precipitation of Coldest Quarter).

Table 2
Based on phylogenetic generalized least squares (PGLS) regression models of 52 species of the section *Cyclobalanopsis*, the average functional traits were used as responses to the two groups of climate principal components.

Climates	Traits	Estimate coefficient	p	Multiple R^2	Adjusted R^2
PC1	Fruit volume	0.5131	0.0470*	0.0766	0.0582
	Fruit shape	0.0190	0.3900	0.0148	−0.0049
	Fruit maturation period	0.0151	0.4499	0.0115	−0.0083
	Cotyledonary petiole morphology/Embryonic axis position	0.0032	0.4736	0.0103	−0.0095
	Dormancy type	−0.0035	0.8638	0.0006	−0.0194
PC2	Fruit volume	−0.2506	0.3824	0.0153	−0.0044
	Fruit shape	−0.0523	0.0199*	0.1037	0.0858
	Fruit maturation period	−0.0053	0.8086	0.0012	−0.0188
	Cotyledonary petiole morphology/Embryonic axis position	−0.0019	0.6978	0.0030	−0.0169
	Dormancy type	0.0028	0.9057	0.0003	−0.0197

Note: Significance levels: *, $p < 0.05$; **, $p < 0.01$.

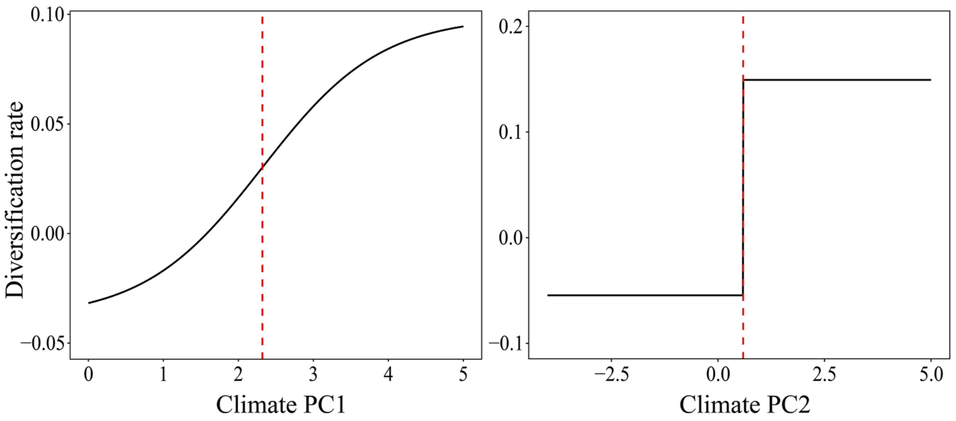

Fig. 4. Relationship between the diversification rate of the section *Cyclobalanopsis* and the principal components of climate variables based on QuaSSE analysis.

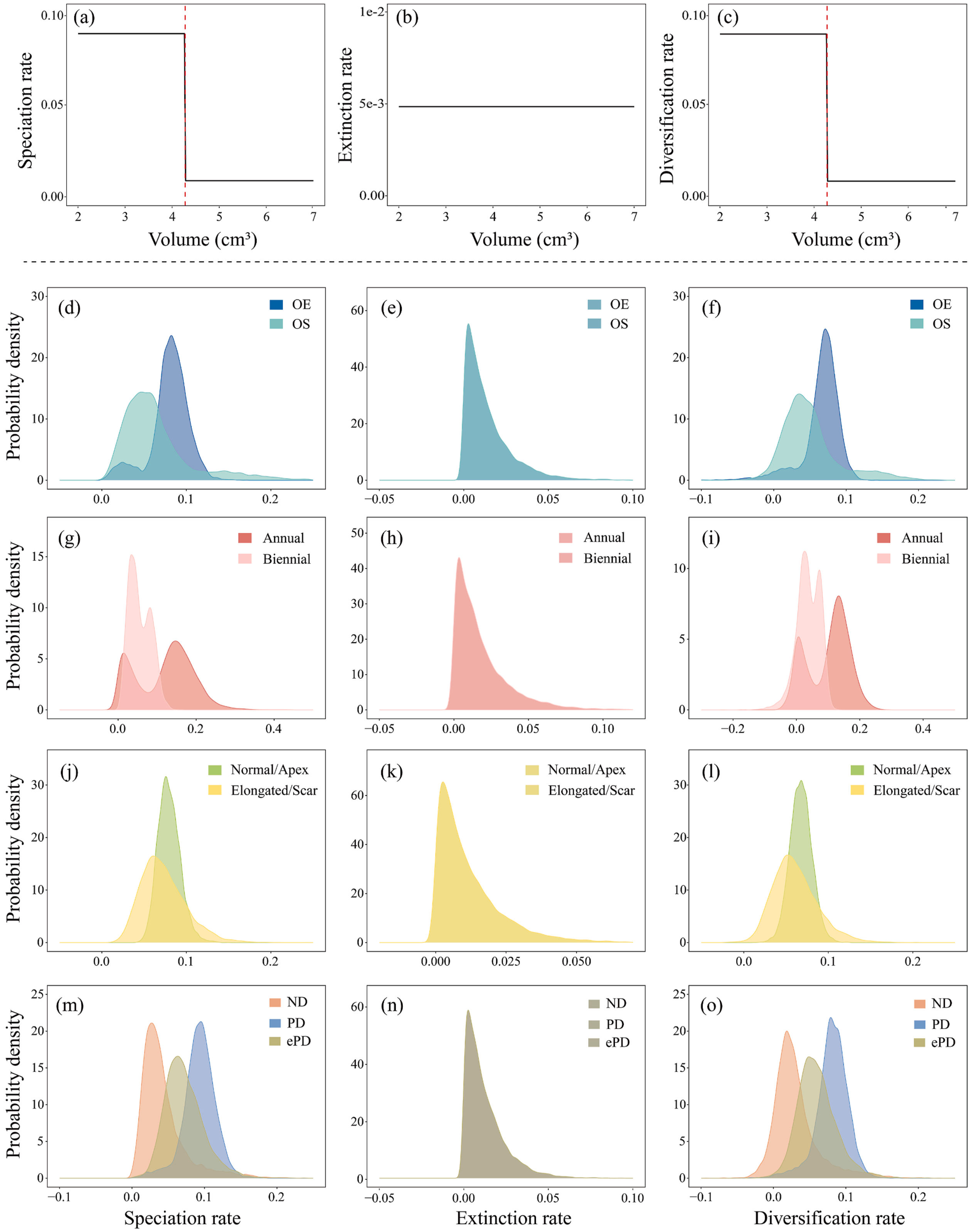

Fig. 5. Comparative of speciation rate, extinction rate, and diversification rate of fruit traits: fruit volume (a–c), fruit shape (d–f), fruit maturation (g–i), cotyledonary petiole morphology or embryonic axis position (j–l), dormancy type (m–o). Fruit volume was inferred using the QuaSSE model; fruit shape, maturation, and cotyledonary or embryonic traits using the BiSSE model; and dormancy type using the MuSSE model. Trait abbreviations are shown in Table 1.

respectively). MCMC analyses under the best-fitting models indicated that species with oblong ellipsoid fruits have a higher net diversification rate than those with oblate spheroid fruits, primarily due to an elevated speciation rate (Fig. 5d–f). In addition, although biennial-fruiting species are more, annual-fruiting species exhibit higher speciation and net diversification rates (Fig. 5g–i). Further analyses revealed that species with embryonic axes located near the apex display higher speciation and net diversification rates than those with embryonic axes near the scar or with elongated cotyledonary petioles, although these differences were less pronounced (Fig. 5j–l). The best-fitting MuSSE model was also the equal μ model (Table S10, AICc = 434.82). The results indicated that species with PD exhibit higher speciation rates, leading to a higher net diversification rate (Fig. 5m–o). Finally, the best-fitting HiSSE model (Table S11) estimates for four binary traits corroborate that species with oblong ellipsoid fruit shapes, an embryonic axis near the apex, and normal (short) cotyledonary petiole morphology exhibit the highest net diversification rates (Fig. S3a-c). Notably, the HiSSE model for fruit maturation period inferred that biennially maturing species have higher diversification rates, a result that contrasts with the BiSSE analysis (Fig. S3b).

4. Discussion

4.1. Diversification of fruit traits

Ancestral state reconstruction indicated that the most likely ancestral traits of the section *Cyclobalanopsis* included small, oblong ellipsoid fruits with a biennial maturation period, normal cotyledonary petioles, the embryonic axis positioned near the apex, and a typical Type-IA germination strategy (Jaganathan and Phartyal, 2024, Fig. 2). This trait combination may reflect early lineages' adaptation to stable climatic environments through gradual resource allocation and synchronized germination.

However, empirical analyses based on 52 species revealed a high degree of fruit trait diversification within the section *Cyclobalanopsis*. The maximum difference in acorn volume among extant species exceeds 30-fold, a variation that strongly influences key ecological processes such as habitat selection, growth rate, survival, tolerance to herbivory, and mechanisms of plant dispersal (Farnsworth, 2000; Fenner and Thompson, 2005; Wang et al., 2014; Kraft et al., 2015). For instance, large fruits may enhance seedling establishment under shaded conditions, whereas small fruits may be better suited to disturbed or resource-limited habitats. In addition, fruit shape has diversified from the ancestral oblong ellipsoid form toward more oblate spheroid types. Spherical fruits are more likely to be consumed by rodents, while elongated fruits are more accessible to birds, potentially shifting the dominant dispersal vectors and shaping spatial patterns of establishment (Lord, 2004). Fruit maturation period also varies among species, ranging from one to two years, and plays a key role in the spatiotemporal dynamics of dispersal and colonization (Mendoza et al., 2017; Cortés-Flores et al., 2019).

Phylogenetic signal analyses further revealed contrasting levels of evolutionary conservatism among fruit traits. Fruit shape, cotyledonary petiole/embryonic axis position, and seed dormancy type all exhibited strong phylogenetic signals. For example, the Helferiana clade has evolved a suite of highly specialized traits—including dormancy associated with delay in shoot emergence, i.e. ePD, elongated cotyledonary petioles, and an embryonic axis positioned below the scar (Sun et al., 2021; Jaganathan and Phartyal, 2024; Table 1). These traits are phylogenetically conserved and also display clear adaptive value, functioning to reduce seed predation risk and mitigate drought stress. The extension of the cotyledonary petiole allows the embryonic axis to emerge away from the fruit body, thereby reducing vulnerability to granivores. Meanwhile, the positioning of the embryonic axis below the scar, which exacerbates water loss, is counterbalanced by rapid root germination, enabling efficient water absorption and maintaining adequate hydration for the epicotyl (Sobrino-Vesperinas and Viviani, 2000; Xia et al., 2012; Willis et al., 2014; Li et al., 2023; Jaganathan and Phartyal, 2024). Fruit volume and maturation period, by contrast, showed weak phylogenetic signals, suggesting that these traits are more evolutionarily labile and likely shaped by ecological factors. Their high phenotypic plasticity and low phylogenetic constraint indicate a greater potential for adaptive divergence under variable environmental conditions.

4.2. Climatic drivers of fruit trait evolution

To further investigate the influence of environmental factors on the evolution of fruit traits, we analyzed the climate adaptation patterns of trait variation by integrating phylogenetic information with principal component axes extracted from 19 bioclimatic variables. The results revealed clear lineage-level climatic differentiation within the section *Cyclobalanopsis*. For example, the Semiserrata clade is predominantly adapted to the hot and humid environments associated with the East Asian summer monsoon, whereas most species in the Cyclobalanoides and Helferiana clades occur in regions dominated by continental climates influenced by the Siberian winter monsoon, characterized by greater interannual and diurnal temperature fluctuations (Spicer, 2017; Jin et al., 2024). Against this climatic backdrop, fruit traits displayed distinct separation along the principal component axes, offering a framework for understanding the ecological mechanisms driving trait evolution.

Further comparative analyses revealed significant differences among fruit traits in their degrees of phylogenetic conservatism and climatic responsiveness. Seed volume exhibited a weak phylogenetic signal within the section *Cyclobalanopsis* (Table S5), suggesting that its evolution is largely independent of phylogenetic history and instead reflects a high degree of ecological plasticity. Correspondingly, seed volume showed strong associations with temperature-related climatic gradients (Table 2), especially under conditions of high mean annual temperature and low temperature seasonality, where individuals tend to develop larger fruits. This may be attributed to the accumulation of carbon assimilates during an extended growing season, which supports the development and maturation of larger fruits and enhances reproductive investment and ecological adaptability. Previous studies have also indicated that warming can promote early cell division and expansion during fruit development, whereas low temperatures may inhibit organogenesis, induce membrane damage, or activate stress-related metabolic pathways, thereby constraining fruit growth (Rodríguez et al., 2011; Flaishman et al., 2015; Yadav et al., 2023). Therefore, despite its limited phylogenetic constraint, seed volume appears to be highly responsive to climatic conditions and may serve as a key functional trait for assessing plant adaptive potential under future climate change.

In contrast, fruit shape exhibits a relatively strong phylogenetic conservatism in the section *Cyclobalanopsis* ($K = 0.619$, $p < 0.01$; Table S5), suggesting that this trait tends to remain stable among closely related species. However, despite this phylogenetic constraint, fruit shape still shows a significant response to precipitation gradients (Table S2), indicating a degree of adaptive plasticity. In regions with abundant rainfall, oblong ellipsoid fruits are more common, whereas in drier or more seasonally variable environments, fruits tend to become more flattened or spherical. This morphological divergence may be associated with differences in dispersal syndromes or with water-related constraints influencing fruit development strategies (Lord, 2004). Previous studies have shown that variation in water availability can alter the anisotropic growth of fruit tissues, affecting shape indices and developmental pathways (Yu et al., 2024), and species-specific responses to precipitation may be highly heterogeneous.

Taken together, the evolution of fruit traits in the section *Cyclobalanopsis* appears to be shaped by the joint effects of phylogenetic history and ecological selection. Fruit volume shows strong climatic sensitivity and ecological plasticity, while fruit shape, though evolutionarily conserved, is still capable of adaptive shifts along specific environmental gradients. These findings support an "interaction between phylogenetic constraint and environmental selection" model of trait evolution, in which phylogenetic background provides a structural framework for trait development, while climatic drivers promote divergence and innovation. The complex climatic regimes of East Asia—especially the interplay between the summer monsoon and the Siberian winter monsoon—have contributed to niche diversification within the section *Cyclobalanopsis* (Wang et al., 2012). This pronounced climatic seasonality and geographic gradient likely facilitated lineage-specific differentiation in climate adaptation (Xia et al., 2016).

4.3. *The role of climate and traits in driving diversification*

Our quantitative analyses reveal that climatic niche variables have a significant influence on species diversification. Specifically, diversification rates increase almost linearly with climate PC1 (temperature), suggesting that enhanced temperature adaptability may continuously open new ecological opportunities. In contrast, along PC2 (precipitation), diversification rates show a sharp increase once a threshold value of 0.59 is surpassed, indicating that major shifts in precipitation regimes may trigger rapid lineage radiations (Fig. 4). Branch-specific analyses further indicate a notable increase in diversification rates in the section *Cyclobalanopsis* around the Oligocene–Miocene boundary (Figs. 1b and S1). Paleobotanical evidence suggests that the East Asian monsoon intensified during the early Miocene, resulting in a significant increase in regional precipitation. We propose that this climatic shift acted as a pivotal environmental driver promoting rapid diversification within this lineage. As the stability of regional precipitation surpassed a critical threshold, the physiological constraint imposed on recalcitrant seeds that require maintaining moisture content above 20 percent for viability was markedly alleviated (Jaganathan, 2021). This relaxation likely enhanced their potential for broader geographic dispersal (Pritchard et al., 2022), thereby facilitating the expansion of the section *Cyclobalanopsis*.

Among multiple fruit traits, seed volume exhibits a nonlinear relationship with diversification rate: species with seed volumes smaller than approximately 4.3 cm^3 maintain high speciation and net diversification rates, whereas those exceeding this threshold show a marked decline (Fig. 5a–c). This pattern aligns with the hypothesis that smaller seeds enhance dispersal and colonization potential, thereby promoting diversification (Geritz, 1998; Eriksson et al., 2000; Parolin, 2000; Seidler and Plotkin, 2006; Lei et al., 2012; Galetti et al., 2013). In contrast, while larger seeds may provide competitive advantages at the individual level—especially under resource-limited or shaded environments (Linkies et al., 2010)—their limited dispersal capacity could constrain species expansion and subsequent diversification.

In terms of fruit morphology, species with oblong ellipsoid fruits exhibited higher speciation rates and net diversification, a pattern consistently supported by both BiSSE and HiSSE models (Figs. 5d–f and S3). The duration of fruit maturation also had a significant impact on diversification potential. Although biennial maturation is more prevalent across individual lineages, annual species—owing to their higher reproductive frequency and faster responsiveness to environmental changes—exhibited elevated net diversification rates (Fig. 5g–i), aligning with previous findings on the influence of fruit maturation on diversification (Abels et al., 2016; Westerhold et al., 2020; Meijer et al., 2024). However, results from the HiSSE model, which incorporates hidden evolutionary factors, indicated that species with biennial maturation may in fact experience higher diversification rates (Fig. S3). Given the pronounced imbalance in character state representation within our dataset (42 biennial vs. only 10 annual species), the BiSSE results may be biased due to the limited representation of annual-maturing species. Therefore, the evolutionary dynamics of this trait are likely influenced by additional ecological or phylogenetic factors. The evolution of internal structures also exhibits a certain degree of phylogenetic constraint and association with diversification. The ancestral state—characterized by a normal cotyledonary petiole and an embryonic axis positioned near the apex (Type-IA)—is a morphological configuration widely present in *Quercus*, known for its strong ecological adaptability and resistance to environmental stress (Sobrino-Vesperinas and Viviani, 2000; Xia et al., 2012; Jaganathan and Phartyal, 2024). Lineages retaining this ancestral trait exhibit higher diversification rates (Figs. 5j–l and S3), suggesting that this structural combination may have facilitated rapid lineage expansion during the early stages of the section *Cyclobalanopsis* evolution.

Phylogenetic analysis of germination types indicate that PD is associated with higher diversification rates across multiple lineages (Fig. 5m–o). PD allows seeds to synchronize germination with favorable environmental conditions, thereby enhancing establishment success in novel habitats (Donohue et al., 2005). The sensitivity of PD to environmental cues such as temperature, light, and moisture is considered a physiological foundation for the ecological expansion and diversification of the section *Cyclobalanopsis* (Finch-Savage and Leubner-Metzger, 2006). By contrast, the emergence of ND and ePD likely represents derived strategies evolved under the increasingly disturbance-prone climatic regimes of the Miocene. While these dormancy types may confer advantages in terms of accelerated life cycles and enhanced resource acquisition, their long-term contribution to diversification potential remains to be fully assessed (Willis et al., 2014).

Within East Asia's varied climates, fruit traits in the section *Cyclobalanopsis* likely evolved as adaptations to environmental pressures while simultaneously driving the ecological spread and species diversification. Although this study cannot confirm direct causation, the strong correlation between fruit trait evolution and diversification rates underscores their central role in shaping the group's macroevolutionary success.

5. Conclusion

We have demonstrated that the variation in diversification rates within *Quercus* section *Cyclobalanopsis* is driven by climatic niche innovation and fruit trait evolution since the Miocene. The origins of the section *Cyclobalanopsis*, coupled with ancestral fruit traits, can be traced to southern and southwestern China during the middle Eocene to early Oligocene, coinciding with the emergence of evergreen broad-leaved forests (Jin et al., 2024; Zhang et al., 2024b; Meng et al., 2025; Zhao et al., 2025). Subsequently, the uplift of the Tibetan Plateau during the late Oligocene to early Miocene, along with global climatic changes, facilitated the gradual establishment of the East Asian subtropical monsoon and the South Asian tropical monsoon systems (Spicer, 2017; Li et al., 2025). Among them, the East Asian subtropical monsoon played a key role in driving the rapid evolution of the section *Cyclobalanopsis*, while the South Asian tropical monsoon promoted localized coevolution of fruit traits.

Further exploration that integrates ecological and genomic methodologies promises to deepen our understanding of how plant traits adapt and influence species diversification amidst changing environmental dynamics. By combining diverse macroevolutionary frameworks with phylogenetic analyses, this study provides valuable insights into the evolutionary processes in subtropical evergreen broadleaf forests. Our findings suggest that the rich diversity within the section *Cyclobalanopsis* may result from complex interactions between climate niche dynamics and the evolution of functional traits. Climate niches shape the growth environment and ecological niche distribution, while the evolutionary trajectory of functional traits influences the competitive advantage and resilience of plants across varied climatic contexts. It is worth considering comparative phylogenetic studies including other related genera within Fagaceae to understand broader evolutionary patterns and identify common drivers of diversification are important to provide more insights into the evolutionary and ecological significance of recalcitrant seeds. We believe Fagaceae might be a model family to carry out such works.

CRediT authorship contribution statement

Liang-Hai Yang: Writing – original draft, Visualization, Software. **Ganesh K. Jaganathan:** Writing – review & editing, Writing – original draft. **Si-Di Liang:** Software, Formal analysis. **Si-Si Zheng:** Data curation. **Hong-Hu Meng:** Writing – review & editing. **Xi-Qing Sun:** Formal analysis, Data curation. **Xin Ning:** Data curation. **Ru-Ning Hou:** Data curation. **Xin Zhong:** Data curation. **Tian-Rui Wang:** Data curation. **Bin-Jie Ge:** Data curation. **Gregor Kozlowski:** Writing – review & editing. **Yi-Gang Song:** Writing – review & editing, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pld.2025.07.004.

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