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The remotely sensed carousel of spring green-up: Do individual trees reshuffle their phenological ranks across years?

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ABSTRACT

Within temperate deciduous forests, spring leaf-out timing varies markedly among individuals of the same stand, yet whether this variation reflects persistent phenological strategies or year-specific reshuffling remains unresolved. Addressing this question requires individual-resolved, multi-year observations rarely achievable at scale with conventional monitoring. Here, we leveraged high-resolution PlanetScope satellite imagery, enabling individual crown resolution, to track spring canopy greenness of 50 European beech (*Fagus sylvatica*) individuals in a managed stand in the central Apennines (Tuscany, Italy) at five key stages of green-up over five years (2020–2024). We quantified intra-stand variability from green-up onset to the early summer canopy plateau and assessed the inter-annual consistency of within-stand phenological hierarchy using Kendall's coefficient of concordance and pairwise Spearman's rank correlations. Phenological ranks were significantly repeatable across years, yet consistency was strongly modulated by phenological phase. It peaked once canopy expansion was complete and collapsed during the preceding active leaf-expansion phase, which emerged as a tipping point where year-specific spring conditions most strongly reshuffled individual rank positions. At the individual level, four recurrent trajectory types were distinguished: trees with consistently high (consistently high archetype) or consistently low ranks (consistently low archetype), and two reshuffling types (variable archetypes) whose ranks changed in opposite directions between years. The coexistence of these strategies within a structurally homogeneous stand may reflect individual, possibly genetic, differences in phenological response and is consistent with a population-level bet-hedging mechanism, whereby phenological diversity buffers collective performance across variable spring conditions, distributing risk across the population rather than concentrating it. These findings challenge the assumption of fixed intra-population phenological niches and highlight the need for individual-scale frameworks in both empirical phenology and process-based modeling, particularly for southern populations facing accelerating climate change.

1. Introduction

Spring leaf-out is a pivotal phenophase in temperate deciduous forests, marking the onset of canopy development and strongly shaping seasonal carbon uptake, water exchange, and trophic interactions (Chen et al., 2022). In such ecosystems, broad-scale patterns of spring phenology are primarily governed by photothermal forcing interacting with dormancy processes, and phenology responses may largely vary across latitude (Meng et al., 2021) and elevation (Skvareninova et al., 2024).

However, within a single forest stand, where individuals experience broadly similar daylength cues and regional weather, leaf-out timing can still diverge markedly and individuals within a single stand may differ by days to weeks (Malyshev et al., 2022; Lin et al., 2024). This crown-level asynchrony can affect within-stand light competition and the timing of canopy closure, thereby influencing understory light windows and competitive outcomes among functional groups (Roberts et al., 2015). It may also mediate vulnerability to late frost events, because early flushing individuals can experience disproportionate damage during cold snaps (Vitasse et al., 2025; Bascietto et al., 2018).

Inter-individual variation in leaf-out likely reflects a combination of genetic differences and phenological strategies (Vitasse, 2013; Lazic

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et al., 2024; Kembrytė et al., 2022), ontogenetic and structural effects (e.g., age- and size-related differences in microclimate exposure or resource status) (Malyshev et al., 2022; Panchen et al., 2014; Osada and Hiura, 2019), and microenvironmental heterogeneity (e.g., irradiance, competition status) (Zellweger et al., 2020; Adams et al., 2021). Evidence for individual-condition effects has been reported across temperate deciduous systems, where tree size and light environment can correlate with leaf phenology (Marchand et al., 2020; Delpierre et al., 2017; Malyshev et al., 2022). Genetic structuring can also covary with phenological forms in beech, suggesting that within-stand phenology may partly reflect stable, biologically meaningful differences rather than observational "noise" (Kembrytė et al., 2022; Lazic et al., 2024). At the same time, microclimatic variation experienced by buds and leaves can diverge from standard meteorological measurements, exerting strong control over phenological timing (Vitasse et al., 2021; De Frenne et al., 2021).

A central open question is therefore not only how much individuals differ, but how consistently they differ through time. If individual trees maintain stable phenological "ranks" (i.e., the same trees repeatedly flush early or late), then inter-individual variability can be interpreted as a repeatable spectrum of strategies with predictable behavior across years. Conversely, if ranks reshuffle substantially among years, predictability at the crown level may be limited, and "early" and "late" phenotypes may largely reflect year-specific cueing, carry-over effects, or stochasticity.

Empirical evidence supports both perspectives. In temperate deciduous forests, individual phenological ranks have been shown to mostly repeat from year to year, and rank position can correlate with growth, consistent with persistent differences among individuals (Cole and Sheldon, 2017). Long-term monitoring of different deciduous forests similarly reported strong within-stand rank consistency (Delpierre et al., 2017), identifying subsets of early and late flushers that differed by several days (Malyshev et al., 2022). Yet, rank consistency is not guaranteed and can vary with trait, year, and context. For instance, Capdevielle-Vargas et al. (2015) found that trees showing early leaf unfolding in one year could rank among the latest in the following year, with no consistent phenological order detectable across time, suggesting that within-stand phenological plasticity may represent an adaptive strategy to buffer against unpredictable climatic variation. Even in studies reporting repeatability, ranks are not fully conserved across all individuals and years, and repeatability can differ between spring leaf-out and autumn senescence (Delpierre et al., 2017).

Within beech stands, multi-year assessments have documented pronounced phenological plasticity, implying that interannual cueing can alter absolute timing and relative ordering depending on spring conditions (Malyshev et al., 2022). Additional work indicates that inter-individual variability in spring phenology can be linked to prior-year autumn phenology and tree size, mechanisms that can introduce year-specific carry-over effects and reduce rank stability (Fu et al., 2014; Marchand et al., 2020). Finally, within-population variability itself can change with temperature conditions, implying that inter-individual budburst variation is driven by warming rate (Malyshev et al., 2022) and may compress or expand among years, thereby challenging the assumption of fixed phenological separation (Lin et al., 2024). Within-stand phenology may therefore resemble a carousel, where individuals shift up and down in relative timing across years, rather than maintaining fixed early/late positions. Together, these findings call for a targeted, crown-level assessment of rank stability, treating it as an outcome of interacting drivers.

Answering this local-scale phenology question requires observations that are individual-resolved, frequent enough to capture rapid spring transitions, and sustained over multiple years. High-resolution satellite imagery offers a promising tool to address this gap. Constellations such as PlanetScope provide near-daily observations at meter-scale spatial resolution, enabling repeated tracking of canopy greenness dynamics at spatial grains that can approach individual crowns in many stands. This approach is especially attractive for testing rank consistency because it couples dense temporal sampling with multi-year coverage, allowing phenological ordering to be evaluated repeatedly under varying spring conditions and management contexts (Wu et al., 2021; Wang et al., 2024).

In this study, we leverage high-resolution remote sensing to analyze interannual and inter-individual variability of spring phenology at crown-level in a European beech (*Fagus sylvatica*) stand in the Alpe di Catenaia (Tuscany, Italy), managed under a seed-tree system. The specific aims were to (i) quantify intra-stand variability of individual crown-level canopy greenness across the full arc of spring leaf development over a five-year period (2020–2024), (ii) assess whether individual trees maintain repeatable positions in the within-stand hierarchy across years; and (iii) characterize the diversity of phenological strategies coexisting within a single managed beech stand.

2. Data and methods

2.1. Study area

The study was conducted in a European beech (*Fagus sylvatica* L.) stand under a seed-tree silvicultural system located at the Alpe di Catenaia in Tuscany, central Italy (approximately 43.65°N, 11.8°E, ca. 1000–1100 m a.s.l.), extending over 14,000 m^2 (Fig. 1). The stand is situated on the Apennines and is representative of the southern distribution of European beech.

The climate is sub-Mediterranean montane, characterized by cold and wet winters, moderately wet springs, and mild, dry summers. According to the closest available meteorological station (La Verna; 1125 m a.s.l.; 43.707°N, 11.931°E), climatic conditions during green-up differed markedly among the study years (Fig. 2). 2020 was the driest year until May, with the lowest water balance and a slightly negative value already by May (−5 mm). In contrast, 2024 and 2021 had the wettest late winters (308 and 270 mm in the window ending in March), and 2024 remained the wettest year until May (186 mm). By June, the balance was negative in 2020, 2021 and 2022 (−20 to −63 mm) and close to zero in 2024, while 2023 was the only year with a clear surplus (107 mm), following a very wet May. Mean air temperature over the same windows rose from 2.4 to 5.6 °C in March to 10.8–13.8 °C in June. 2024 was the warmest year until May and 2023 the coolest throughout, while 2020 was warmer than 2021–2023 until April and 2022 was the warmest in June. The study period thus included warm springs with contrasting water availability (dry 2020, wet 2024), cooler springs (2021 and 2023), and a spring with intermediate conditions followed by a warm, dry early summer (2022).

2.2. Remote sensing data and NDVI extraction

Individual trees were segmented from LiDAR point clouds acquired on 8th of April 2024 during leaf-off to define stable crown boundaries (Puletti et al., 2024). The drone used for the LiDAR data collection was the DJI Matrice 350 quadcopter, equipped with the Zenmuse L1 LiDAR sensor, with a range accuracy of 3 cm at 100 m and a mean point density of 1500 per square meter. Crown boundaries were drawn as polygons in a Geographic Information System (GIS) environment and kept fixed across all years and acquisition dates to ensure temporal comparability of the extracted spectral signal. Each crown polygon served as the spatial unit of analysis throughout the study.

To investigate the remotely sensed dynamics and inter-individual variability of spring phenology at the tree level, we selected 50 European beech individuals (Fig. 1). Trees were selected to ensure a representative sampling of canopy conditions within the study area, while minimizing potential confounding factors such as crown overlap, edge effects, and shading from neighboring trees. Only dominant or co-dominant individuals with clearly identifiable and well-isolated crowns were included, allowing consistent crown delineation and

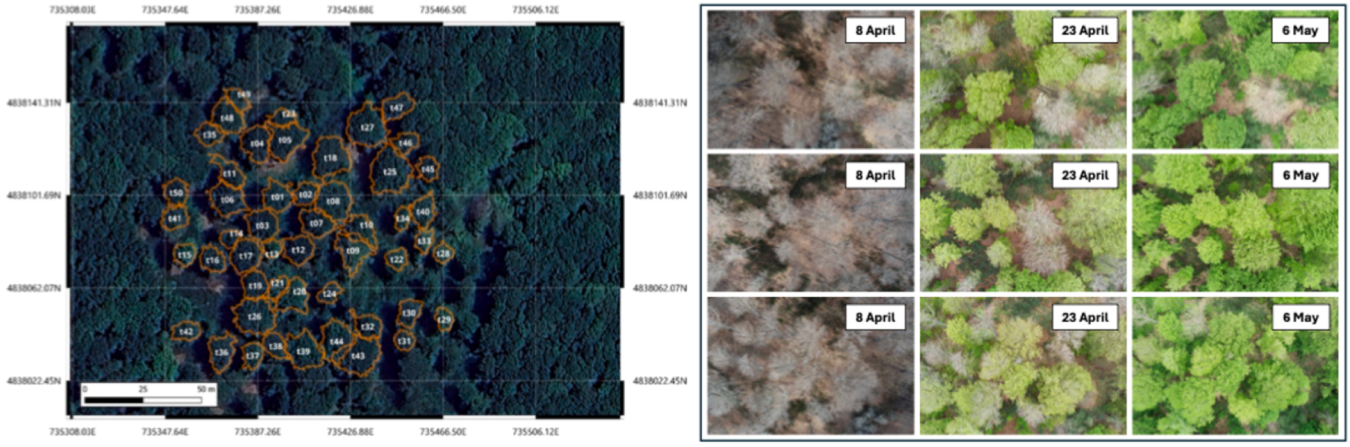

Fig. 1. Location of the stand and the 50 tree crowns (left panel) and drone images of selected plots during spring 2024 (right panel) within the beech stand in Alpe di Catenaia (Tuscany, Italy).

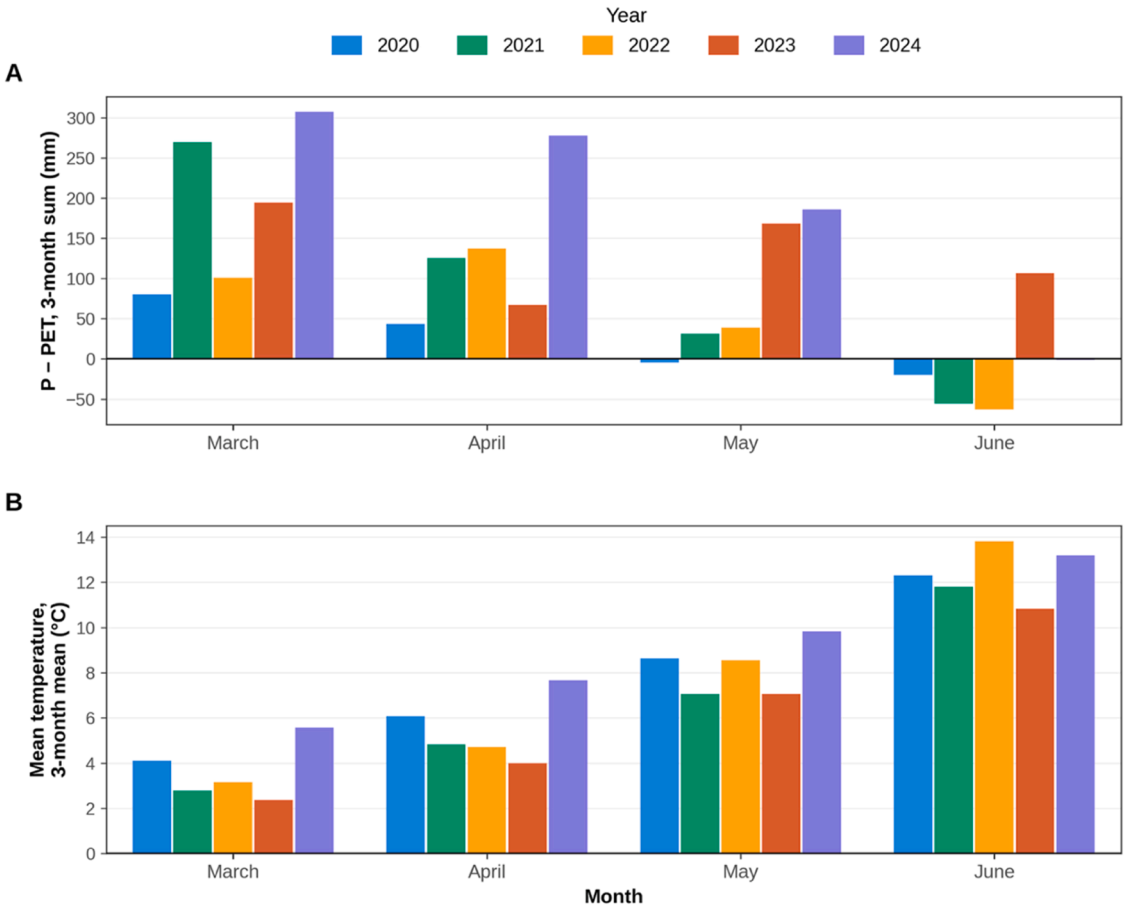

Fig. 2. Climatic conditions during green-up at La Verna station, 2020–2024: (A) climatic water balance (precipitation minus potential evapotranspiration; Hargreaves and Samani, 1985) and (B) mean air temperature, computed over 3-month windows ending in each month from March to June.

reliable pixel extraction across all images and years. Multispectral surface reflectance imagery was acquired from the PlanetScope constellation (Planet Labs PBC), which provides near-daily coverage at approximately 3 m spatial resolution in four spectral bands (blue, green, red, near-infrared). We used the Level 3B Surface Reflectance (SR) product, which is orthorectified and atmospherically corrected. To avoid spatial inconsistencies, we used only full, non-mosaicked PlanetScope scenes, ensuring that all sampled tree crowns were entirely contained within the same image for each acquisition date. For each segmented canopy, for the period 2020–2024, we extracted NDVI (Normalized Difference Vegetation Index; Rouse et al., 1974) values only for pixels fully included (>90%) within the canopy boundaries, corresponding to the central portion of each tree crown, thereby minimizing edge effects and mixed-pixel contamination.

To capture the green-up phase of European beech canopies, for the period 2020–2024, images were selected for five phenologically informative days of year (DOY): 81 (22 March), 93 (3 April), 116 (26 April), 144 (24 May), and 168 (17 June), covering the full arc of spring leaf-out

from bud break to full canopy expansion. These five reference dates were not fixed a priori: they correspond to the time windows in which a cloud-free, non-mosaicked scene covering all 50 crowns was available in every year within a maximum of 7 days, and which at the same time describe the key moments of the spring green-up, from early onset (DOY 81–93) to active leaf expansion (DOY 116), full expansion (DOY 144) and early summer plateau (DOY 168). This allows all trees to be compared within the same seasonal window in every year. The acquisition dates actually used and their offset from the reference DOY are given in Table S1. The five dates are representative of the green-up period rather than an exhaustive sampling of it. The resulting dataset comprised 1250 observations (50 trees × 5 years × 5 DOYs).

2.3. Statistical analysis

To evaluate intra- and interannual variability in the magnitude and timing of spring greenness, a Principal Component Analysis (PCA) was performed on the NDVI dataset configured as 250 observations (50 trees × 5 years) and 5 variables (the five DOYs).

For each year and each DOY, the 50 trees were ranked according to their NDVI value, with rank 1 assigned to the tree with the highest NDVI and rank 50 to the tree with the lowest, on the assumption that higher NDVI reflects more advanced leaf-out and canopy development. This ranking approach describes each tree's position in the stand-level greenness hierarchy at a given phenological moment. This allowed us to standardize inter-individual comparisons across dates and years, reducing the influence of absolute NDVI differences due to external factors (e.g., illumination conditions or residual atmospheric effects) and focusing on relative phenological status among individuals.

Inter-annual consistency of individual phenological ranks was assessed separately for each of the five DOYs. For each DOY, a concordance matrix was constructed with the 50 trees as subjects and the five years as raters, and Kendall's coefficient of concordance W was computed (Kendall, 1948). Kendall's W is a non-parametric statistic that quantifies the overall agreement among multiple raters (here, years) in their ranking of the same set of subjects (here, individual trees): a value of 0 indicates no agreement beyond chance, while a value of 1 indicates perfect concordance across all raters (Kendall, 1948). Kendall's W was tested with a tie-corrected chi-square approximation and with a permutation test in which ranks were shuffled independently within each year (9999 permutations); its 95% confidence interval was estimated by bootstrapping crowns (2000 replicates). Concordance was interpreted following Schmidt (1997), in which $W \approx 0.5$ indicates moderate and $W \approx 0.7$ strong agreement. We used $W = 0.50$ to separate weak-to-moderate from moderate-to-strong concordance: values above this threshold indicate that more than half of the maximum possible agreement is achieved, meaning that individual rank positions are broadly repeatable across years, whereas values below it signal that year-specific variation substantially disrupts the within-stand hierarchy. Additionally, all pairwise Spearman rank correlation coefficients were computed between year pairs for each DOY, yielding 10 pairwise comparisons per DOY. Pairwise Spearman correlations were tested individually, with p-values adjusted for multiple testing across the 50 tests (10 year pairs × 5 dates) using the Benjamini–Hochberg procedure (Benjamini and Hochberg, 1995).

Then, to identify groups of crowns with similar interannual rank trajectories, we applied agglomerative hierarchical clustering (Ward's method on Euclidean distances) to the continuous NDVI ranks (1–50) of the 50 crowns across the five years at the date of maximum rank instability. To explore the structure of the rank trajectories and the resulting clusters, we performed a principal component analysis (PCA) on the same matrix of ranks (50 crowns × 5 years). The number of clusters was selected by comparing the solutions obtained for $k = 2$–6 and retaining the most ecologically interpretable partition. The robustness of each cluster was assessed by bootstrap resampling of crowns (mean Jaccard similarity between original and bootstrap clusters, $B = 500$; Hennig, 2007).

Finally, to characterize individual rank trajectories across the five study years, trees were assigned to within-stand NDVI quartiles (Q1 = bottom 25%, Q4 = top 25%) separately for each year × DOY combination. Quartile transitions between consecutive years (2020–2021, 2021–2022, 2022–2023 and 2023–2024) were summarized, for each DOY, as the percentage of crowns that remained in the same quartile, shifted by one quartile, or shifted by two or more quartiles (Table S2), and as the percentage of crowns in each quartile that remained in it the following year (Table S3). Quartile membership was used only as a descriptive step to visualize rank flows and to simplify the 50 individual rank trajectories into types that can be described. All inferential and quantitative analyses used the full ranks 1–50.

3. Results

Stand-level NDVI trajectories were highly consistent across years, following the same seasonal shape (Fig. 3): a low greenness plateau in early spring (DOY 81–93, mean NDVI 0.47–0.54), a steep rise during active leaf expansion phase (DOY 116), and convergence toward a high summer plateau (DOY 144–168, mean NDVI 0.83–0.90). The 2024 season showed a notably lower NDVI at DOY 81 compared to other years (~0.46), suggesting a later green-up onset. Interannual differences in mean NDVI were largest at DOY 116, where within-stand dispersion also peaked across all years, which represents the moment of maximum inter-individual phenological divergence.

The first two principal components of the PCA together explained 75.9% of the multivariate seasonal structure (Fig. 4). PC1 (45.2% of variance) was dominated by DOY 116, whose loading vector was by far the longest and pointed strongly in the positive direction, reflecting the extremely high NDVI variance at this date. All other DOYs loaded weakly on PC1. To the contrary, PC2 (30.7%) captured a contrast between the summer plateau (DOY 144 and DOY 168 loading positively) and the early green-up phase (DOY 81 and DOY 93 loading negatively), indicating that these two seasonal blocks covary negatively: trees ranking high in early spring tend to rank lower at peak summer, and vice versa. Annual ellipses shifted along PC1 in a non-monotonic pattern: 2024 and 2020 showed centroids displaced toward positive PC1 values, indicating greater inter-individual spread at DOY 116, while 2021 occupied the most negative PC1 position, with 2022 and 2023 intermediate. Notably, the 2024 ellipse was markedly elongated along PC1, while, along PC2, ellipses showed substantial overlap. These findings suggest that inter-annual variation in NDVI is driven primarily by differences in the active leaf expansion phase rather than by uniform shifts across the entire growing season, and that the magnitude of this mid-season variability is itself year-dependent, being particularly pronounced in 2024.

Inter-annual rank concordance was significant at all five dates (chi-

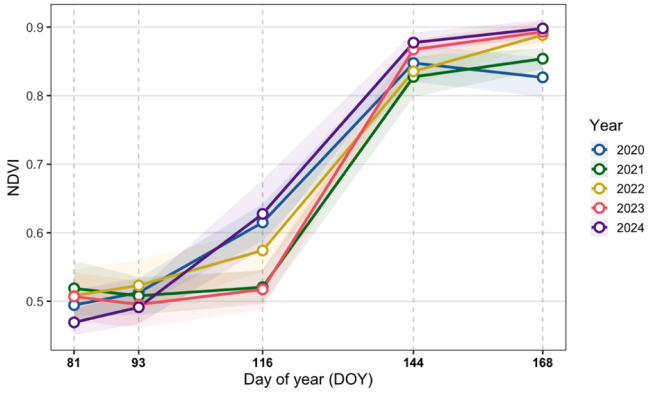

Fig. 3. Mean values of the NDVI distributions for the considered spring DOYs (81, 93, 116, 144, and 168) over the five-year study period (2020–2024).

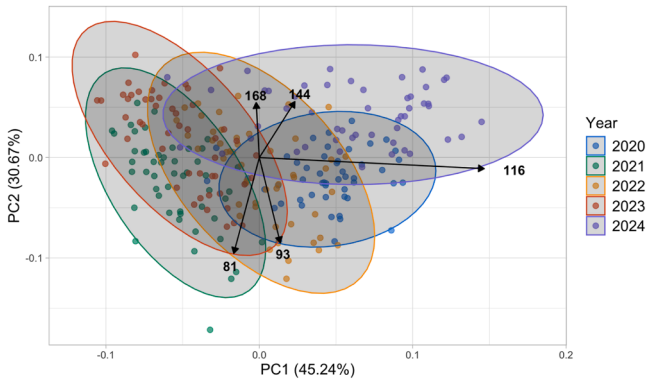

Fig. 4. Principal component analysis (PCA) of spring canopy greenness dynamics for 50 individual beech trees across five years (2020–2024) at the Alpe di Catenaia stand (Tuscany, Italy). Each observation (n = 250, 50 trees × 5 years) is represented as a point colored by year. Shaded ellipses indicate 95% confidence regions computed separately for each year. Black arrows indicate variable loadings (DOY 81, 93, 116, 144, 168).

square and permutation tests, $p < 0.001$; Fig. 5A). W ranged from 0.402 at DOY 116 (95% CI 0.28–0.53) to 0.671 at DOY 144 (0.54–0.77), and its interval did not overlap those of DOY 93 (0.55–0.74) and DOY 144, revealing a clear seasonal pattern in rank stability. The lowest concordance occurred during active leaf expansion (DOY 116), where individual NDVI ranks were most susceptible to year-specific cueing, consistent with this phase concentrating the greatest inter-individual phenological plasticity. The highest concordance was recorded at DOY 144, suggesting that the within-stand hierarchy is most reliably expressed at full leaf expansion.

The Spearman pairwise correlations reveal considerable heterogeneity in pairwise rank consistency both across years and across DOYs (Fig. 5B). Concordance was weakest at DOY 116, where year-specific spring forcing conditions appeared to differentially reorganize the within-stand hierarchy, and 2020 in particular showed systematically lower agreement with subsequent years across multiple DOYs. Concordance peaked at DOY 144, where correlations were the strongest and most uniformly significant across all year pairs, confirming full leaf expansion as the phenological moment when stable individual differences are most clearly and repeatably expressed.

The alluvial diagrams confirmed the mixed picture emerging from the pairwise Spearman analysis: at all five DOYs, flows showed a combination of within-quartile persistence and cross-quartile movement, indicating that neither full rank stability nor complete rank reshuffling characterized any single phenological moment (Fig. 6). The balance between these two tendencies, however, shifted across the season. At DOY 144, parallel flows predominated, with most trees remaining within the same or an adjacent quartile across consecutive years, though a non-negligible fraction crossed quartile boundaries in each transition. At DOY 116, this balance tilted markedly toward instability, with extensive crossing across all year pairs and no stable block of trees maintaining a consistent quartile position throughout the study period, confirming this date as the moment of maximum rank disruption within



Fig. 5. Inter-annual consistency of individual canopy greenness rankings across phenological dates. (A) Kendall's coefficient of concordance (W) computed across the five study years (2020–2024) for each of the five phenological dates (DOY 81, 93, 116, 144, 168), treating the 50 individual trees as subjects and years as raters (n = 50 trees). The dashed horizontal line indicates W = 0.50 as a reference threshold. Error bars: bootstrap 95% confidence intervals (2000 resamples of crowns). (B) Pairwise inter-annual Spearman rank correlations between all ten year-pairs for each phenological date, computed on within-stand NDVI ranks. Each cell reports the Spearman ρ coefficient; asterisks indicate significance level after Benjamini–Hochberg correction for multiple testing across the 50 tests (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$); non-significant correlations are shown without asterisks. Color scale ranges from brown (negative correlation) to dark green (positive correlation).

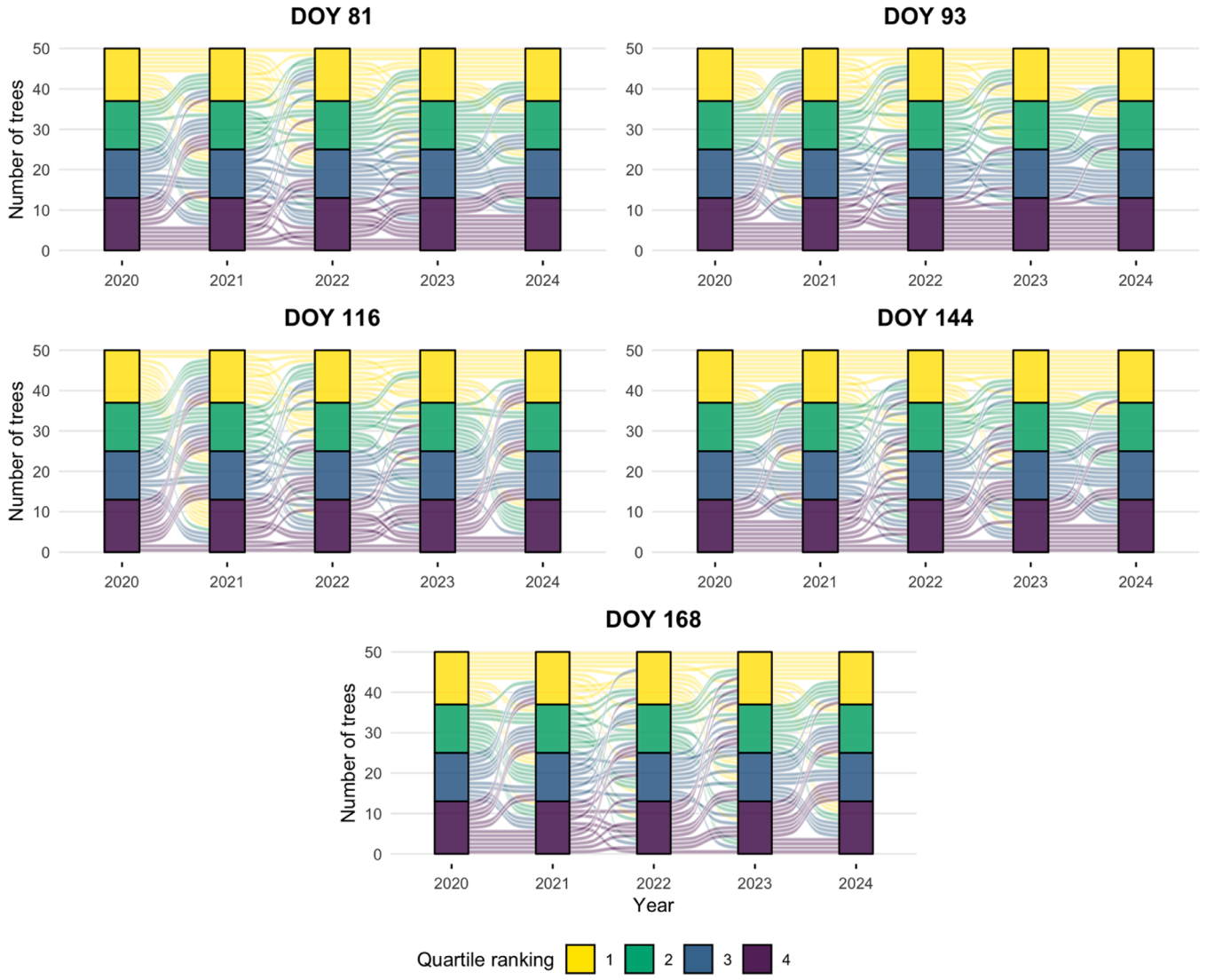

Fig. 6. Alluvial diagrams showing the temporal dynamics of within-stand canopy greenness rank positions for 50 individual beech trees for each of the five phenological dates (DOY 81, 93, 116, 144, 168), across 2020–2024. For each year × DOY combination, trees were assigned to within-stand NDVI quartiles: Q1 (yellow, bottom 25%, lowest NDVI), Q2 (green), Q3 (blue-gray), and Q4 (purple, top 25%, highest NDVI). Each ribbon represents an individual tree tracked across the five study years; ribbon color reflects the quartile assigned in the origin year of each transition.

the seasonal trajectory.

Among the solutions compared (k = 2–6), hierarchical clustering identified four, ecologically meaningful groups of rank trajectories. According to the PCA of the interannual NDVI rank trajectories at DOY 116 (Fig. 7), ranks in 2021–2023 loaded mainly on PC1 and ranks in 2020 and 2024 mainly on PC2. The four clusters occupied the four combinations of rank in the two groups of years. Consistently high (n = 9) and consistently low trees (n = 10) kept their position in both groups of years, whereas variable amplified trees (n = 17) ranked higher in the high-NDVI years (2020, 2024) and variable damped trees (n = 14) in the low-NDVI years (2021–2023). The cluster of variable damped trees was highly stable under bootstrap resampling (Jaccard = 0.89), whereas the clusters of consistently low, variable amplified and consistently high trees were moderately stable (Jaccard = 0.64, 0.60 and 0.64, respectively), indicating that the clusters describe a continuum of trajectories rather than discrete types.

The four clusters thus corresponded to different phenological archetypes (examples in Fig. 8; see Supplementary material for the whole set of trajectories). Consistently high trees (e.g., t27) ranked among the most advanced in all five years, regardless of interannual variation in spring forcing conditions. Consistently low trees (e.g., t18) showed the opposite pattern, remaining in the lower ranking across years, which may reflect individual or microsite characteristics rather than a specific response to interannual conditions. Variable trees alternated between high and low ranks from year to year, responding to year-specific conditions differently from the rest of the population in two opposite ways: amplified trees (e.g., t42) ranked high in the high-NDVI years and low in the low-NDVI years, whereas damped trees (e.g., t31) showed the reverse pattern.

4. Discussion

This study provides a crown-level, multi-year assessment of spring phenological dynamics in a European beech stand, tracking the full green-up trajectory at the individual level. Our results show that within-stand phenology is neither fully deterministic nor purely stochastic, but emerges from a dynamic interplay between persistent inter-individual differences and phenological plasticity. These findings contribute to the ongoing debate on whether within-population phenology reflects stable individual strategies or year-specific reshuffling, and suggest that both mechanisms coexist and interact within the same stand.

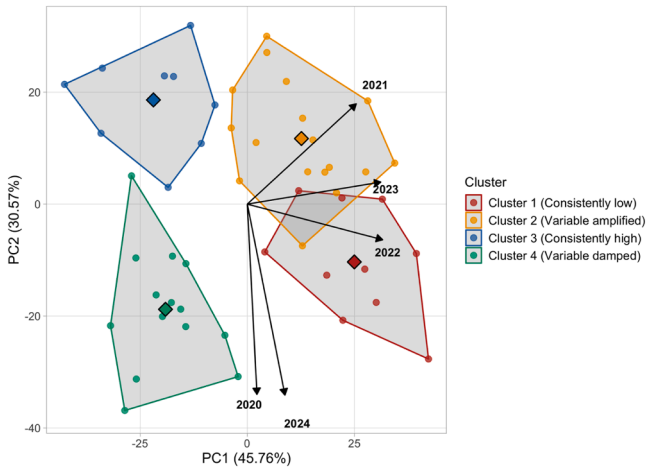

Fig. 7. Principal component analysis (PCA) of the interannual NDVI rank trajectories of 50 individual beech trees at DOY 116. Each point is a crown, described by its NDVI rank (1 = highest NDVI) in each of the five years (2020–2024), and colored by cluster. Polygons are the convex hulls of each cluster and diamonds mark the cluster centroids. Black arrows indicate variable loadings (years) and point toward increasing rank, i.e. lower NDVI.

4.1. Phase-dependent rank stability during canopy green-up

Our results provide clear evidence that within-stand spring green-up in *Fagus sylvatica* emerges as a "phenological carousel". By leveraging high-resolution remote sensing, we show that individual phenological ranks exhibit a significant interannual consistency, with a marked loss of coherence during leaf expansion.

Significant Kendall's W across dates demonstrates that individuals retain a consistent phenological identity, supporting previous works showing that phenological ranks in temperate deciduous trees are not random but reflect persistent individual differences that repeat from year to year. Delpierre et al. (2017) documented strong within-stand rank consistency in leaf-out timing across multiple temperate deciduous species in France, showing that rank position correlated with individual growth performance and biological traits, rather than observational noise. Similarly, Malyshev et al. (2022) identified stable subsets of early and late budburst individuals within a beech stand in Germany, attributing inter-individual variation primarily to differences in sensitivity to spring warming rate rather than to stochastic year-specific responses. Our study extends these findings to a Mediterranean population and a crown-level remote sensing framework, showing that this structure also emerges in canopy greenness dynamics, not only in phenological onset dates.

Our results partially differ from studies reporting weak individual predictability (e.g., Capdevielle-Vargas et al., 2015), likely due to methodological and environmental differences. NDVI integrates both timing and leaf area, potentially capturing more stable structural differences than onset dates alone, while longer time series and recurrent drought conditions in our study may enhance the detectability of persistent individual differences. Indeed, climatic context plays a key role. Under non-stressful conditions, stochastic year-specific variation in microclimate and carry-over effects may dominate over stable genetic differences, reducing rank consistency (Cole and Sheldon, 2017). Under recurrent drought stress, by contrast, the same environmental filter is applied repeatedly, amplifying the expression of stable individual differences in drought sensitivity and phenological strategy (George et al., 2017; DeSoto et al., 2020).

However, the observed repeatability is strongly phase-dependent. Rank consistency peaks at full canopy expansion (DOY 144) but weakens markedly during active leaf expansion (DOY 116), identifying this latter stage as a key window of plasticity. This matters for studies of the drivers of individual phenology: relating individual traits to rank position during active leaf expansion would test a largely reshuffled hierarchy.

The active leaf expansion date emerged as the most unstable point in the seasonal rank trajectory across all analytical frameworks. DOY 116 falls precisely within the window of maximum sensitivity to transient spring forcing conditions, possibly explaining why ranks at this date are most susceptible to year-specific cueing. It showed the greatest absolute NDVI variance (Fig. 3), the widest dispersion in the PCA covariance biplot (Fig. 4), the lowest inter-annual Kendall W (Fig. 5) and the highest rank exchange rate across years (Fig. 6). Rather than representing a smooth transition between spring and summer, this stage functions as a tipping point between two physiologically distinct phases, consistently with the known physiology of beech leaf expansion (Cole and Sheldon, 2017; Delpierre et al., 2020; Malyshev et al., 2022). This reflects the sensitivity of early leaf development to interacting controls of chilling, forcing, and photoperiod, and aligns with evidence that inter-individual

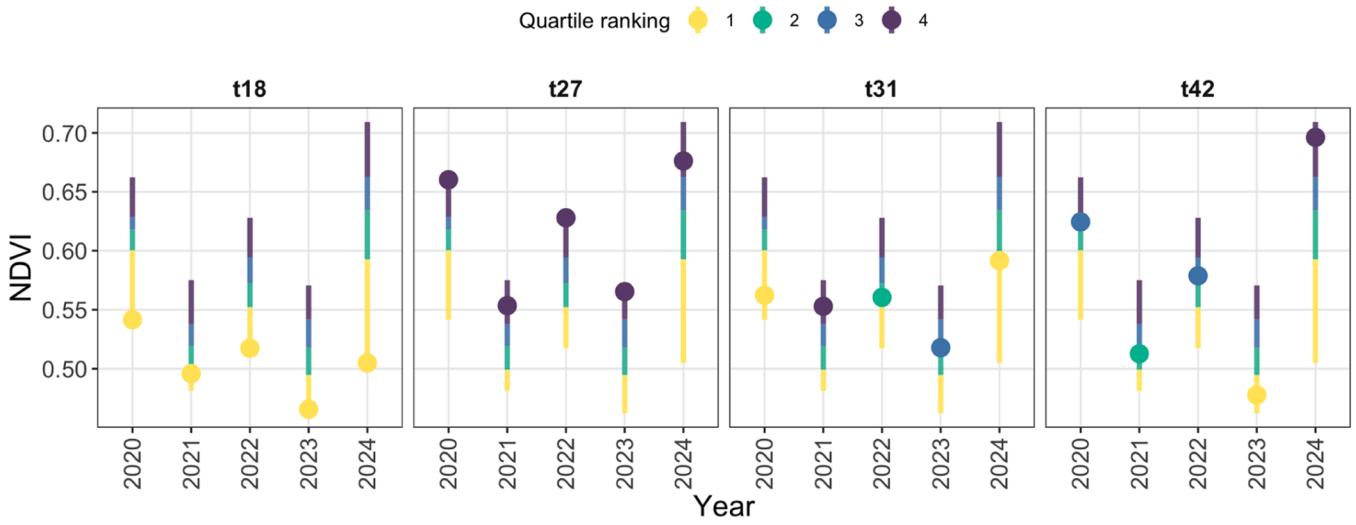

Fig. 8. Within-stand quartile rankings and individual NDVI trajectories across 2020–2024 at DOY 116 for four representative beech trees (t18, t27, t31 and t42) illustrating contrasting phenological clusters. Point color indicates quartile membership within the stand at that year × DOY 116 (Q1 = yellow, lowest NDVI; Q2 = green; Q3 = blue; Q4 = purple, highest NDVI). Vertical bars indicate the full range of NDVI values, color-coded per quartile boundaries, observed across the 50-tree stand at that date and year.

variability in budburst depends on spring forcing dynamics and nonlinear temperature responses (Malyshev et al., 2022; Lin et al., 2024). While previous studies have shown that variability peaks during green-up (Denéchère et al., 2021; Delpierre et al., 2020), our results further demonstrate that this phenological stage is structurally unstable, and small differences in climatic cues can amplify inter-individual divergence, increasing the likelihood of rank reshuffling.

4.2. Within-stand phenological diversity as a bet-hedging strategy

The clustering at DOY 116 (i.e., during active leaf expansion) reveals that, at the individual level, different phenological archetypes coexist within the stand: crowns consistently ranking high, crowns consistently ranking low, and crowns alternating between high and low positions across years. The reshuffling observed at this phase is therefore not random, but structured by how individual crowns respond to interannual conditions.

The climatic contrasts between study years during green-up are consistent with this interpretation. 2020 had the lowest water balance in the three-month windows ending in March, April and May, and the only negative balance by May, whereas 2023 and 2024 were the wettest years. 2020 and 2024 were also the warmest years, whereas 2021 and 2023 were the coolest. The four trajectory types responded differently to these contrasts. Consistently high- and consistently low-ranking crowns kept their relative position in all years, regardless of whether springs were warm or cool, dry or wet. In contrast, the variable archetypes responded in opposite ways: variable-amplified crowns ranked high (i.e., early) at DOY 116 in the two warmest years (2020 and 2024), despite their opposite water balance, and low (i.e., late) in 2021 and 2023, whereas variable-damped crowns showed the reverse pattern. Together, these patterns suggest that the relative rank position of some individuals depends on spring temperature, while others keep their position regardless of spring conditions. This is consistent with evidence that individual phenological ranks may repeat from year to year within stands (Delpierre et al., 2017), but that individuals differ in their response to spring warming (Malyshev et al., 2022), and that spring temperature modulates the spread of leaf-out dates within populations based on individual environment-sensitivity (Zohner et al., 2018; Denéchère et al., 2021). However, with five years, these links remain descriptive and should be tested on longer series.

Our design constrains the structural factors most often invoked to explain within-stand phenological variation. Only dominant or co-dominant trees with well-isolated crowns were selected, so canopy position, shading and crown overlap (Delpierre et al., 2017; Malyshev et al., 2022) are limited by construction. Therefore, the persistence of distinct trajectory types under these structural conditions, and where all individuals experienced broadly similar regional weather, suggests underlying biological differences, likely with a genetic component, consistent with previous findings in beech populations (Kembrytė et al., 2022; Lazic et al., 2024). The coexistence of consistently high, consistently low and variable phenological archetypes suggests that within-population diversity is maintained even under strong climatic forcing, consistent with recent work linking phenological traits to genetic and adaptive variation (Pfenninger et al., 2025).

From an ecological perspective, the diversity of phenological strategies within the stand may function as a population-level buffering mechanism, analogous to bet-hedging (Simons, 2011) and to the portfolio effect described for population diversity (Schindler et al., 2010; Malyshev et al., 2022). Different climatic configurations may favor different phenological behaviors: for instance, early-flushing (i.e., high-ranking) individuals may benefit from warm springs followed by mild summers (e.g., 2020), when a longer leafy season is not offset by summer water stress, while late-flushing (i.e., low-ranking) individuals may be favored in years with cold springs (e.g., 2021 and 2023), when delayed leaf-out reduces exposure to late frosts (Bascietto et al., 2018). Since no single phenological strategy is likely to be optimal across all possible climatic configurations, the maintenance of a distribution of sensitivities within the stand may ensure that risk is distributed across individuals rather than concentrated on the whole population simultaneously (Hughes et al., 2008). This functional role of within-stand phenological diversity has been proposed on theoretical grounds, and our results provide individual-level evidence of the response diversity on which it could rest in a forest stand.

This bet-hedging interpretation acquires particular relevance for southern beech populations, such as those of the central Apennines, where warming and increasing summer drought frequency are expected to intensify. The maintenance of within-stand phenological diversity may be a critical determinant of population persistence under global change (Hampe and Petit, 2005). The stand should thus be viewed not as a homogeneous unit, but as a mosaic of phenological strategies whose diversity underpins its adaptive potential.

5. Conclusions

This study shows that crown-level phenology in European beech is governed by a dynamic interplay between stability and plasticity, likely modulated by phenological phase and climatic context. The leaf expansion period emerges as a critical tipping point where predictability breaks down and rank reshuffling is maximized. Moreover, the coexistence of distinct phenological strategies within a single stand suggests possible trade-offs between early/late growth and stress resilience. These findings challenge the assumption of fixed phenological niches within populations and highlight the need to explicitly consider intra-stand variability in both empirical and modeling frameworks. Our findings also highlight a key limitation of aggregated approaches: averaging across individuals obscures critical dynamics such as rank reshuffling, phase-dependent variability, and seasonal inversion. By leveraging high-resolution imagery, this study demonstrates that individual-level phenological dynamics can be resolved remotely over multiple years, bridging the gap between ground observations and coarse satellite analyses. Future work should aim to link phenological types to physiological traits and attribute individual rank positions to their drivers combining crown-level phenology (via satellite, phenocams or ground surveys) with crown traits, microclimate and genetic data, to better predict phenological responses to climate change.

CRediT authorship contribution statement

Mara Di Giulio: Writing – original draft, Investigation, Formal analysis, Data curation. **Carlo Ricotta:** Writing – review & editing, Supervision, Conceptualization. **Nicola Puletti:** Writing – review & editing, Data curation. **Sofia Bajocco:** Writing – review & editing, Writing – original draft, Supervision, Methodology, 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.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2026.111618.

Data availability

Research Link Provided
Spring NDVI time series from PlanetScope imagery (Original data) (Figshare)

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