

Comparative study of the distribution and phenology of *Quercus cerris*, *Quercus frainetto* and *Quercus petraea* in Bulgarian forests

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Abstract

This study examined the distribution and phenology of forests dominated by *Quercus cerris* L. (QC), *Quercus frainetto* Ten. (QF) and *Quercus petraea* sensu lato (QP) across Bulgaria. Ecological variables, including altitude, latitude, longitude, aspect and slope, were analysed to characterise species-specific habitat preferences. Phenological events, such as the start of the vegetation period (SVP), the end of the vegetation period (EVP) and the length of the vegetation period (LVP), were also compared. The results showed that QC and QF were more common on flat terrain, whereas QP preferred mountainous areas. QC tended to dominate shaded slopes, QF occurred mainly on sunny exposures, and QP was more evenly distributed across both. QC exhibited the latest leaf unfolding (20 April $\pm$ 4.8 days) and the earliest EVP (15 October $\pm$ 12.8 days), resulting in the shortest growing season (178.1 $\pm$ 13.8 days). In contrast, QF and QP began vegetation period almost simultaneously (16–18 April $\pm$ 4.8–6.6 days) and ended at similar times (20–23 October $\pm$ 9.4–12.9 days), with comparable vegetation periods (187–188 days). Observed features enhance our understanding of the ecological and phenological differences among the three oak species. They can be utilised to improve the efficient, evidence-based management of oak forests in Bulgaria, which may be crucial in the face of climate change challenges.

Key words: end of vegetation period, length of vegetation period, oak forests, start of vegetation period.

Introduction

Genus *Quercus* is one of the most significant groups of woody angiosperms in the Northern Hemisphere in terms of species diversity, ecological dominance and economic importance (Nixon 2006, Gil-Pelegrín et al. 2017). It comprises estimated 430 species of trees and shrubs

(Carrero et al. 2020), mainly deciduous, and occupies a variety of environments, including temperate, subtropical, and tropical regions (San-Miguel-Ayán et al. 2016). Few oak species are the most prevalent in Bulgarian hardwood forests – *Quercus cerris* L. (QC), *Quercus frainetto* Ten. (QF), and *Quercus petraea* sensu lato (QP), the latter of which includes

three sessile oak species recognised in Bulgaria: *Quercus petraea* (Matt.) Liebl., *Quercus dalechampii* Ten., and *Quercus polycarpa* Schur (Ganchev and Bondev 1966; Nicolescu et al. 2025). According to Stefanov (1943a,b, 1944), natural oak forests adapted to the plains and lower mountain slopes were extensively clear-felled in the past to meet agricultural needs, provide pasture, and supply fuel for nearby settlements. Despite historical logging pressures, stands containing these species still represent over a third of Bulgaria's forest area (Alexandrov and Tonchev 2024), with forests dominated by them covering 14.1% of the country's total forest area (NFI 2023). In many instances, the three species coexist in mixed oak forests, with different levels of dominance depending on site conditions. Stefanov and Ganchev (1953) also observed that oaks face significant challenges in colonising new areas due to their heavy seeds, limited germination viability, and high seed predation. Combined with their relatively slow growth, these characteristics emphasise the phytogeographic significance of oaks.

QC is distributed throughout southern Europe, from central and northern Spain to the Balkan Peninsula, extending to Switzerland in the north and Syria in the south (Stefanov 1934). Stefanov (1943a) notes that among all oaks found in Bulgaria, QC is notable for its widespread distribution. The author notes that among all oaks found in Bulgaria, QC is distinguished by its widespread distribution, except in mountainous regions (above 800–900 m a.s.l.) and in the Thracian plain. According to Vannini et al. (2022), it is more light-demanding than QP and susceptible to late spring frosts, but relatively tolerant of drought and air pollution. QF mainly occurs on the Balkan Peninsula

and in southern Italy (San-Miguel-Ayanz et al. 2016). Stefanov (1943a) emphasises that the species' distribution indicates adaptation to the continental climate and resilience to soil drought, which explains its widespread presence in Northern Bulgaria, particularly in the Northeast. Chatziphilippidis and Spyroglou (2006) describe it as a light-demanding, meso-xerophilous species typical of transitional climates between Mediterranean and continental areas, with hot summers and cold winters. QP is common throughout much of Europe, particularly in hilly and lower mountainous regions (Stefanov 1943a), which is why it is often called 'the oak of the mountains' (Nicolescu et al. 2025). It is regarded as drought-tolerant, often found on light, well-drained, rocky soils and acidic substrates, frequently on slopes and ridges (San-Miguel-Ayanz et al. 2016). Other authors, however, report that it flourishes in fertile, deep, and moist soils (Nicolescu et al. 2025) or limestone soils (Stefanov 1943a). Stefanov (1943a) attributes the species' absence in north-eastern Bulgaria and its sporadic presence in the Deliorman region to the limited number of humid localities in the area. High variability demonstrates its extensive phenotypic plasticity, which explains why some populations are classified as subspecies or even separate species in certain countries (Nicolescu et al. 2025). Nevertheless, this variability allows adaptation to different environments and enhances its resilience amid climate change (Sáenz-Romero et al. 2017).

The timing of phenological events is a significant determinant of the productivity and species distribution in temperate forests. Numerous studies (Vitasse et al. 2009, 2011; Čufar et al. 2012; Schieber et al. 2013; Gressler et al. 2015; Flynn and Wolkovich 2018; Peaucelle et al. 2019;

Piao et al. 2019; Lukasová et al. 2020; Ciocîrlan et al. 2022; Gafenco et al. 2022; Anev 2023, 2025; Skvareninova et al. 2024) indicate that the phenology of temperate deciduous trees varies with altitude and latitude due to differences in temperature, photoperiod and other environmental factors. According to Hopkins' bioclimatic law (Hopkins 1918), temperatures in temperate latitudes progressively decrease with elevation and distance from the equator, delaying spring phenophases, such as budburst, flowering and leaf unfolding, while advancing autumn events. This results in a shorter growing season at higher altitudes and latitudes, reducing the available time for growth and reproduction. Local factors, such as slope, aspect and topography create additional microclimatic variation, so phenological timing can vary even within the same altitude range. Schuster et al. (2014) found that cold-air pools significantly affect the growing season of deciduous trees, with individuals on mid-slope positions often having an advantage over those at valley bottoms. Long-term studies on temperate woody species demonstrate that three main cues govern budburst and leaf unfolding: spring forcing temperatures, increasing photoperiod, and the duration and intensity of winter chilling (Flynn and Wolkovich 2018).

Remote sensing techniques, such as satellite imagery and unmanned aerial vehicles, offer effective tools for monitoring phenology. Numerous studies (Bucha and Koren 2017, Lukasová et al. 2019, Gray and Ewers 2021, Soudani et al. 2021, Ciocîrlan et al. 2022, Grabska-Szwagrzyk and Tymińska-Czabańska 2024) demonstrate that the variations in vegetation's ability to absorb primarily red and infrared radiation, as measured by multispectral cameras, indicate distinct phenological

stages and can be quantified through spectral indices. These indices track variations over time and space in phenological events, with statistical algorithms aiding in determining their timing and relationship to environmental factors.

Although the ecology and biology of *Quercus* species in Europe have been broadly studied, some issues remain difficult to resolve. These issues relate to how long-lived organisms, like oaks, respond to changing climate conditions, which develop much faster than woody plants can adjust either in the short term through physiological changes or across generations in the long term.

This study aimed to improve understanding of the distribution and phenology of forests dominated by three of Bulgaria's most widespread oak species. The results are expected to deepen knowledge of their ecology and support evidence-based forest management strategies, which are essential in the face of climate change challenges.

Object and Methods

This study focuses on Bulgarian forests mainly composed of three common oak species: *Quercus cerris* L. (QC), *Quercus frainetto* Ten. (QF) and *Quercus petraea* sensu lato (QP). The latter includes three oak species recognised in Bulgaria: *Quercus petraea* (Matt.) Liebl., *Quercus dalechampii* Ten. and *Quercus polycarpa* Schur, all of which are listed in the national forest inventory as sessile oak. For the purposes of this study, and according to Welle et al. (2022), a forest stand was considered dominated by one of the species if at least 80% of the main tree layer consisted of that species.

Tree species composition and stand

polygons were sourced from the National Forest Inventory database, current as of 2022, and available at <https://iag.bg/> (Fig. 1). The polygons for the stands conformed to the boundaries outlined during the forest inventory. Before the analysis, a validity check algorithm was applied to the vector layer geometries, and no errors were detected.

The extent of QC-dominated forests is nearly the same as that of QP-dominated forests and surpasses the area of QF-dominated forests. The QP-dominated forests have the highest average age, while the QC-dominated forests are the youngest (Table 1).

The National Forests Inventory database and satellite raster imagery were processed using QGIS (v. 3.40.9). Mean stand coordinates (latitude and longitude)

Table 1. Area and age of studied forests

Variants	Area, ha	Area, %	Age, years $\pm$ SD
QC-dominated forests	183,684	4.83	56.8 $\pm$ 25.6
QF-dominated forests	169,690	4.46	60.5 $\pm$ 30.2
QP-dominated forests	183,872	4.83	67.2 $\pm$ 28.0

Note: The areas are presented both in hectares and as a percentage of the total forested area of Bulgaria.

were calculated using the ‘native:meancoordinates’ tool. The EuroDEM raster layer (EuroGeographics 2025) was used to derive altitude, slope, and exposure. The raster was reprojected to EPSG:32635 with the ‘gdal:warpproject’ tool (GDAL v. 3.10.2), and slope and exposure rasters

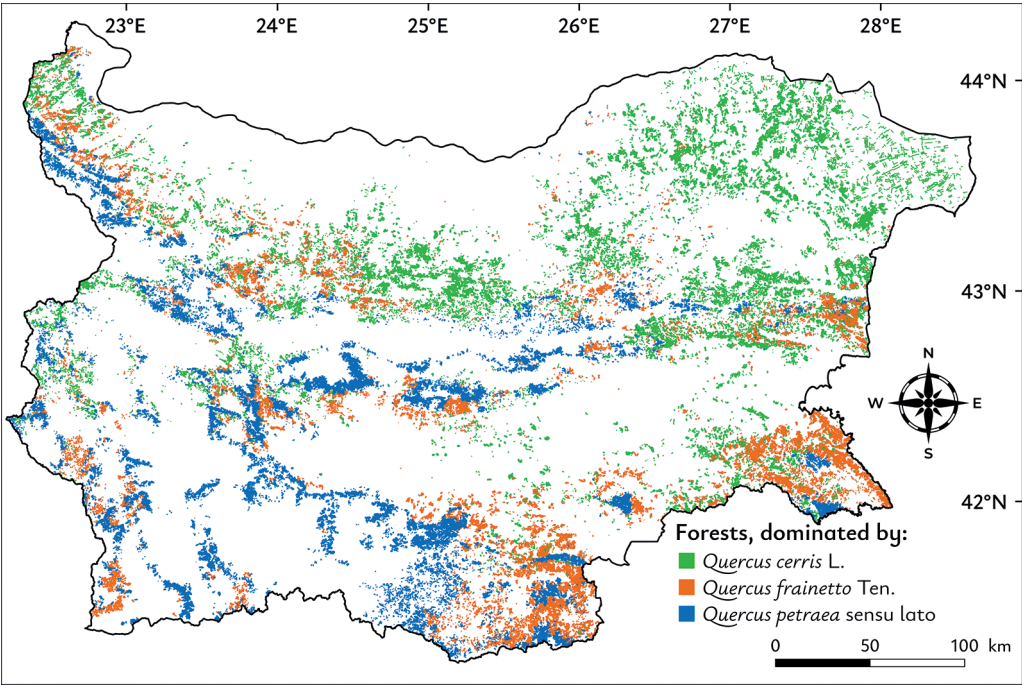


Fig. 1. Geographical distribution of forests dominated by *Q. cerris* (54,343 stands), *Q. frainetto* (40,684 stands) and *Q. petraea* (40,298 stands) in Bulgaria.

were generated with the 'r.slope.aspect' tool (GRASS GIS v. 2.12.99). Because the exposure raster represents circular data ($0^\circ = 360^\circ = \text{north}$), direct averaging would produce incorrect values. To address this, the exposure values were dissected into two components: 'Exposure_y', indicative of the north–south orientation through a cosine function, varying from $-1.0 = \text{south}$ to $1.0 = \text{north}$; and 'Exposure_x', indicative of the east–west orientation through a sine function, varying from $-1.0 = \text{west}$ to $1.0 = \text{east}$. Zonal statistics ('native:zonalstatisticsfb') were then used to compute average values ('Exposure_y_mean' and 'Exposure_x_mean') of these two rasters for each stand. The geographic angle of mean exposure was reconstructed using the function specifically created for this case:

CASE

WHEN degrees(atan2('Exposure_y_mean', 'Exposure_x_mean')) < 0

THEN degrees(atan2('Exposure_y_mean', 'Exposure_x_mean')) + 360

ELSE degrees(atan2('Exposure_y_mean', 'Exposure_x_mean'))

END

Phenological events were derived from the Copernicus Land Monitoring Service, using satellite imagery from the High-Resolution Phenology and Productivity series (WEkEO 2025) of the Copernicus programme (<https://land.copernicus.eu/>). The analysis used the Seasonal Trajectory of the Plant Phenology Index (ST-PPI) (Jin and Eklundh 2014; Smets et al. 2022), particularly the start of the season (SOSD), end of the season (EOSD), and length of season (LOSD) rasters for season 1 from the years 2017 to 2023. For each stand, the SOSD, defined as the spring day when the ST-PPI reaches 25 % of its maximum annual value, was used to estimate the average start date of

the vegetation period (SVP); EOSD, defined as the autumn day when the ST-PPI drops to 15 %, was used to estimate the average end date of the vegetation period (EVP); and LOSD, defined as the difference between EOSD and SOSD, was used to estimate the average length of the vegetation period (LVP) in days. Twenty-two raster images were analysed for each phenological event across each year from 2017 to 2023 ($N = 462$).

Images were reprojected using 'gdal:warp' and mosaicked with 'gdal:buildvirtualraster' (GDAL v. 3.10.2). Zonal statistics ('native:zonalstatisticsfb') were then employed to calculate mean values of phenological events for each stand's polygon. The final dataset, combining geographic and phenological attributes, was exported with the 'gdal:gdal2xyz' tool and transferred into MS Excel (Office 365, Microsoft) for visualisation and statistical analysis. Statistical processing was performed using built-in functions and VBA scripts (VBA v. 7.1, Microsoft). One-way ANOVA followed by Tukey's post hoc test was applied to compare geographic indicators and phenological events among the three oak-dominated forest types. The slope of the linear regression between latitude, longitude, and altitude, on one hand, and the SVP, EVP and LVP, on the other, was used to evaluate the impact of geographical coordinates on the timing of phenological events.

Results

Distribution

Species-specific variation in distribution by latitude and longitude was observed when comparing forests dominated by QC, QF, and QP. QC-dominated forests

were primarily located in North and East Bulgaria, while QP-dominated forests were mainly found in South and West Bulgaria. QF-dominated forests were spread throughout Bulgaria, except in the North-East. The distribution range in latitude was narrowest in QC and broadest in QF, and in longitude it was narrowest in QP and broadest in QC. QC and QF were more prevalent on flat terrain, whereas QP was mainly associated with mountainous regions (Fig. 2A,B).

Despite the notable difference in the average altitudes of forests dominated by QC and QF (mean $\pm$ SD: QC = 357.4 $\pm$ 205.6 m, QF = 380.0 $\pm$ 200.5 m), their similar ranges of variation (5–95 %: QC = 114.9–818.0 m, QF = 101.7–782.2 m) suggest comparable ecological importance for this indicator. Conversely, forests dominated by the QP (mean $\pm$ SD: 749.4 $\pm$ 334.7 m) are rarely (<5 %) found below 390 m a.s.l. (5–95 %: 392.3–1110.3 m),

which corresponded to the average altitude for forests dominated by QC and QF. In accordance with the vertical distribution patterns of these forest species, QC and QF were predominantly found on flat and gentle slopes, whereas QP was mainly located in sloped mountainous regions (Fig. 3A,B).

The distribution of forests dominated by the three studied species varied also with terrain exposure (Fig. 4A–C). While QC preferred shady exposures (56.8 %), this preference decreased in QP (51.9 %). In QF-dominated forests, the presence of sunny and shady slopes was nearly equal, and their tolerance for fully southern slopes was notable.

All three studied species tended to avoid western exposures, likely due to the prevailing westerly movement of air masses over Bulgaria. Nevertheless, while QC avoided slopes oriented west-southwest, QP avoided slopes oriented west-north-

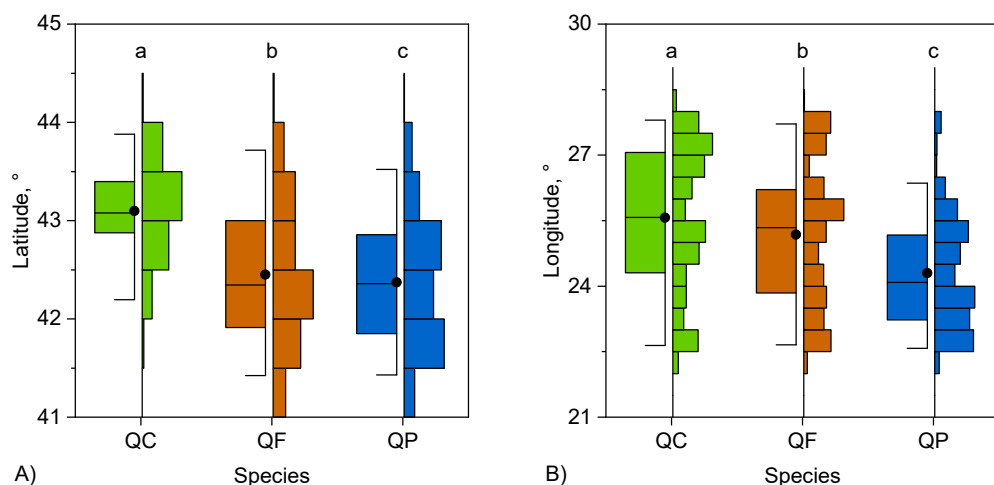


Fig. 2. Distribution extent of *Q. cerris* (QC), *Q. frainetto* (QF) and *Q. petraea* (QP) dominated forests by: A) latitude, B) longitude.

Note: Mean values are indicated by a solid dot, the median by a line, the box range shows the 25–75% quartiles, and the whiskers extend to the 5–95% range. Histograms display the distributions with a bin size of 0.5°. Means that do not share a letter differ significantly (one-way ANOVA with Tukey test, p -value < 0.05).

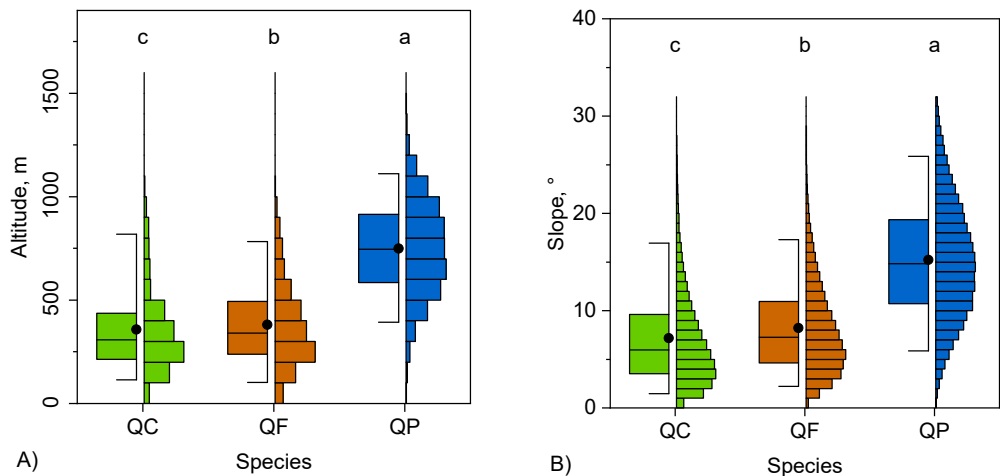


Fig. 3. Orography extent of *Q. cerris* (QC), *Q. frainetto* (QF) and *Q. petraea* (QP) dominated forests by: A) altitude, B) slope.

Note: Mean values are indicated by a solid dot, the median by a line, the box range shows the 25–75 % quartiles, and the whiskers extend to the 5–95 % range. Histograms display the distributions with a bin size of 100 m in altitude and 1° in slope. Means that do not share a letter differ significantly (one-way ANOVA with Tukey test, p -value < 0.05).

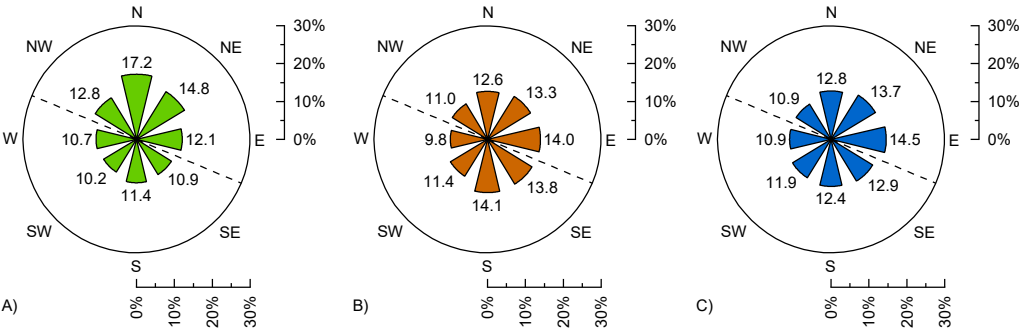


Fig. 4. Distribution of terrain exposures in forests dominated by A) *Q. cerris* (QC), B) *Q. frainetto* (QF) and C) *Q. petraea* (QP).

west, and the QF was least frequently observed on slopes directly exposed to the west.

Phenology

Within the noted disparities in the distribution of QC, QF, and QP-dominated forests, species-specific differences emerged both at the start and, more prominently, at the

end of the vegetation period (Fig. 5A–C).

In QC-dominated forests, the SVP occurred around 20 April (± 4.8 days), and the EVP occurred around 15 October (± 12.8 days), leading to a shortened LVP of 178.1 days (± 13.8). The longest LVP of 188.0 (± 12.4) days occurred in QP-dominated forests, primarily because of a later EVP on 23 October (± 9.4 days), rather than an earlier SVP on 18 April (± 6.6

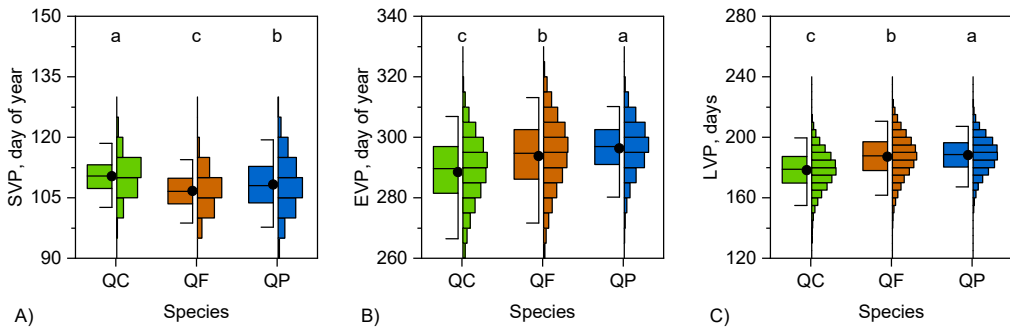


Fig. 5. Phenological events: A) start of vegetation period (SVP), B) end of vegetation period (EVP), and C) length of vegetation period (LVP) in forests dominated by *Q. cerris* (QC), *Q. frainetto* (QF) and *Q. petraea* (QP).

Note: Mean values are indicated by a solid dot, the median by a line, the box range shows the 25–75 % quartiles, and the whiskers extend to the 5–95 % range. Histograms display the distributions with a bin size of five days. Means that do not share a letter differ significantly (one-way ANOVA with Tukey test, p -value < 0.05).

days). The earliest SVP was observed in QF-dominated forests on 16 April (± 4.8 days). However, in these forests, EVP occurred earlier than in QP-dominated forests, on 20 October (± 12.9 days). This chronology resulted in an LVP of 187.1 days (± 14.7), which, despite being similar in length, remained slightly shorter than the LVP in QP-dominated forests.

In the two species most closely associated with plain conditions (QC and QF), SVP was reached relatively quickly, typically within two weeks, for 90 % of these forests. Conversely, in the more montane QP, SVP was significantly delayed, reaching nearly 22 days for 90 % of the forests dominated by this species. The EVP period was considerably longer than SVP, exceeding one month in the examined forests. EVP occurred most rapidly in forests primarily composed of the more mountainous QP species, around 30 days for 90 % of these forests. In contrast, for the more plains-adapted species, QC and QF, this period extended to 40–41 days.

Spring phenology at QC was most

strongly associated with latitude, with SVP occurring 2.3 days earlier per degree northward and 1.3 days later per 100 m increase in elevation, while longitude had no significant effect. Conversely, in QP, altitude had a greater influence, delaying SVP by 2.1 days per 100 m, whereas a one-degree northward shift advanced SVP by 1.8 days. The spring phenology in QF was not significantly influenced by latitude, longitude, and altitude, and occurred largely synchronously within its range in Bulgaria.

The autumn phenology in QC was significantly affected by geographical coordinates, with a one-degree eastward shift advancing EVP by 2.3 days, and a one-degree northward shift delaying it by 2 days later. Elevation had a minor effect on QC's autumn phenology, amounting to less than one day per 100 metres of elevation gain. In QF, longitude was the main factor, advancing EVP by 2.1 days per degree east. For QP, EVP occurred 1.5 days earlier per degree northward.

These trends were evident in LVP,

which increased by 4.3 days in QC with a degree shift to the north and decreased by 2.4 days with a shift to the east. In QF, longitude had the most significant effect, with a one-degree eastward shift reducing LVP by 2.4 days. In QP, LVP was most sensitive to altitude, shortening by 1.7 days per 100 m increase.

Discussion

This study confirmed that QC was associated with flatter conditions in Northern, Eastern, and especially Northeastern Bulgaria, and is nearly absent in southwestern Bulgaria due to the more mountainous terrain and higher altitude there. These findings align with those of other authors (Stefanov 1943a). QP preferred more mountainous areas in Southern, Western, and particularly Southwestern Bulgaria. Although QF exhibited a wide range across Bulgarian forests, it was most prominently dominant in hilly and flat regions within the northwestern-southeastern Bulgaria strip. Some authors, such as Mérian et al. (2011), suggested that the amount of precipitation during the active growth period (May to July) limits the distribution of QP. Perkins et al. (2018) and Peters et al. (2023) proposed that this may have resulted from the anisohydric traits of the species, which can lead to a more prolonged drought memory due to high investments in maintaining photosynthetic activity. In Bulgaria, the species' preference for southern and western regions appeared to be more closely associated with the mountainous terrain of these areas than with their hydrothermal regimes, as the species dominates forests from the Western Stara Planina to the Eastern Rhodopes and Strandzha. However, Šimková et al. (2023) highlighted

that droughts occurring in June and July mainly restrict the growth of QC, with temperature having only a minor influence. Stefanov (1943b) also notes that although it avoids terrain with high groundwater levels, the QP is sensitive to late spring droughts, which explains its preference for more mountainous, drained, but better periodically moistened areas by rain. Additionally, Móricz et al. (2021) observed that QP exhibited lower growth plasticity in response to drought compared to QC. The authors noted that QC responded dynamically to fluctuations in soil water availability, showing significantly decreased growth rates during droughts, a strategy that likely helps in conserving reserves for subsequent recovery and survival. The greater potential for recovery after a dry period in QC compared to QP was further confirmed by Mészáros et al. (2022). This, combined with better resistance to low temperatures due to later leafing, explains the more widespread presence of QC in Northern and especially in Northeastern Bulgaria. On the other hand, Stefanov (1943a) points out that, compared to other studied oaks, the QC has almost annual fruiting and significantly more successful natural regeneration, which may be responsible for its wide distribution. The preference for different terrain exposures in QC and QF probably reflects different strategies in water absorption, and therefore, differences in their geographical distribution. Although QF extends into the foothills of Northern Bulgaria, it is less dominant than QC in Northeastern part of Bulgaria, where the climate is likely too continental for this species. In the central and western parts of Northern Bulgaria, where both species coexist in mixed oak forests, they dominate slopes with different exposures – QF on south- and south-east-facing slopes, and QC on north- and

northeast-facing ones. It should be noted that, due to the preference for the flatter conditions of the QC and the QF, their distribution is heavily affected by human activity (Stefanov 1943b). The predominantly coppice forests (Alexandrov and Tonchev 2024) may regenerate through various mechanisms related to overcoming competition from grass and shrub vegetation, which in the QC could explain its stronger presence in shaded rather than sunny exposures. However, Popović et al. (1997) noted that QF has a narrower ecological range than QC in most aspects, especially concerning light and soil moisture, although it is more drought-tolerant and requires higher light availability.

The observed differences in phenological events were likely driven by ecological variations among the studied species and by the differing conditions of their respective forest habitats. As a more continental species (San-Miguel-Ayanz et al. 2016), QC emerged the latest, which probably enhanced its resilience to late spring frosts. Unlike European beech, in which the investment in winter bud formation begins in the middle of the previous year (Anev 2023, 2025), species within the genus *Quercus* do not show such preparatory processes. This creates a challenge for species that produce new leaves early, as they need to store more winter reserves in the xylem parenchyma to enable rapid leaf emergence. Conversely, species that unfolded earlier and over a longer period, such as QP, benefited from using assimilates produced by young leaves to support the later phases of leaf and shoot development. Numerous studies (Liepe 1993, Deans and Harvey 1995, Ducousso et al. 1996, Sáenz-Romero et al. 2017, Gafenco et al. 2022) conducted in comparative trials of sessile oak have shown that the budburst phenology varies with latitude,

with southern populations leafing earlier than northern ones. Gafenco et al. (2022) reported that budburst in sessile oak followed longitudinal and altitudinal tendencies rather than latitudinal ones, with lower-elevation eastern provenances leafing earlier than higher-elevation western ones, suggesting that less accumulated heat is required to trigger budburst. However, these findings contrasted with those of Jensen (2000), who found in comparative trials of sessile oak and pedunculate oak that northern provenances budded earlier than southern provenances, which agreed with our results. Nonetheless, certain studies have also documented similar clinal variations along altitudinal gradients (Alberto et al. 2011, 2013), which may be attributed to the species' high physiological tolerance to heat. The earliest leaf development observed in QF indicated a preference for more Mediterranean conditions and likely explained its weaker presence in Northeastern Bulgaria, where late spring frosts could disrupt the vegetation period. Across all species, EVP lasted longer than SVP. However, while in QP the difference between the two phenophases was only ten days, in QC and especially in QF, this difference exceeded two and a half times. The two species characterised by rapid and short SVP phases (QC and QF) had a slower and prolonged EVP, whereas, in contrast, the slow-developing QP completed the vegetation period quickly. This may reflect the more contrasting conditions in the mountain's habitats where QP predominates.

Conclusions

This study highlighted the distinct ecological and phenological features of the three most common oak species in Bulgarian

forests. Both QC and QF favoured flatter areas but differed in exposure preferences. Specifically, QC preferred shaded slopes, whereas QF was often found in sunny terrains. Meanwhile, QP occurred on steeper slopes, mountainous regions, reflecting its tolerance for cooler and more variable conditions. QC dominated the flat, low-lying areas of Northern and Eastern Bulgaria, exhibiting a broad longitudinal distribution and strong adaptation to continental conditions through late leaf unfolding and short vegetation periods. QF primarily inhabited hilly terrains across Southern Bulgaria, showing the widest latitudinal and longitudinal range, as well as earlier leaf development, reflecting adaptation to warmer, more Mediterranean climates, yet limiting its presence in the colder Northeast. QP prevailed in the mountainous regions of Southern and Western Bulgaria, displaying the widest altitudinal range and the most extended vegetation period due to delayed leaf senescence. Phenological rhythms varied geographically: QC was the most influenced by latitude and altitude, QP by altitude, and QF showed the least spatial dependence. These distinct ecological and phenological strategies shape distribution of studied oak species across Bulgaria and provide insights into their potential responses to future climatic shifts.

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