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Climate-driven shifts in tree phenology: global patterns, trends, and ecological implications

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Shifts in the seasonal timing of tree phenological events, including budburst, leaf emergence, flowering, and fruiting, are among the most sensitive biological indicators of climate change. We conducted a systematic review of 145 empirical studies published between 2004 and 2024, encompassing 116 tree species across tropical, subtropical, temperate, and boreal biomes, to synthesize global trends, dominant climatic drivers, and ecological consequences of phenological changes. Temperature emerged as the primary driver in temperate and boreal systems, where spring leaf-out and flowering advanced by 2.5–5.1 days/°C of warming. In contrast, phenology in tropical and subtropical ecosystems was more strongly regulated by precipitation and drought variability, with increased rainfall advancing flowering and fruiting by 3–5 days and drought stress delaying events by 7–10 days. Additional influences included photoperiod, solar radiation, relative humidity, elevated CO_2, soil moisture, and urban heat island effects, while extreme events such as heatwaves and late frosts frequently disrupted expected phenological patterns. These shifts have far-reaching implications for growing-season length, carbon uptake, evapotranspiration, nutrient cycling, and trophic synchrony, with cascading effects on biodiversity and ecosystem resilience. Despite this importance, evidence remains geographically biased toward Europe and North America, and mechanistic understanding is constrained by reliance on observational approaches and limited representation of species-specific responses in dynamic global vegetation models. Integrating long-term monitoring, remote sensing, trait-based data, and machine learning into modelling frameworks is essential to improve the projections of vegetation–climate feedbacks under future climate scenarios.

Environmental significance

Climate-driven shifts in tree phenology represent one of the most sensitive biological responses to global climate change, with far-reaching consequences for forest productivity, biodiversity, and ecosystem services. By synthesizing evidence from 145 studies across multiple biomes, this work highlights how changes in temperature, precipitation, and extreme events are reshaping the timing of leafing, flowering, and fruiting in tree species worldwide. These phenological shifts influence carbon sequestration, water cycling, nutrient dynamics, and trophic synchrony, thereby affecting ecosystem resilience and climate–vegetation feedbacks. By identifying geographic biases, key climatic drivers, and critical knowledge gaps, this study provides valuable insights for improving ecological models, guiding climate-adaptive forest management, and informing conservation strategies under ongoing global environmental change.

1. Introduction

Forests are critical components of the Earth's system. Forests substantially contribute to global carbon storage, playing a central role in regulating climate, biodiversity, and ecosystem services.[1] However, rapid human-driven changes in climatic conditions, such as rising global temperatures, changes in precipitation patterns, and an increased frequency of extreme events, have intensified ecological disruptions across forest ecosystems worldwide.[2,3] Phenology (the timing of recurring biological events) is one of the most sensitive and easily observable biological indicators of climate change. Shifts in phenological events such as leaf-out, flowering, fruiting, and senescence influence not only individual plant health but also ecosystem-level processes, including carbon sequestration, energy exchange, and species interactions, which collectively affect biodiversity.[4,5] These cascading effects have profound implications for forest productivity, carbon dynamics, and food web stability, underscoring the need to understand how climate drivers shape phenological responses globally. While localized

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and species-specific studies provide valuable insights, a comprehensive synthesis that integrates patterns across biomes and climatic gradients is essential for predicting ecosystem resilience and informing adaptive management strategies in a warming world.[6,7] Trees, as long-lived and structurally dominant organisms, exhibit a unique sensitivity to climatic variability. Their life history traits and growth cycles are closely tied to seasonal environmental cues.[8,9] Historical records of phenology such as centuries-old observations of cherry blossom dates in Japan and leaf-out patterns in European forests have provided some of the earliest biological indications of climate warming.[10] These long-term datasets underscore that even subtle shifts in temperature and precipitation regimes can lead to noticeable modulations in phenophases. Beyond serving as indicators, phenophases play a crucial role in regulating ecosystem functioning, influencing the timing of carbon uptake, transpiration, and nutrient cycling. Consequently, understanding phenological dynamics is vital for predicting forest productivity, species competition, and the stability of ecosystem services in the context of global climate change.[3]


Karuna Gusain

Karuna Gusain: She is a Research Scholar pursuing PhD at the G. B. Pant National Institute of Himalayan Environment, Almora, Uttarakhand, India, and is focused on analysing the impacts of the urban environment on the phenological and biochemical responses of tree species. Her research examines how urban climate stressors such as altered temperature regimes, air pollution, and modified hydrological conditions affect tree growth cycles, physiological traits, and ecosystem functions. With a strong interest in climate–vegetation interactions, her work contributes to improving understanding of urban forest resilience and supports the development of climate-smart urban greening and sustainability strategies.


Kajal Gautam

Kajal Gautam: She has completed her PhD in Chemistry from UPES Dehradun, specializing in plant nanobionics to enhance the bioremediation capabilities of indoor plants for air and soil pollution using nanoparticle-based approaches. Her research expertise includes material synthesis, material chemistry, and energy storage, and she has contributed to several interdisciplinary projects spanning nanotechnology, environmental remediation, and energy storage. She has published multiple papers in reputed international journals, including Nanoscale Advances, Materials Advances, Advanced Biology, Scientific Reports, ChemSusChem, and the Journal of Energy Storage. Her work focuses on developing sustainable, nanotechnology-driven solutions that bridge fundamental science with practical environmental applications.


Mohit Bhatt

Mohit Bhatt: He has completed his PhD in Materials Science at UPES Dehradun, with expertise in energy storage applications including engineering of electrode nanomaterials for batteries and supercapacitors. His research focuses on the design, synthesis, and electrochemical evaluation of advanced electrode materials, and he has authored several research papers published in reputed international journals, including the Journal of Energy Storage, ChemSusChem, Materials Advances, Scientific Reports, Nanoscale Advances, and RSC Advances. In addition to his core research in energy storage, he is actively involved in interdisciplinary collaborations in plant nanobionics and environmental applications, aiming to develop sustainable, material-driven solutions to environmental challenges.


Hukum Singh

Hukum Singh: Dr Singh is a Senior Scientist and an environmental plant physiologist at the Forest Research Institute, Dehradun, and specializes in plant resilience to climate change, elevated CO_2, heavy metals, and air pollutants, advancing environmental sustainability. With over 200 publications, he has mentored numerous postdoctoral, doctoral, and master's students. Dr Singh has received prestigious awards, including the SERB-DST Fast Track Young Scientist Award, UCOST Young Scientist Award, AsiaFlux Travel Fellowship, VIFRA Outstanding Faculty Award, and M. S. Swaminathan Research Fellow Award. His work employs advanced techniques to address critical environmental challenges, making significant contributions to plant physiology and climate adaptability research.

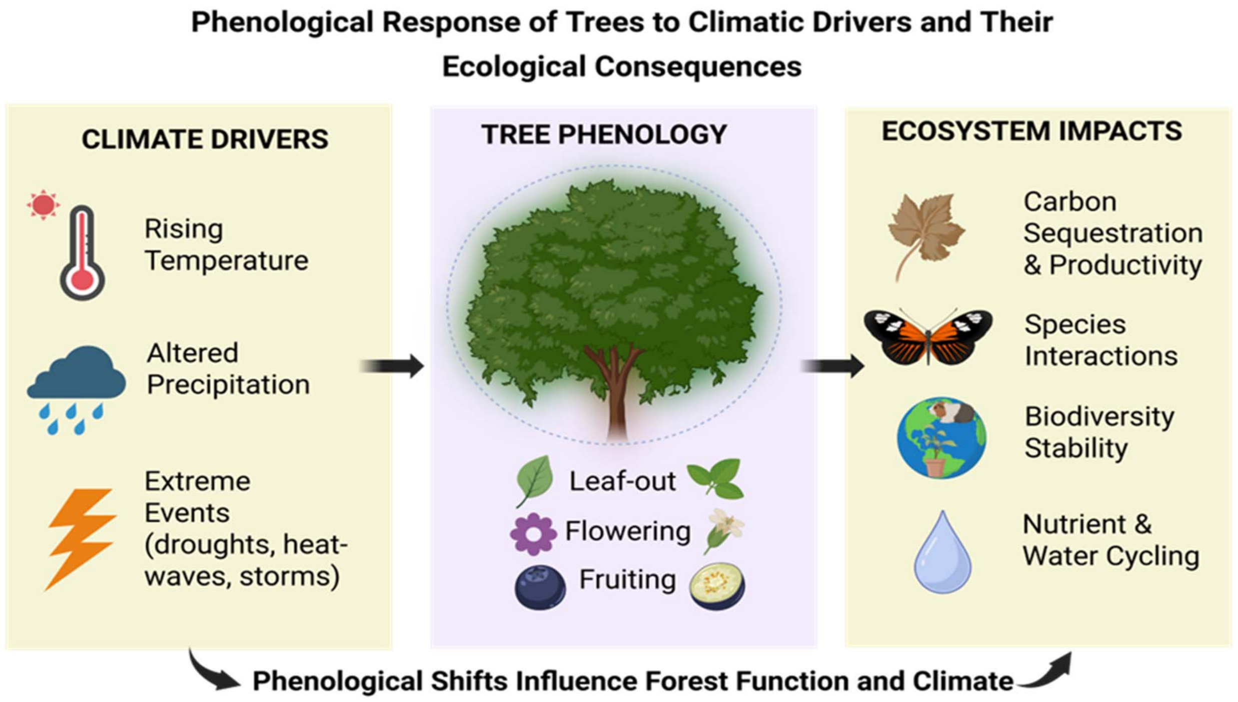

Fig. 1 Conceptual framework illustrating how climatic drivers (temperature rise, altered precipitation, and extreme events) influence tree phenology (leaf-out, flowering, fruiting, and senescence), leading to cascading ecosystem impacts (carbon sequestration, productivity, biodiversity, species interactions, and nutrient cycling). Phenological shifts, in turn, feedback into the climate system (created using https://www.biorender.com/).

1.1 Climate sensitivity of tree phenology and ecological implications

Phenology is susceptible to climatic variabilities, particularly temperature, precipitation, and photoperiod.[11,12] The change in these climatic variabilities has intensified shifts in tree phenology, emerging as one of the most visible biological indicators of global climate change.[13,14] To illustrate the ecological consequences of these shifts, Fig. 1 summarizes the pathways through which altered phenological timing influences

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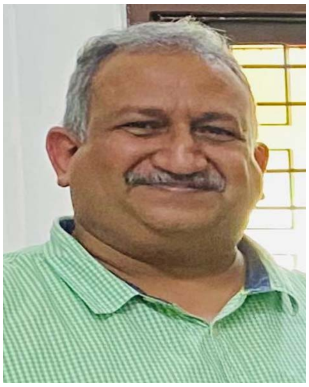

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forest productivity, species regeneration, biodiversity, and ecosystem services, including carbon sequestration. These phenological shifts have profound implications for forest functioning and ecosystem stability.[15,16]

Phenological shifts have been documented across biomes and latitudinal gradients, with substantial advances in spring events such as budburst and flowering and delays in autumn events, including leaf senescence.[17] These shifts are primarily attributed to increased minimum temperatures and altered seasonal variability.[18,19] For instance, the studies have reported earlier budburst in temperate trees in Europe,[20] increased flowering intensity in tropical regions,[21] and altered reproductive cycles in high-altitudinal and moisture-sensitive species.[22,23] However, phenological responses are species-specific and depend on regional climates, elevation, forest type, and even tree age or size.[24,25] Few species have displayed high phenological plasticity, allowing them to flexibly adjust dates of flowering and leafing, while others show conservative responses, possibly making them susceptible to climate mismatches.[26] Furthermore, phenological mismatches between trees and dependent organisms, such as pollinators and herbivores, are increasingly reported to raise concerns about disrupted ecological interactions and reduced forest resilience.[27,28]

Therefore, understanding climate-induced phenological changes is an important measure for developing adaptation and mitigation strategies in forest management, conservation planning, and agriculture.[29,30] Phenological monitoring with precision and accuracy enables predictive modelling of tree growth and productivity under different climatic scenarios, particularly in economically viable species like *Quercus robur*, *Fagus sylvatica* and *Betula pendula*.[31,32] Changes in budburst timing in fruit trees like *Malus domestica* and *Prunus* sp. have direct implications for yield, frost risk, and pollination success.[33,34] Likewise, phenological plasticity can serve as an indicator of climate adaptation potential in reforestation and afforestation efforts.[35] Despite substantial progress, significant uncertainties remain in predicting phenological responses due to the interactive and often non-linear influence of multiple drivers. While temperature and photoperiod are widely recognized as dominant cues, other factors such as soil moisture, nitrogen deposition, elevated atmospheric CO_2, and urban heat islands increasingly modulate phenological timing.[36,37] Moreover, the combined effects of extreme events like droughts, heatwaves, and late frosts present additional challenges by altering physiological thresholds for budburst and flowering.[4] A notable research gap exists for tropical and subtropical ecosystems, which remain underrepresented in phenology studies compared to temperate regions, despite their significant role in global carbon dynamics.[38] Hence, addressing these complexities requires integrative approaches that combine long-term observational data with advanced process-based models to capture species-specific and biome-specific sensitivities to climate change.[39]

Additionally, technological advancements such as LiDAR, satellite-based remote sensing, including hyperspectral imagery, and machine learning have revolutionized phenological studies by enabling continuous, high-resolution monitoring of phenophases across various landscapes.[40–42] Despite these advancements, gaps remain in understanding the cumulative impact of climatic drivers like drought, heatwaves, and chilling requirements on phenological development in tree taxa.[15,43]

1.2 Rationale of the systematic review

Various studies have observed climate-phenology relationships in trees, showing fragmented, localised, and species-specific or region-specific shifts in phenological patterns. Existing meta-analyses are either limited to specific phenophases or

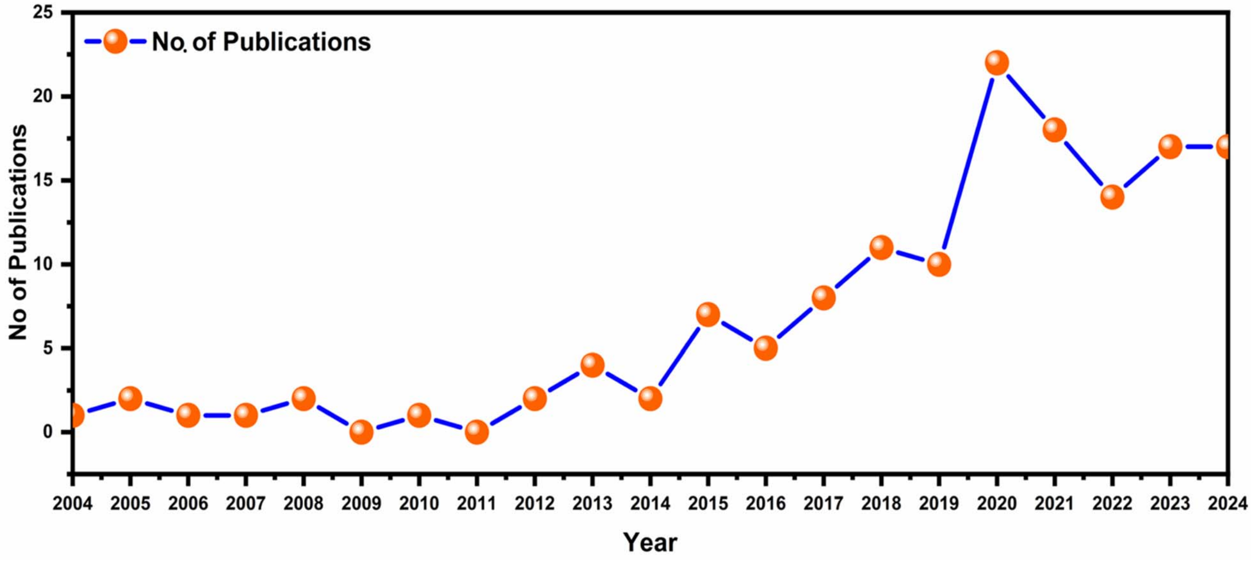

Fig. 2 Temporal distribution of the published papers on tree phenology and climate variability between 2004 and 2024. The trend indicates a substantial increase in publications during the last five years, reflecting growing research attention to this field.

biogeographical zones, thereby lacking a comprehensive synthesis across continents, forest types/biomes, and climatic gradients.[44] Moreover, there is a limited understanding of how multiple climatic drivers like temperature, precipitation, photoperiod, and drought interact to modulate phenological patterns across different tree species.[45]

To address this gap, we conducted a systematic review of 145 peer-reviewed research articles published between 2004 and 2024. To illustrate the temporal evolution and research emphasis on tree phenology under changing climatic conditions, Fig. 2 shows the annual distribution of studies included in this review. The review aimed to identify global patterns, trends, and drivers of phenological shifts in tree species in response to climate change by incorporating different forest types/biomes (evergreen, deciduous, and mixed), climatic zones (tropical to temperate), and phenophases (leafing, flowering, fruiting, budburst, *etc.*). Importantly, the present study reviewed a broad spectrum of climatic and environmental drivers, including temperature and precipitation, as well as nuanced variables such as photoperiod, urban heat islands, relative humidity, nutrient availability, solar radiation, and ENSO (El Niño-Southern Oscillation) events. Additionally, stress factors such as drought, fire sensitivity, and heat stress were frequently linked to shifts in phenology, suggesting that multiple overlapping drivers shape temporal responses in tree phenology.

Of the total studies, 55 reported robust statistical associations, including R^2 values, p-values, correlation coefficients, and other inferential metrics. This provided a strong foundation for meta-analytic synthesis, enabling cross-study comparisons of phenological sensitivity to specific climatic variables. Furthermore, this review accounts for methodological heterogeneity, including differences across field-based observations, remote sensing techniques, and controlled experimental designs. While not the primary focus, this dimension is addressed in a dedicated section that highlights how methodological choices may influence the detection and interpretation of phenological shifts.

Through this systematic synthesis, we aim to

- Identify consistent patterns of phenological changes across tree species and climatic zones.
- Quantify the association between phenological changes with climatic drivers and associated environmental stresses and.
- Focus on key research gaps and emerging frontiers in phenological monitoring.

A schematic overview of the methodological workflow adopted in this systematic review is presented in Fig. 3.

2. Methodology

2.1 Review framework and reporting standard

This systematic review was conducted in accordance with the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) 2020 guidelines. The aim was to provide

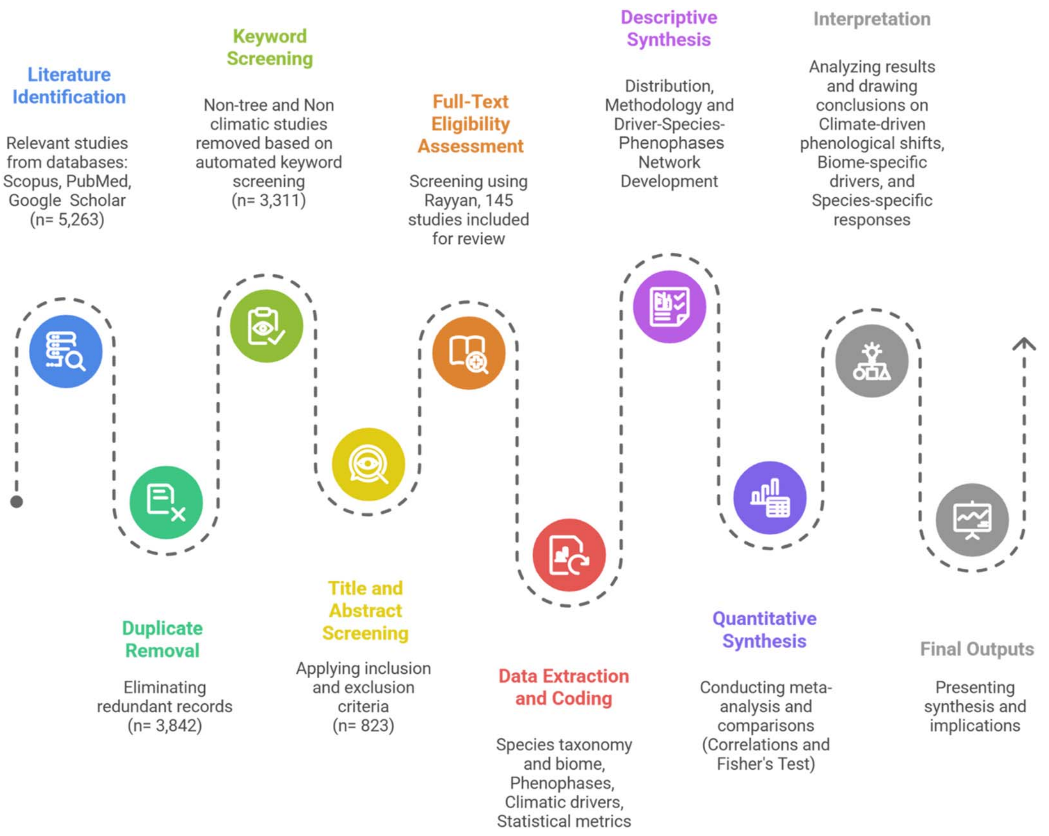

Fig. 3 :Schematic of the workflow followed in this systematic review, illustrating the key steps from literature search and study screening to data extraction, synthesis, and interpretation of the climate-driven shifts in tree phenology (created using Canva).

a global synthesis of phenological shifts observed across various tree species and their associations with different climatic variables. The complete PRISMA flow diagram detailing the screening process is presented in Fig. 3.

2.2 Research framework

To ensure clarity and focus, we structured this review using a modified PICoST approach:

Population (P): tree species (tropical/sub-tropical and temperate) across global forest ecosystems. Interest (I): observed phenological events including budburst, flowering, fruiting, and leafing. Context (Co): climatic influences on phenological changes (*e.g.*, temperature, precipitation, photoperiod, and drought).

Study design (S): empirical field-based or modeling studies examining phenological-climatic relationships.

Timeframe (T): articles published between 2004 and 2024.

2.3 Research question

How have phenological shifts in trees been documented globally in response to different climatic drivers, and what patterns emerge across species, regions, and phenophases?

2.4 Search strategy and database selection

A systematic literature search was conducted across Scopus, ScienceDirect, PubMed, and Google Scholar. To capture both broad and specific studies, we applied the following Boolean combinations of keywords:

- "Tree phenology" AND "climate change"
- "tree" AND "phenology" AND ("temperature" OR "precipitation" OR "photoperiod" OR "drought" OR "climatic variables") NOT "animals"
- "Tree phenology" AND ("climate variability" OR "environmental drivers" OR "global warming" OR "urban heat island")

The search was restricted to the title, abstract, and keywords fields. Only peer-reviewed journal articles published in the English language were considered. The inclusion of multiple databases minimized publication bias and ensured broad coverage.

2.5 Eligibility criteria

To ensure relevance and quality, the following inclusion and exclusion eligibility criteria were used to select the articles for this review: studies were included if they: (i) reported empirical evidence of phenological changes in tree species, (ii) explicitly examined at least one climatic driver in relation to a phenophase, and (iii) focused on key phenological events such as budburst, leaf emergence, flowering, fruiting, or senescence. Only peer-reviewed journal articles published in English between 2004 and 2024 were considered. The selected time frame was chosen to align with the period during which phenological research expanded substantially, driven by the increased availability of long-term observational datasets, standardized phenophase definitions, and advances in statistical analysis and remote sensing techniques. Before 2004, very few empirical studies on the relationships between tree phenology and climate were available, and those that existed often lacked consistent methodological detail or quantitative climatic linkages, limiting their comparability. Studies published after 2024 were excluded because they fell beyond the predefined search cut-off date used for literature retrieval and screening.

Exclusion criteria were applied to: (i) review papers, conceptual papers, editorials, and theses; (ii) studies focusing exclusively on crops, grasses, or non-tree species; (iii) articles where phenological observations of trees could not be quantitatively or qualitatively linked to specific climatic variables; and (iv) studies lacking sufficient methodological detail, such as unclear or inconsistent phenophase definitions, inadequate description of observational methods, or missing or incomplete climatic data.

2.6 Screening and selection process

The initial search across multiple databases identified 5263 records. After removing 1421 duplicate entries, 3842 unique records remained for screening. To efficiently reduce irrelevant studies, automated keyword-based filtering tools were first applied to titles and abstracts, which excluded 531 records that clearly did not meet the basic inclusion criteria. The remaining 3311 records were then subjected to a detailed title and abstract review. This step resulted in the retention of 823 studies for full-text evaluation, while 425 articles were excluded because they did not specifically examine tree phenology, lacked relevant climatic variables, or lacked empirical evidence.

To ensure a thorough and unbiased selection, the bibliographic data for the retained studies were exported in the CSV format and imported into the Rayyan web tool, which facilitated blinded screening and consistent application of the eligibility criteria. During the full-text review, 253 articles were excluded, primarily because they lacked sufficient methodological information or did not explicitly quantify or assess the linkage between phenological observations and climatic variables. Ultimately, 145 studies met all predefined inclusion criteria and were included in the systematic review and meta-analysis. The stepwise refinement process from initial identification to final inclusion is illustrated in the PRISMA 2020 flow diagram (Fig. 4), providing a clear overview of the screening and selection workflow.

2.7 Data extraction and coding

To ensure consistency and comprehensiveness in synthesizing data across diverse studies, we developed a structured data extraction protocol. This protocol was implemented through a standardized data extraction sheet designed to capture all relevant variables aligned with the objectives of our systematic review and meta-analysis.

2.8 Data extraction process

For each eligible study, key variables were recorded, which are as follows: (i) biological taxonomy, comprising the scientific name of each species; (ii) geographic and ecological context,

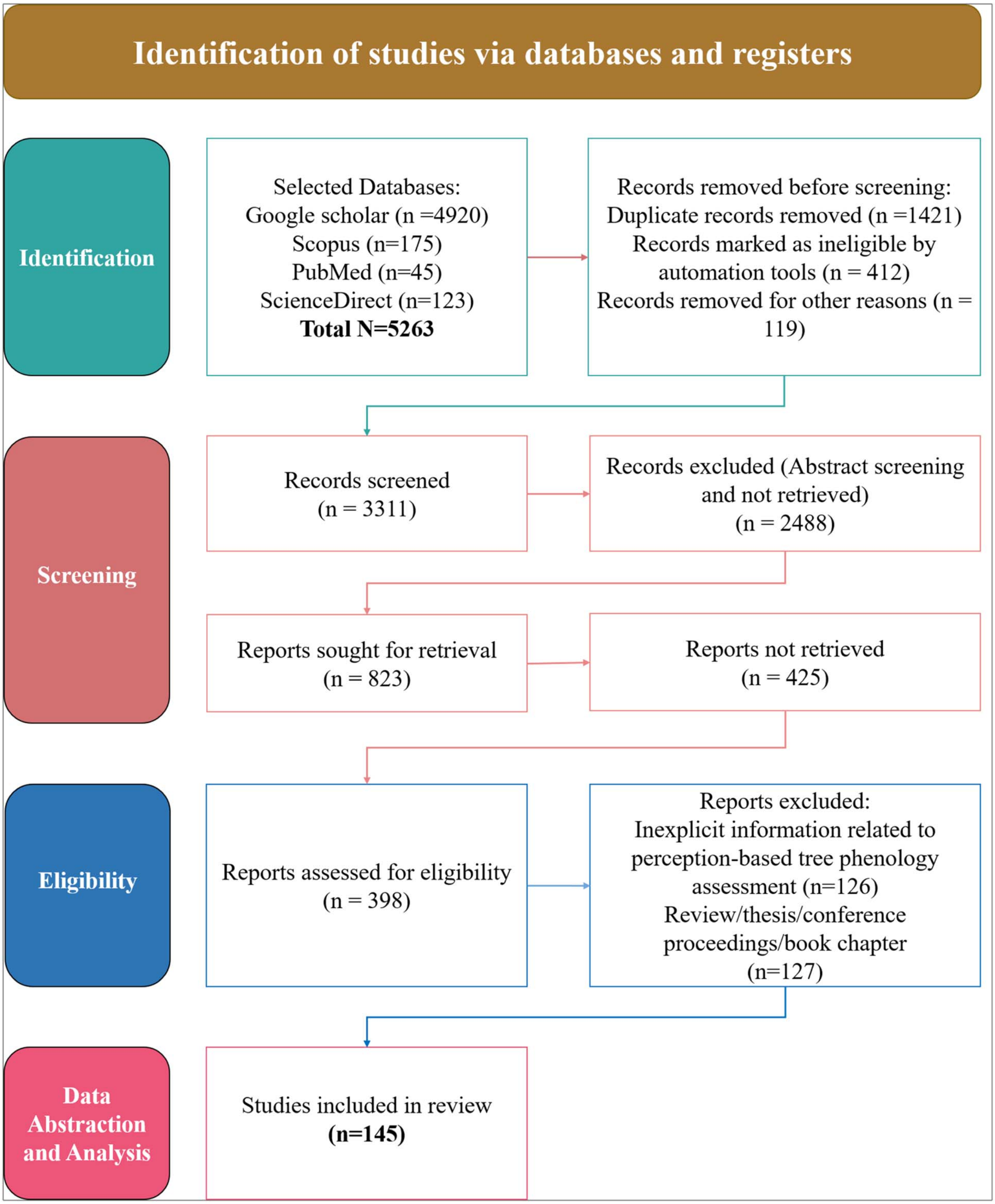

Fig. 4 PRISMA 2020 flow diagram. Overview of the screening and selection process for studies included in the systematic review on the phenological shifts in tree species in response to climate change. The diagram illustrates the process of identifying records from databases, removing duplicates, screening and excluding records, assessing full-text articles for eligibility, and determining the final number of studies included in the review.

such as country, region, and biome type (*e.g.*, temperate deciduous, boreal, and tropical rainforest); (iii) phenological phases under investigation, including budburst, leaf-out, flowering, fruiting, and senescence; (iv) climatic drivers examined, such as temperature, precipitation, photoperiod, solar radiation, and humidity; (v) phenological response type, categorised as advancement, delay, or no change; (vi) quantitative metrics, such as correlation coefficients, regression slopes, effect sizes, and associated significance values; and (vii) study characteristics, including methodological design (field observation, remote sensing, herbarium records, experimental manipulation, or modelling), as well as temporal resolution, duration of observation, and sample size when reported.

2.9 Coding scheme

A coding framework was applied to harmonise extracted data and minimise ambiguity. Species names were standardised using accepted taxonomic databases to resolve synonyms and spelling variations. Climatic variables were grouped into broad categories (*e.g.*, temperature, precipitation, and photoperiod) with further subdivision where applicable (*e.g.*, spring mean temperature and winter minimum temperature). Phenophases were harmonised using established definitions from phenological classification systems. The direction of phenological response was binary coded (0 = delay, 1 = advance), with ordinal scales applied where gradients were reported. Effect size types were categorised as correlation coefficients, slope estimates, or other statistical measures, and wherever possible, correlation coefficients were either extracted directly or converted to enable meta-analytic standardisation. Uncertainty estimates including standard errors, variances, or confidence intervals were also recorded to allow appropriate weighting of studies during meta-analysis.

2.10 Reviewer training and inter-coder reliability

We conducted the data extraction process. Before full extraction, we performed calibration using a small subset of studies ($n = 10$) to ensure consistency in the interpretation and application of the coding scheme. During full extraction, disagreements or ambiguities were flagged and resolved through structured discussions. A subset of 20 randomly selected studies (10 of the final pool) were double-coded to assess inter-coder reliability using Cohen's kappa (k) for categorical variables and intraclass correlation (ICC) for continuous variables. The average inter-coder agreement was high ($k > 0.85$, ICC > 0.90), indicating strong consistency in the coding process.

2.11 Data management

All extracted data were managed using Microsoft Excel and RStudio, with built-in validation rules to minimize entry errors. Metadata logs were maintained to document any transformations or assumptions made during the data harmonization process.

2.12 Analysis

We performed analysis using the *R* statistical software and Microsoft Excel for data organization and preliminary cleaning. The final database consisted of studies that reported quantitative associations between climatic variables and phenological events in tree species, along with metadata such as species taxonomy, geographic region, and direction of phenological response. Following data extraction, we performed a series of transformations to prepare for meta-analytic synthesis. Where studies reported correlation coefficients (r-values) between climatic variables and phenophases, we applied Fisher's z-transformation to normalize the effect sizes and stabilize variance across different sample sizes. The corresponding sampling variance for each Fisher's z was computed using the formula $\mathrm{var}(z) = \frac{1}{n-3}$, where n is the sample size of the original study.

Moreover, studies without reported sample sizes were excluded from meta-analytic computations but retained for descriptive synthesis. We then merged this transformed dataset with additional coded attributes, including phenophase timing (early, delayed, and ambiguous), climatic drivers (*e.g.*, temperature, precipitation, and photoperiod), biome type and study design (field-based, remote sensing, and modeling). Each combination of species, phenophase, and climatic variable was treated as a distinct observation.

In cases where studies reported multiple phenophase-climate relationships, each pair was separated into unique rows to preserve precision in analysis. In addition to meta-analytic synthesis, we conducted descriptive analyses to summarize trends in phenological responses. Cross-tabulations were created to examine the frequency and distribution of adaptation patterns across phenophase types, regions, species groups, and climatic variables. Studies that lacked sufficient information to classify the timing of response or settlement context (*e.g.*, urban v/s natural forest) were coded as ‘indeterminate’ or ‘ambiguous’ and were excluded from subgroup analyses but retained in general summaries.

3. Result and discussion

3.1 Geographical distribution of the studies

The studies included in this systematic review exhibit a broad global distribution, encompassing forested regions across six continents. To visualize the spatial distribution and regional concentration of phenological research, Fig. 5 maps the geographic coverage of the included studies.

A total of 145 articles were geographically mapped using QGIS, revealing that research on phenological shifts in tree species is particularly concentrated in temperate and subtropical forest zones. Notably, the United States stands out with the highest number of studies (19), followed closely by Germany (11), reflecting significant research investment in these regions. Other countries with high representation include India, China, Brazil, and the United Kingdom, each contributing between 8 and 12 studies. In Europe, a dense cluster of studies originate from countries such as France, Italy, Spain, and Norway, indicating strong regional interest in climate-phenology linkages. In Asia, contributions span both tropical and temperate zones, with substantial input from South Korea, Japan, and Southeast Asian nations, including Thailand, Malaysia, and Vietnam. African countries, such as the Democratic Republic of the Congo, Cameroon, and Uganda, also contribute, albeit with fewer studies, reflecting a growing interest in phenological research across tropical forests. South America features contributions from Brazil, Colombia, and Uruguay, while Australia represents the Southern Hemisphere's temperate forests. This

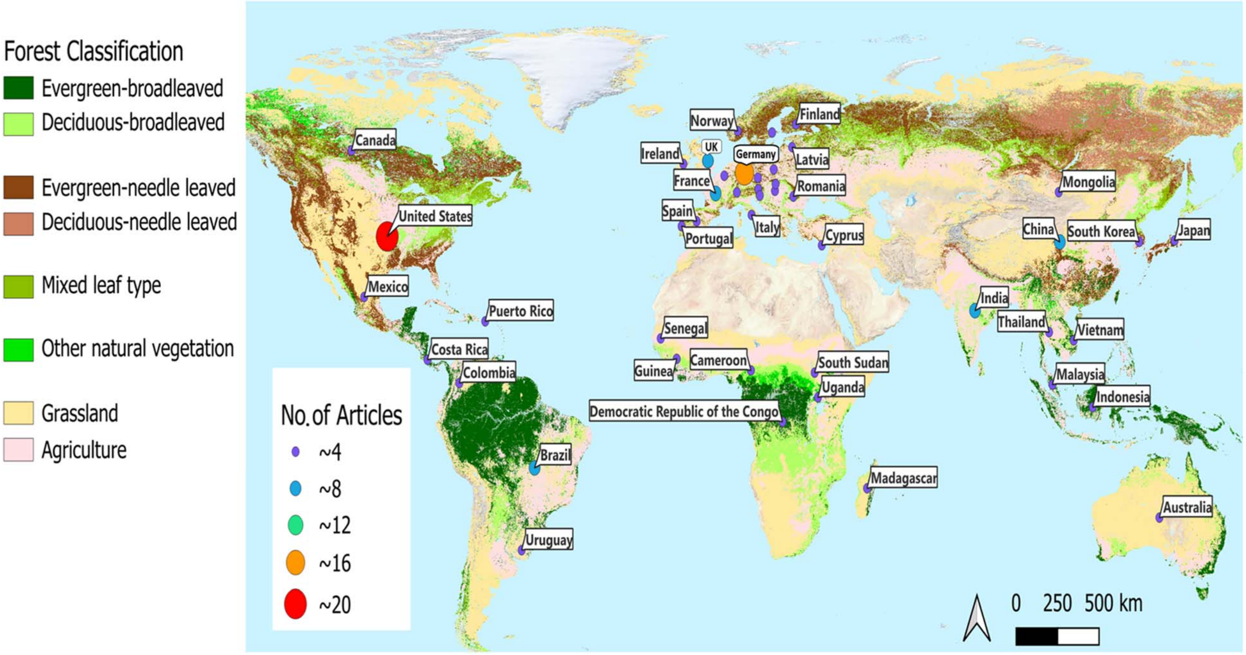

Fig. 5 Geographic distribution of studies on tree phenology and climate change. Spatial representation of the number of articles included in the systematic review across different countries, overlaid on a global forest classification map. Marker size and colour indicate the number of articles per country. Background colours represent dominant vegetation types, including evergreen broadleaved, deciduous broadleaved, evergreen needle-leaved, deciduous needle-leaved, mixed leaf types, grasslands, agriculture, and other natural vegetation.

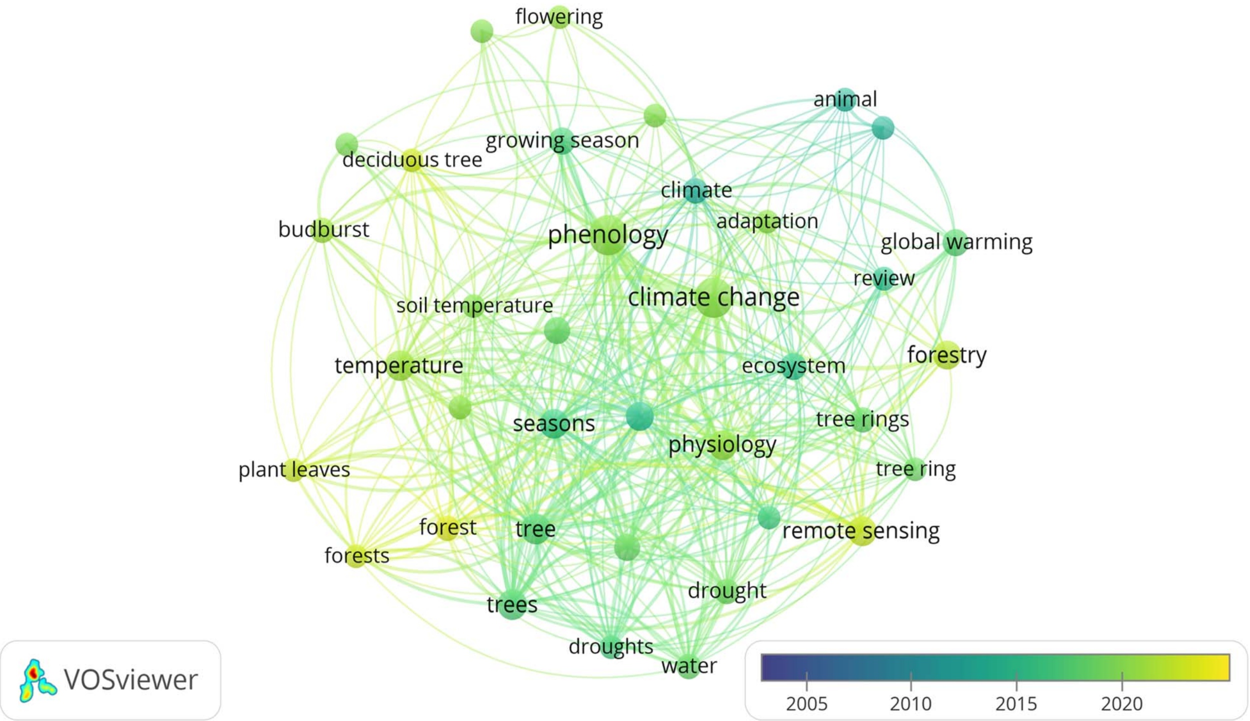

Fig. 6 Keyword co-occurrence network. A visualization map generated using VOS viewer, showing the most frequently co-occurring keywords across the reviewed literature. Node size reflects keyword frequency, while link thickness indicates the strength of co-occurrence between terms. Colours represent clusters of related research themes, such as climate change, temperature, seasons, trees, phenology, and ecosystems. The overlay colour scale (2004–2024) indicates the average publication year of keywords, highlighting temporal trends in research focus.

pattern of the geographic spread of studies highlights a global concern about how climate variability affects tree phenology. However, a clear bias persists toward data-rich regions in the Global North.

3.2 Network analysis of the keywords

To better understand the evolution of research on phenological shifts in tree species, we utilized the VOS viewer to create a keyword co-occurrence map based on the literature, as presented in Fig. 6. This network diagram highlights four main clusters of closely related topics. At the center of the map is a green cluster centered on broad environmental themes, including climate change, temperature, and seasons. These are the most frequently discussed topics and form the foundation of most studies in this field. The yellow cluster brings together keywords such as trees, budburst, plant leaves, and phenology, indicating a growing interest in species-specific and seasonal biological responses. A blue cluster features terms such as biological models, species specificity, and altitude, showing how modelling and ecological variability are often used to understand phenological trends. The purple cluster includes keywords such as plant physiology and region names like China, Europe, and Germany, reflecting a focus on physiological processes and region-specific studies. The colours of the keywords also indicate when they were most commonly used in the literature: older topics appear in blue, while newer research trends are shown in yellow. Notably, keywords such as trees, budburst, and leaf unfolding have become more prominent in recent years. Larger nodes in the network represent keywords that appear more frequently, while thicker connecting lines show stronger relationships between topics. This network diagram reveals the field's diversity and interconnectedness, highlighting the need for a comprehensive review that integrates findings across species, regions, and climate drivers.

3.3 Methodological approaches in reviewed studies

The studies included in this review employed a diverse array of methodological approaches, reflecting the varied challenges and objectives in tree phenology research. To summarize the methodological distribution across the reviewed studies, Table 1 provides an overview of the methods employed. The predominance of modelling and field-based approaches reflects the historical trajectory of phenological research, which initially relied heavily on statistical and simulation-based modelling to extrapolate trends across broader spatial and temporal scales. Field studies remain the gold standard for capturing fine-scale

Table 1 Summary of major methodological approaches used to study phenological shifts in tree species, including their frequency of use, strengths, and limitations

Methodology category	Usage frequency (%)	Strengths	Limitations	References
Field observations	22	High phenophase resolution, species-specific, direct observation of events	Labour-intensive, limited spatial scope, potential for observer bias	46–48
Remote sensing	15	Large spatial coverage (regional to global), consistent and frequent data collection, and long-term historical archives	Coarse spatial resolution (mixed pixels), cloud contamination, indirect measure of phenology	40 and 49
Phenocams/digital cameras	5	High temporal resolution, bridges the gap between group and satellite data, provides a direct visual record	Limited field of view, can be affected by changing light conditions, requires power and data infrastructure	50
Controlled experiments	7	Allows for manipulation of variables (temperature and CO_2), establishes casual relationships, can test future climate scenarios	Artificial conditions may not reflect natural complexity, often limited to seedlings or small plants, can be costly	15, 51 and 52
Modeling/simulation	28	Predictive capabilities for future scenarios, can integrate multiple data types, helps in understanding underlying mechanisms	Relies heavily on assumptions, requires extensive data for parameterization and validation, model complexity can be a barrier	53
Herbarium/historical data	9	Provides a unique long-term historical perspective (>100 years), cost-effective source of past phenological data	Data can be spatially and temporally sparse, potential for collector bias, phenological stage is a single point in time	54
Process-based approaches	9	Focuses on physiological mechanisms driving phenology, enhances mechanistic understanding and predictive accuracy	Highly complex, demands extensive data on plant physiology and environmental conditions for proper parameterization	55
Integrated/multimodal	2	Synergizes strengths of different methods, reduces uncertainty by cross-validating data, provides a holistic view of phenology	Methodological and data integration can be technically complex, requires expertise across multiple disciplines	56 and 57
Drone-based	3	Very high spatial resolution (individual plant level), flexible deployment for targeted monitoring, bridges the scale between ground plots and satellite pixels	Limited spatial coverage and flight time, data processing can be complex and intensive, subject to weather and regulations	58

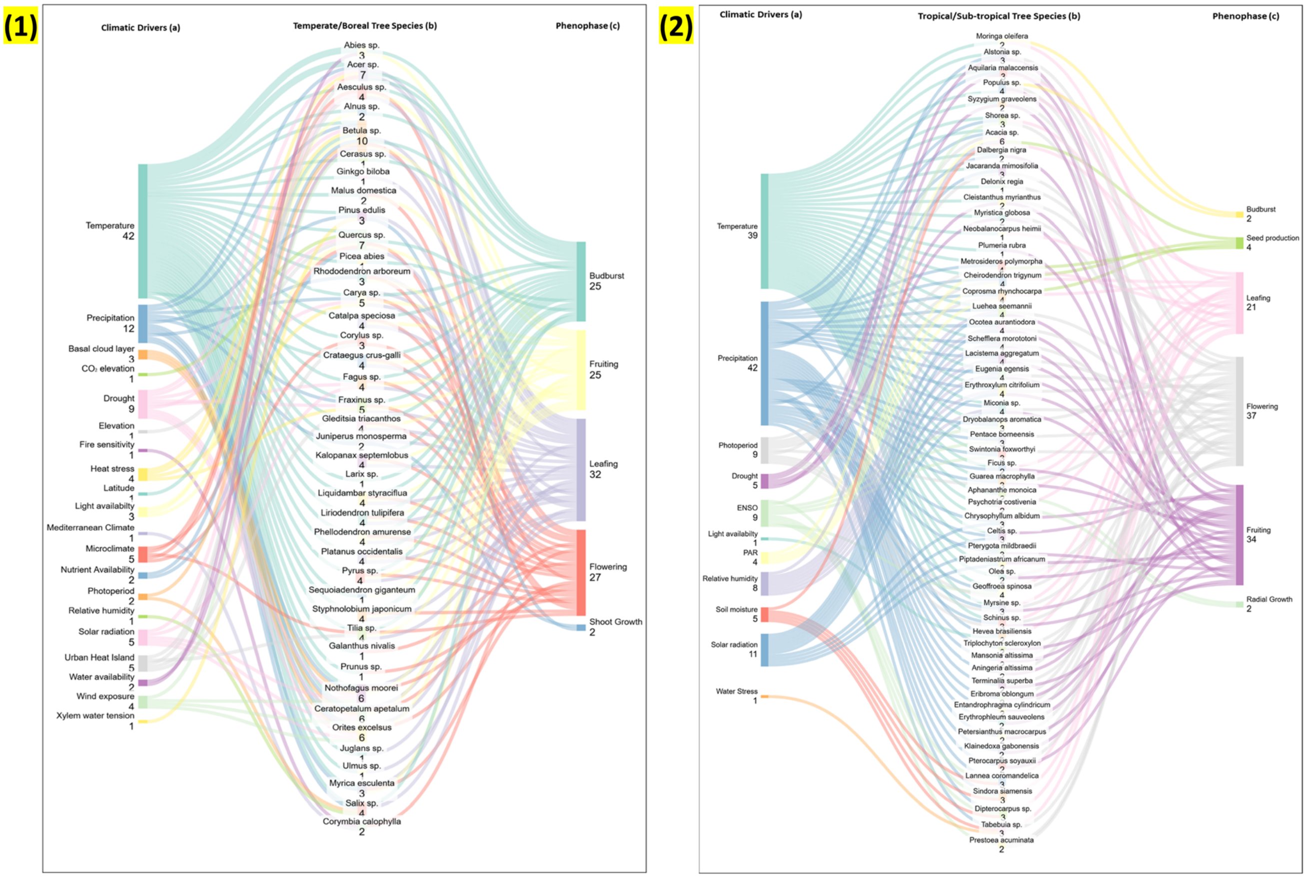

Fig. 7 (1) Sankey diagram illustrating the relationships among climatic drivers, temperate/boreal tree species, and phenophases. The diagram illustrates the relationship between different climatic drivers (left) and temperate and boreal tree species (middle), as well as their associated phenophases (right). The width of the connections represents the frequency of reported associations in the reviewed literature. (a) Total number of times each climatic factor was reported as influencing phenological events. (b) Number of studies or records involving each species. (c) Frequency of each phenological event reported. Created using https://www.sankeymatic.com/. (2) Sankey diagram illustrating the relationships among climatic drivers, tropical/sub-tropical tree species, and phenophases. The diagram illustrates the relationship between different climatic drivers (left) and tropical and subtropical tree species (middle), as well as their associated phenophases (right). The width of the connections represents the frequency of the reported associations in the reviewed literature. (a) Total number of times each climatic factor was reported as influencing phenological events. (b) Number of studies or records involving each species. (c) Frequency of each phenological event reported. Created using https://www.sankeymatic.com/.

phenophase details, but their logistical demands, such as sustained site access, seasonal labour, and species-level expertise, naturally limit spatial coverage. In parallel, modelling approaches leverage existing datasets and climate projections, allowing researchers to explore large-scale patterns and forecast future scenarios, but they depend critically on the availability and quality of input data, which may be regionally or taxonomically biased.

3.4 Categorization of phenological responses

In this review, we examined a range of phenological events associated with temperate and boreal tree species in response to climatic drivers. The primary phenological events analysed include budburst, leafing, flowering, fruiting, and shoot growth. These events represent key developmental transitions that are highly sensitive to environmental cues, particularly temperature and photoperiod.[59–61] Across the studies, budburst consistently linked its timing to spring temperature accumulation and chilling requirements during winter dormancy.[62–64] In temperate deciduous species, earlier budburst was generally associated with warmer pre-season temperatures, while some species displayed non-linear responses due to photoperiod limitations.[51,65–67] Leafing phenology is often measured as leaf-out or leaf expansion and has the third-highest research frequency. Leaf-out dates have shown marked advancements in response to warming, with the magnitude of shift varying among species and functional groups.[68,69] Early successional and pioneer species generally exhibited stronger temperature sensitivity than late-successional or shade-tolerant species,[56,70,71] suggesting that climate change may alter competitive hierarchies in forest ecosystems. Fruiting shows the second-highest research frequency, revealing significant shifts in timing in response to warming trends.[72–74] Altered fruiting schedules may influence seed dispersal dynamics, recruitment success, and food web interactions, particularly for frugivorous fauna.[75] Flowering phenology emerged as the highest studied event that displayed both advancement and delays, depending on species-specific life-history strategies and local climatic regimes.[76–78] In some species, flowering time was strongly correlated with spring temperature, while in others it was modulated by photoperiod or precipitation as the major climatic drivers.[79,80] The reviewed studies also highlighted that shifts in flowering phenology can have a drastic impact on pollinator interactions, reproductive success, and genetic diversity.[81,82] Other phenological events such as shoot growth, seed production, and radial growth received less research attention. Overall, these phenophases exhibited species-specific, region-specific, and phenophase-specific sensitivities to climatic drivers. This emphasizes the need for multi-phenophase monitoring within the same species and across geographical gradients to fully understand climate change impacts on forest phenology.[83,84]

3.5 Climatic drivers, tree species and phenophase linkages

Across the two biomes, a total of 742 driver-species-phenophase linkages were recorded from 145 studies. In temperate and boreal forests, temperature dominated the climatic drivers, accounting for 42 discrete linkages, followed by precipitation (12 linkages) and drought (9 linkages). Less frequently examined drivers included solar radiation (5), microclimate (5), and heat stress (4). Temperature-driven responses were most often linked to leafing (32 linkages, of all phenophase records), flowering (27), budburst (25), and fruiting (25), with shoot growth infrequently reported (2). To illustrate the relative importance of climatic drivers and phenophase responses in temperate and boreal forests, Fig. 7(1) summarizes the observed driver-phenophase linkages. Species with the highest driver connectivity included *Betula* sp. (10 linkages) and *Quercus* sp. (7), indicating high sensitivity to multiple climatic stimuli.

In tropical and sub-tropical forests, precipitation emerged as the leading driver (42 linkages), marginally ahead of temperature (39). Secondary drivers like solar radiation (11), photoperiod (9), ENSO (9), relative humidity (8), drought (5), and soil moisture (5) displayed greater diversity than temperate/boreal forests. Phenophase patterns differed markedly, with flowering (37 linkages) and fruiting (34) dominating, followed by leafing (21), seed production (4), budburst (2), and radial growth (2). To highlight these biome-specific contrasts in driver dominance and phenophase sensitivity, Fig. 7(2) presents the corresponding linkage patterns for tropical and subtropical forests. High connectivity tropical species included *Acacia* sp. (6 linkages) and *Erythroxylum citrifolium*, *Metrosideros polymorpha*, and *Ocotea aurantidora*, *etc.* (4 linkages each).

These patterns indicate biome-specific differences in both climatic drivers and phenological shifts, with temperature-centric leafing and budburst dominating in temperate/boreal forests. They also reflect physiological constraints in tree species, which are primarily limited by heat accumulation and the timing of frost. At the same time, precipitation-driven flowering and fruiting are most prominent in tropical/subtropical forests. The diversity of secondary drivers in tropical systems suggests more complex climatic interactions, potentially reflecting greater environmental heterogeneity and the influence of multiple seasonality signals.

Factors such as photoperiod, soil moisture, and microclimate are underrepresented across both biomes (less than 10%), which may represent research gaps rather than true biological irrelevance, especially in tropical forests, where microclimate buffering could modulate phenology. Since the dataset encompasses 116 unique tree species, it is evident that some species/phenophases are more extensively studied than others, resulting in an uneven distribution of link thickness in the Sankey diagrams. This highlights taxonomic bias and may affect global generalizations.

3.6 Meta-analytical assessment of climatic driver-phenophase associations

Analysis of 91 total climatic driver-phenophase associations from 55 studies that satisfied the inclusion criteria was included in the meta-analysis. To illustrate these patterns, Fig. 8a and b summarize the climatic driver-phenophase associations across temperate/boreal and tropical/sub-tropical tree species, respectively. Temperate species show a pronounced predominance of advancing responses to increasing temperatures, with 69.4% of temperature-related associations being negative, indicating earlier onset of phenophases, and 30.6% showed delays, which were mostly linked to species with specific chilling requirements that were unmet under warmer winter conditions, like *Fagus sylvatica*, *Quercus petraea*, *Picea abies*, *Myrica esculenta*, and *Rhododendron arboreum.* These exceptions primarily involved late-successional or high-chilling species, where warming may disrupt the accumulated cold requirements. Precipitation-linked responses were overwhelmingly advanced (87.5%), with the sole delay observed in *Pinus edulis*, suggesting that rainfall generally facilitates earlier phenophases in temperate systems. However, water-energy timing mismatches can cause delays. Photoperiod associations were evenly divided between advances and delays. Delays were observed in *Quercus robur* and *Prunus avium*, while advances were noted in *Galanthus nivalis* and *Myrica guianensis*. This bi-directionality likely reflects species-specific reliance on light cues *versus* thermal or hydric signals. Drought delayed phenology in two-thirds of cases, consistent with stress-constrained growth, but advances occurred in *Fagus sylvatica*, *Quercus robur*, and *Betula pendula*, possibly representing drought-induced stress-escape strategies. Soil moisture and elevation gradients both uniformly delayed phenophases in *Malus domestica*, *Sophora chrysophylla*, and *Fagus sylvatica*. However, urban heat island (UHI) effects consistently advanced phenology across species such as *Malus domestica* and *Quercus leucotrichophora*. Relative humidity uniformly delayed development, whereas solar radiation was mainly associated with advances (85.7%), except in *Pinus edulis*. Light availability and photosynthetically active radiation (PAR) each produced universal advances, while microclimatic variation was more mixed (60% advances, 40% delays). Fire sensitivity uniformly delayed phenophases, with *Pinus edulis*, *Corymbia calophylla*, and *Pinus strobus* all showing marked delays.

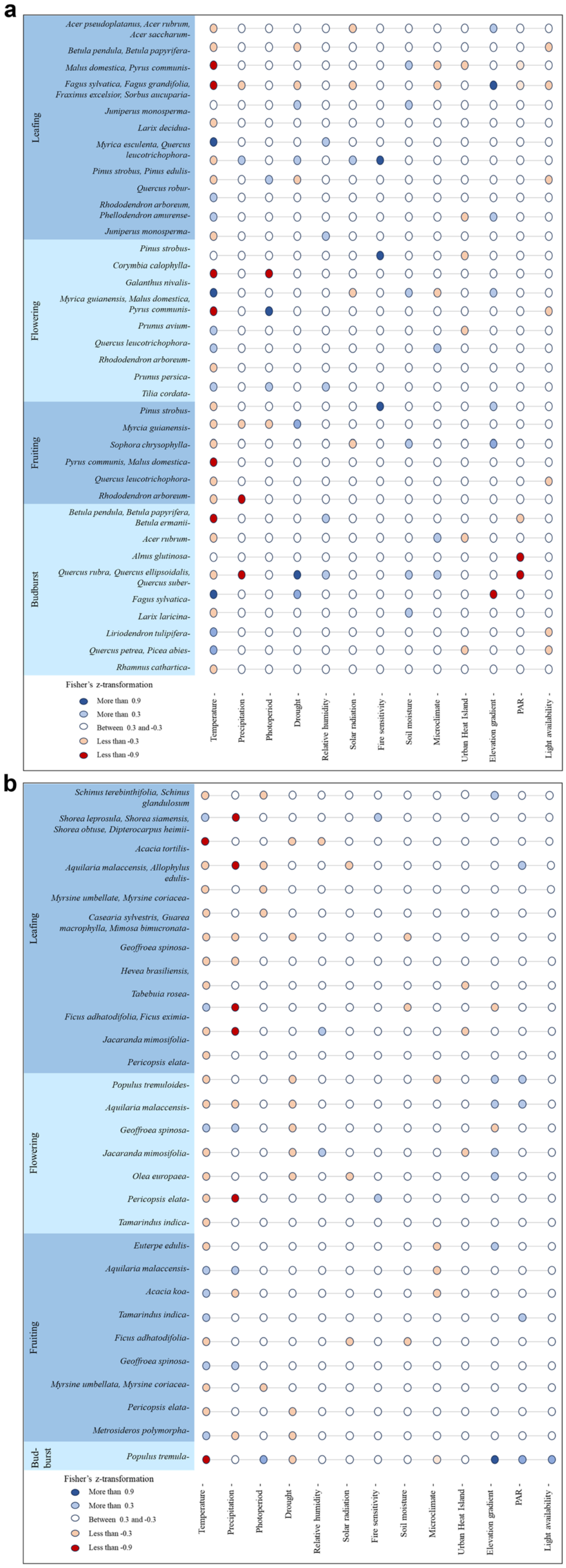

Fig. 8 (a) Bubble plot showing Fisher's z-transformation values for correlations between temperate/boreal tree species phenophases (leafing, flowering, fruiting, and budburst (rows) and climatic/environmental drivers (columns)). Blue circles represent positive correlations (delay) and red circles represent negative correlations (advance), with the color intensity indicating the strength of the correlation. (b) Bubble plot showing Fisher's z-transformation values for correlations between tropical/sub-tropical tree species phenophases (leafing, flowering, fruiting, and budburst (rows) and climatic/environmental drivers (columns)). Blue circles represent positive correlations (delay) and red circles represent negative correlations (advance), with the color intensity indicating the strength of the correlation.

Tropical/sub-tropical tree species also exhibit 68.9% advances in different phenophases in response to temperature, and 31.3% delays, such as the flowering of *Geoffroea spinosa* and the leafing of *Shorea siamensis*, *Shorea leprosula*, and *Dipterocarpus heimii.* Precipitation advanced phenology in 78.6% species but delayed it in 21.4% including flowering and fruiting in *Geoffroea spinosa* and fruiting in *Aquilaria malaccensis.* Photoperiod advanced phenology in 88.9% of species, while 11.1% of species delayed budburst, often due to reduced light exposure caused by cloud cover in *Populus tremula*. Relative humidity delayed phenology in 96.5% of species, but advanced the leafing of *Acacia tortilis*. Drought, solar radiation, urban heat island effects, and soil moisture advanced phenology in all species, with no exceptions. Fire sensitivity was linked exclusively to delayed phenology. Microclimatic conditions also uniformly advanced phenology in all species, highlighting the influence of local temperature and humidity anomalies. Elevation gradients delayed phenology in 90% of species, with advances (10%) in leafing of *Ficus adhatodifolia* and *Ficus eximia*, and flowering of *Geoffroea spinosa*, at lower altitudes. Finally, PAR and light availability both delayed phenology in all species, underscoring the suppressive effect of reduced light energy. Collectively, these findings indicate that in tropical trees, moisture and light-related drivers often outweigh temperature in determining phenological timing, with many responses shaped by hydrological seasonality, canopy light regimes, and disturbance events.

To aid interpretation of these region-specific phenological responses and to improve accessibility for a broader interdisciplinary readership, Tables 2 and 3 summarise the tree species and genera included in the meta-analysis for temperate/boreal and tropical/sub-tropical regions, respectively. For each taxon, the tables provide the scientific name alongside the commonly used name, general geographic distribution, and principal commercial or ecological uses where applicable. This consolidated overview facilitates cross-referencing of species-specific patterns discussed above and enhances the applied relevance of the phenological responses reported across contrasting bioclimatic zones.

3.7 The dominant, yet complex, role of temperature

The most consistent finding across the studies is the strong influence of temperature on the timing of spring phenophases. A large number of studies provided clear evidence that rising spring temperatures are leading to an earlier onset of leaf unfolding, flowering, and needle emergence.[14,116,117] This advancement is fundamentally linked to the accumulation of thermal units, or growing degree days (GDDs), required to initiate developmental processes. As the temperature increases, these thermal thresholds are met earlier in the year, thereby

Table 2 Temperate/boreal tree species included in the meta-analysis, with common names, uses, and geographic distribution

Scientific name	Common name	Country	Uses	References
Acer pseudoplatanus	Sycamore maple	Switzerland	Timber (furniture, instruments, flooring, kitchenware); urban planting; dye source; traditional sap and bark uses; ornamental/windbreak	13 and 45
Acer rubrum	Red maple	USA	Timber (furniture, pulp, flooring); ornamental landscaping; sap for syrup/sweetener; traditional medicinal uses (bark infusions for inflammation and wounds); wildlife habitat and food source; antioxidant extracts used in skincare	19, 53 and 64
Acer saccharum	Sugar maple	USA	Sap for maple syrup; hardwood timber; ornamental; traditional Indigenous uses; wildlife support; antioxidant extracts	19, 53 and 85
Alnus glutinosa	Common alder	Germany, Norway	Timber; bark for tanning/dyeing; soil improvement and erosion control; wildlife habitat; traditional medicinal uses	86
Betula ermanii	Erman's birch, gold birch	Japan	Ornamental; land reclamation; timber; traditional bark and sap uses; medicinal properties	83
Betula papyrifera	Paper birch, canoe birch, white birch	USA	Ornamental and crafts; timber products; traditional medicinal bark and sap uses; wildlife support	52, 64 and 87
Betula pendula	Silver birch	Europe	Timber; ornamental and reforestation; traditional medicinal uses; sap products; bark tar	18, 51 and 88
Corymbia calophylla	Marri, red gum	Australia	Timber; medicinal bark and leaf uses; beekeeping; ornamental/shade tree; wildlife habitat; resin uses	60
Fagus grandifolia	American beech	USA	Timber; edible nuts; wildlife support; traditional bark and leaf uses; ornamental shade tree	89
Fagus sylvatica	European beech	Europe	Timber; medicinal bark and buds; edible nuts; leaves for food; ornamental and traditional uses	50, 57 and 90
Fraxinus excelsior	Common ash, European ash	Central Europe	Timber; traditional medicinal uses; ornamental; agroforestry; seeds for oil; homeopathic uses	14
Galanthus nivalis	Common snowdrop	Germany	Medicinal (Alzheimer's treatment); homeopathic uses; traditional immunity and cognitive support	91
Juniperus monosperma	Oneseed juniper	USA	Food; medicinal teas; dyes; fuel/timber; sacred uses; ornamental; soil stabilization; flavoring/aromatic	92
Larix decidua	European larch	Europe	Timber; medicinal resin; bark for fuel; ornamental/restoration; aromatherapy/Bach flower uses	56
Larix laricina	Tamarack	USA	Traditional medicinal uses: timber, resin/bark supplements, dietary supplements, and uses of roots and bark/twigs	64
Liriodendron tulipifera	Tulip tree	USA	Timber; ornamental; traditional medicinal uses; nectar source; tinder/cordage; antioxidant/anticancer leaf extracts	89
Malus domestica	Apple, domestic apple	Germany, Latvia	Edible fruit; medicinal uses; cosmetics; traditional bark/leaf uses; food and phytochemicals	34, 65 and 93
Myrica esculenta	Box myrtle, bayberry, kaphal	India, Nepal	Traditional medicinal uses; antioxidant/anti-inflammatory/antimicrobial properties; fruits for food/drinks	94

Table 2 (*Contd.*)

Scientific name	Common name	Country	Uses	References
Myrcia guianensis	Candleberry	Brazil	Traditional medicinal uses; antioxidant/antimicrobial/anti-inflammatory; cosmetic and weed control potential	95
Phellodendron amurense	Amur cork tree	USA	Anti-inflammatory agent, antimicrobial and antibacterial, digestive and urological health, metabolic support, skin conditions	89
Picea abies	Norway spruce	Switzerland	Timber; Christmas trees; ornamental; medicinal extracts; antioxidant/antimicrobial; fire-starting/cultural uses	13
Pinus edulis	Pinyon pine, two-needle pinyon	Africa	Edible seeds; timber; firewood; traditional resin/needle uses; ornamental; climate studies	15
Pinus strobus	Eastern white pine	Ontario, Quebec, Nova Scotia, Newfoundland, Labrador	Timber; ornamental; traditional medicinal uses; teas/syrups; resins; vitamin C needles	35
Prunus avium	Sweet cherry, wild cherry	Europe	Edible fruit; medicinal uses; hardwood; ornamental/afforestation; bioactive compounds	44 and 96
Prunus persica	Peach	France	Edible fruit; cosmetics; traditional medicinal uses; extracts/oils; caution for seeds	97
Pyrus communis	Common pear, European pear	Germany	Edible fruit; traditional medicinal uses; timber; dyes; bioactive compounds	34
Quercus ellipsoidalis	Northern pin oak, hill's oak, jack oak	USA	Ornamental; wildlife habitat; land rehabilitation; timber; edible seeds; medicinal tannins	64
Quercus leucotrichophora	Banj oak, ban oak, brown oak, woolly oak	India	Fuel, fodder, timber, traditional medicinal uses, wildlife support, and erosion control	94 and 98
Quercus petraea	Sessile oak	Europe	Timber; animal fodder; tannins; fuel; biodiversity/wildlife support	80, 99–101
Quercus robur	English oak, common oak, pedunculate oak	Europe	Homeopathic uses; astringent/antiseptic bark; traditional medicinal uses	18 and 51
Quercus rubra	Northern red oak, red oak, common red oak	USA	Timber; ornamental; wildlife support; traditional medicinal uses	31, 53 and 89
Quercus suber	Cork oak	Portugal	Bark (multiple uses); timber; tanning; agroforestry; medicinal uses; biodiversity	102
Rhamnus cathartica	Common buckthorn, European buckthorn, purging buckthorn	USA	Medicinal and homeopathic uses; dyes; lubricating seed oils	64
Rhododendron arboreum	Tree rhododendron, Burans (or Buransh), Lali Gurans	India	Medicinal, food products, firewood, and craft wood uses	94 and 103
Sorbus aucuparia	Rowan, mountain ash, European mountain ash	Europe	Food, medicinal, cosmetic, carpentry, and ecological restoration uses	13 and 45
Sophora chrysophylla	Māmane (or Mamani)	USA	Timber, traditional medicine, cultural uses, wildlife conservation, and erosion control	30
Tilia cordata	Littleleaf linden, small-leaved lime	Europe	Medicinal teas, cosmetics, lightweight timber, edible leaves, and antioxidant benefits	11, 46 and 104

advancing the start of the growing season. This phenomenon has been documented globally, from temperate forests in Europe and North America to high-altitude ecosystems, confirming it as a near-universal biological indicator of climate change. However, the relationship between warming and phenological advancement is more complicated than a simple linear progression. Earlier, studies revealed a weakened phenological response to warming in recent decades.[12,31] This suggests that the initial strong response of plants to warming may be saturating or encountering new limiting factors. One of the most significant of these countervailing forces is the effect of winter temperatures on chilling requirements. Many temperate and boreal plant species have evolved to require a period of cold exposure (chilling) to break dormancy before

Table 3 Tropical/sub-tropical tree species included in the meta-analysis, with common names, uses, and geographic distribution

Scientific name	Common name	Country	Uses	References
Acacia koa	Koa, Koa acacia	United States (island of Hawaii)	Premium timber for crafts and instruments; traditional Hawaiian uses; reforestation, dyes, and medicinal value	30
Acacia tortilis	Umbrella thorn, Sejal	Senegal	Fodder, fuelwood, and timber; soil improvement (N-fixation, erosion control); traditional medicine; agroforestry and restoration species	105
Allophylus edulis	Chal-chal, Cocú/Kokû	Brazil	Medicinal (anti-inflammatory, antioxidant, analgesic); digestive/respiratory support; timber, ornamental, and reforestation use	106
Aquilaria malaccensis	Agarwood, Aloewood, Eaglewood	India	Aromatic products and rituals; traditional medicine; construction wood and bark textiles; critically endangered	47
Casearia sylvestris	Guaçatonga, wild sage	Brazil	Medicinal (anti-inflammatory, antiulcer, antimicrobial, wound healing); GI, cardiovascular, and antitumor potential	106
Dipterocarpus heimii	Chengal, Chengai	Malaysia, Sumatra, Thailand	Heavy construction and marine timber; flooring and cooperage; resin for varnishes and lacquers	71
Euterpe edulis	Juçara palm, Jussara palm	Brazil	Fruit for food products; heart of palm; light timber; antioxidant-rich pulp with medicinal potential; agroforestry species	107
Ficus adhatodifolia	Shortleaf fig, wild banyantree	Brazil	Latex used traditionally as an anthelmintic; reported anti-inflammatory/antioxidant activity with safety concerns	108
Ficus eximia	Brazilian fig	Brazil	Low-value timber; used as a shade tree in agroforestry and landscaping; traditionally used in folk medicine for gastrointestinal, respiratory, and inflammatory ailments	108
Geoffroea spinosa	Palu di Taki, Palu di Taki-taki, Oba Shimaron	Brazil	Fruit for food and medicinal use; timber for furniture, fuel, and construction; ornamental and tropical resource	109
Guarea macrophylla	Jatuauba, Bilheiro, Marinheiro	Brazil	Timber for furniture/construction; fuelwood; medicinal uses (anti-inflammatory, antimicrobial, cytotoxic); seeds potentially toxic	106
Hevea brasiliensis	Rubber tree, Para rubber tree	Colombia	Latex for rubber; seed oil for biofuels/chemicals; timber for furniture/fuel; traditional medicine and famine food uses	110
Jacaranda mimosifolia	Blue Jacaranda, Neeli Gulmohur	Australia	Ornamental; traditional medicine for wounds/infections/pain; timber for carpentry/instruments; bioactive extracts with antioxidant, antimicrobial, and anticancer potential	111
Metrosideros polymorpha	Lehua, lehuaahihi	United States (island of Hawaii)	Construction and tools; fuelwood; flowers/buds for leis and childbirth; nectar for birds/honey; ecologically vital; threatened by ROD.	30
Mimosa bimucronata	Maricá, Alagadiço, Amorosa, Angiquinho	Brazil	Ecological restoration and landscaping; firewood, honey, timber; medicinal leaves; thorny, considered a weed	106
Myrsine coriacea	Leathery Colicwood	Brazil	Traditional medicine (anti-inflammatory, antioxidant, antimicrobial); coffee shade, reforestation, basic timber	106
Myrsine umbellata	Umbrella myrsine	Brazil	Traditional medicine (stomach, skin, liver, leprosy); bioactive compounds; landscaping; food/pharma potential	106

Table 3 (*Contd.*)

Scientific name	Common name	Country	Uses	References
Olea europaea	Olive tree	Cyprus	Edible fruit/oil; medicinal (antioxidant, anti-inflammatory, metabolic, immune); cosmetics; durable wood; bioactive compounds	112
Pericopsis elata	Afrormosia, African Teak	Ghana	Durable hardwood (furniture, flooring, boat building); agroforestry shade; medicinal uses; endangered	113
Populus tremula	European aspen, common aspen	Spain, Turkey, Japan, Korea	Medicinal (anti-inflammatory, analgesic, febrifuge, digestive, urinary); wood and charcoal; metabolic health potential	67
Populus tremuloides	Quaking Aspen, Trembling Aspen	USA	Medicinal (pain, digestive, urinary, anti-inflammatory); wood for pulp/furniture; bark/buds for herbal remedies	23
Schinus glandulosum	Scentless rosewood	Brazil	Medicinal (wound-healing, analgesic, anti-inflammatory, antibacterial)	106
Schinus terebinthifolia	Brazilian peppertree, Christmas berry	Brazil	Spice, ornamental, medicinal (anti-inflammatory, antimicrobial, wound-healing); invasive/allergenic	106
Shorea leprosula	Meranti, light red Meranti	Malaysia, Sumatra, Thailand	Timber (furniture, flooring, plywood), traditional medicine, ecological restoration	71
Shorea obtusa	Taengwood, Balau, Burma sal, Siamese	Vietnam, Malaysia, Sumatra, Thailand	Timber (construction, flooring, boats), resin (incense/medicine), leaves (biodegradable, antioxidant/antimicrobial)	114
Shorea siamensis	Meranti, dark red Meranti	Vietnam, Malaysia, Sumatra, Thailand	Timber (construction/furniture), resin (caulking/incense), medicinal bark (dysentery/skin)	114
Tabebuia rosea	Pink trumpet tree, rosy trumpet tree, or pink poui	Uganda	Ornamental, medicinal (fever/pain/anemia/cancer), durable wood, shade/eco-use; antioxidant and anti-inflammatory potential	115
Tamarindus indica	Tamarind tree, imli	West Africa (Sudan-Guinea)	Culinary, medicinal (digestion/inflammation/fever/antivenom), industrial (gum, timber)	73

they can respond to spring warmth. As winters grow milder, the accumulation of chilling hours decreases. Insufficient chilling may delay or even prevent budburst, thereby counteracting the advancing effect of a warm spring.[118,119] This antagonistic interplay between reduced chilling and increased forcing explains a significant portion of the observed heterogeneity in phenological trends, where some species or populations show delayed, rather than advanced, spring phenology under warming scenarios.[120]

The complexity of these interactions poses a significant challenge for predictive modelling. Process-based phenological models that incorporate both chilling and forcing requirements (two-phase models) generally outperform simpler, single-phase thermal time models in explaining historical data. Even these sophisticated models show substantial divergences in their projections of future phenological events, particularly in their representation of the end of the chilling period under novel climatic conditions.[20] This uncertainty highlights a critical research gap. The fundamental physiological mechanisms governing dormancy release and their interactions with temperature, which remain poorly understood, limit our ability to project the future of the growing season accurately.

3.8 Impacts of phenological shifts

The reviewed studies collectively demonstrate that phenological shifts primarily driven by climate change have profound and multifaceted impacts on tree physiology, ecological interactions, ecosystem functions, and overall environmental resilience, as summarized in Table 4. These shifts, often recognized as advances in spring events (budburst and leaf-out) and variable changes in autumn events (delays or advances in senescence), alter tree health, community dynamics, and biogeochemical cycles. Below are the key impacts synthesized from empirical literature, highlighting both positive and negative consequences across scales.

3.8.1 Physiological and growth impacts. Phenological advancements in spring events increase vulnerability to environmental stressors. For instance, earlier leaf-out (up to 2.5 days/°C in temperate species) heightens exposure to late-spring frosts, with frost injury rates rising from 3% to 78% under drought conditions in some deciduous trees. This leads to delayed budburst in subsequent years (0.6–2.4 days) and reduced leaf toughness/thickness, compromising growth. Conversely, delays in autumn senescence (2.1–25.8 days post-drought) extend growing seasons but can exacerbate water

Table 4 Multidimensional impacts of phenological shifts

Category	Drivers/patterns	Observed impacts	Consequences	References
Physiological and growth impacts	- Spring advancement (up to 2.5 days/°C) - Delayed senescence (2.1–25.8 days) - Elevation-dependent delays (up to 28 days later at 1450 m v/s 550 m)	- Frost injury ↑ (3% to 78% under drought) - Delayed budburst (0.6–2.4 days) - Reduced leaf toughness/thickness	- Higher vulnerability to frost and drought - Carbon allocation trade-offs (storage > growth) - Mortality ↑ in extreme years	18, 29, 43, 114 and 121
		- Drought shortened the growth season despite longer potential - Growth suppression: 36% basal area increment reduction - El Niño: deciduousness extended 2–3 to 5 months, ↑ mortality 45–50% - Fir shows higher plasticity than oak/beech	- Narrowed elevational suitability ranges	
Ecological implications	- Advancing spring phenology (19%↑ leafing probability)	- Mismatches: trees v/s pollinators, frugivores, herbivores	- Reduced pollination and dispersal	48, 99, 122–124 and 128
	- Exotic urban trees = delayed phenology	- Reduced invertebrate abundance (urban caterpillars peak early)	- Lower biodiversity resilience	
	- Edge microclimates advance reproduction (by 20 days)	- Reproductive asynchrony (bimodal patterns in tropics)	- Altered competition and resource use	
	- Extended interspecific differences (IDSP)	- Drought 2015↓ reproduction	- Higher disease/frost trade-offs	
		- Early-flushing oaks escape mildew but risk frost - Late-flushing avoids frost but faces disease - 8% radiation differences (Europe v/s N. America)	- Habitat loss and northward range shifts (*Pinus strobus*)	
Ecosystem function and carbon cycling	- Growing season length ↑ 3.1 days per decade	- NEE ↓ 3.99 TgC annually (Europe)	- Reduced carbon sink capacity	11, 13, 72, 102, 125 and 126
	- Thermal seasons advance faster (12.6 days per decade)	- Longer seasons ↑ respiration (1 Tg respiration to −2.28 TgC NEE)	- Stronger drought stress in lowlands, relief in highlands	
	- Arid systems: pre-rain green-up (>20 days early in 70% areas)	- NPP ↑ under CO_2 fertilization if nutrients are sufficient	- Improved nutrient recycling under stress	
	- Rainfall variability in tropics (+23% in 12 years)	- Nutrient resorption efficiency ↑ 22% in dry years - Drought intensity: +81% lowlands, −84% highlands - Fruiting ↑ with rainfall, but dry deficits delayed peaks	- Instability in tropical carbon dynamics	
Water cycling	- Earlier leaf-out extends the transpiration period	- Higher evapotranspiration demand	- Intensified water stress in dry regions	41, 102 and 112
	- Delayed senescence prolongs water demand	- Faster soil moisture depletion	- Redistribution of drought effects by elevation	
	- Elevation-dependent drought effects	- Low elevation drought stress +81%, high elevation −84%	- Possible buffering in arid/semi-arid regions	
	- Pre-rain green-up in arid systems	- Green-up improves adaptation to rainfall timing		
Disturbance and stress impacts	- Earlier/longer growing season alters exposure to frost, pests, and pathogens	- Early-flushing oaks escape mildew but suffer frost damage	- Higher pest/pathogen pressure	53, 99 and 124
	- Prolonged drought increases pest susceptibility	- Late phenology avoids frost but increases disease exposure	- Trade-offs between frost avoidance and disease risk	
		- Extended leaf periods favour pest outbreaks	- Greater variability in the disturbance regime	

Table 4 (*Contd.*)

Category	Drivers/patterns	Observed impacts	Consequences	References
Forest composition and range shifts	- Species-specific phenological plasticity - Elevation and latitude gradients	- Fir adapts better than oak/beech at higher altitudes - *Pinus strobus* projected to lose habitat under warming scenarios	- Shifts in competitive advantage - Range contractions or northward migrations - Long-term changes in forest	35 and 121
Socio-economic and management implications	- Longer pollen/reproductive seasons - Forestry and agriculture dependent on timing of leafing/flowering - Urban phenology mismatches	- Extended allergy seasons in humans - Reduced forestry yields in dry years - Urban trees less synchronized with insect cycles	- Public health burdens ↑ (allergies, air quality) - Reduced timber/crop productivity - Challenges for adaptive forest and urban management	82, 122, 129 and 130

stress, as seen in *Pyrenean birches* where drought shortened the growth season and reduced ring thickness despite longer potential seasons.[18,43]

Non-structural carbohydrates (NSCs) play a buffering role, with mobilization supporting survival under extreme conditions like late frosts or droughts; however, growth is often suppressed (*e.g.*, 36% reduction in basal area increment during dry years) to favor storage, indicating trade-offs in carbon allocation.[29] Interannual variability further amplifies impacts. El Niño events extended deciduousness from 2–3 to 5 months in tropical dry forests, increasing dieback and mortality by 45–50%.[114] At higher elevations, phenological delays (28 days later budburst at 1450 m compared to 550 m) narrow suitability ranges and strengthen directional selection for earlier traits. However, phenotypic plasticity varies by species; for example, fir matches optima better than oak or beech.[121]

3.8.2 Ecological implications.

Shifts disrupt synchrony in ecological interactions, leading to mismatches. Earlier spring phenology (*e.g.*, 19% increase in leafing probability over decades) creates phenological decoupling with pollinators, frugivores, and herbivores.[122] In urban settings, exotic trees exhibit delayed phenology, causing caterpillar peaks to precede tree peaks and reducing invertebrate abundance.[123] Reproductive phenology shows high intraspecific synchrony but community-level asynchrony, with bimodal patterns in tropical forests potentially buffering biodiversity. However, drought in 2015 reduced reproduction without trait-based predictability, threatening frugivore-dependent species.[48] Mismatches also affect hazards like early-flushing oaks that escape mildew but risk frost at lower elevations, while late-flushing types avoid frost but face disease.[99] In forests, extended interspecific differences in spring phenology (IDSP) alter competitive dynamics and resource use, with 8% differences in radiation exposure between Europe and eastern North America.[124] Fragmentation exacerbates this, with edge microclimates advancing reproduction by 20 days on warmer edges, influencing synchrony and intensity.[95] Overall, these shifts contribute to biodiversity loss, as evident in projected habitat declines and northward shifts for species like *Pinus strobus* under climate scenarios.[35]

3.8.3 Ecosystem function and carbon cycling impacts.

Phenological changes significantly influence carbon dynamics and nutrient cycling. Growing seasons extended by 3.1 days per decade in temperate regions, but thermal seasons advanced 4 times faster (12.6 days per decade),[11] leading to mismatches that reduced net ecosystem exchange (NEE) by 3.99 TgC annually in European forests. Longer seasons increase heterotrophic respiration, offsetting carbon uptake (each 1 Tg respiration reduces NEE by 2.28 TgC).[125] In arid systems, pre-rain green-up (70% of areas >20 days early) enhances resilience but indicates adaptation to insolation cues, potentially boosting net primary productivity (NPP) under CO_2 fertilization if nutrients are not limiting.[126]

Nutrient resorption efficiency increased by 22% in dry years, linked to delayed senescence and pigment degradation, improving nitrogen and phosphorus recycling.[102] However, shifts amplify drought at lower elevations (+81% intensity) while mitigating it at higher elevations (−84%), altering forest composition and productivity.[13] In tropical forests, increased rainfall (23% over 12 years) boosted fruiting intensity, but dry-season deficits delayed peaks, impacting carbon sequestration and ecosystem stability.[72]

The diverse impacts of phenological shifts emphasize their crucial role in influencing tree resilience, ecological interactions, and ecosystem services amid climate change. While longer growing seasons and adaptive responses, such as the mobilization of nonstructural carbohydrates (NSC), provide some resilience, increased vulnerabilities to frost, drought, and ecological mismatches present serious risks to biodiversity and carbon cycling. These findings underscore the urgent need for improved predictive models and adaptive management strategies to reduce negative effects and capitalize on potential benefits, ensuring the sustainability of forest ecosystems in a warming world.

3.8.4 Water cycling.

Climate-driven phenological shifts are projected to significantly alter water cycling in forest ecosystems by 2100, with implications for evapotranspiration (ET), soil moisture, and watershed hydrology across all biomes.[88] Under SSP1-2.6 to SSP5-8.5 scenarios, growing season extensions of 18–52 days, driven by temperature increases (up to 1.7 °C over

60 years) and precipitation variability (+23% in some tropical regions), will intensify ET, particularly in boreal and temperate forests where spring leaf-out advances (up to 3.0 days per decade) in species such as *Picea abies* and *Quercus robur*.[88] Machine learning models (RMSE 7.03–7.33 days) predict earlier leaf flushing (April–July in the tropics, advanced by 2.5 days/°C in temperate zones), increased ET, and depleted soil moisture, especially at low elevations, where drought intensity may rise by 81%. In tropical forests, enhanced rainfall can boost fruiting intensity, but ENSO-driven dry-season deficits may delay reproductive phenophases (October–February), increasing runoff and erosion risks.[113] Soil moisture dynamics will be further strained by earlier budburst (10.2 ± 3.7 days earlier by 2051–2080 under RCP 8.5) and prolonged canopy duration (5–8 months in tropical species with groundwater access), reducing groundwater recharge in Mediterranean systems such as *Quercus suber*.[100] High-elevation forests may mitigate these impacts, with delayed budburst (up to 28 days at 1450 m) preserving soil moisture.[121] However, lowland temperate forests face heightened water stress, exacerbated by late frost risk (frost injury increased from 3% to 78%).[43] Photoperiod effects (1.7 days per latitudinal degree) and chilling deficits in warmer winters can modulate water use by delaying dormancy release, particularly in species such as *Acer rubrum*.[127] Adaptive responses, such as pre-rain green-up in arid species (70% of regions >20 days early) and high phenotypic plasticity in *Fagus sylvatica*, may buffer water stress, but trade-offs, such as reduced growth for carbohydrate storage under drought (36% basal area reduction), limit resilience.[102] Management strategies including drought-tolerant provenance selection, precision irrigation (saving up to 48% of water in orchards), and integration of microbial influences on phenology (10 days delays in budbreak) will be critical.[112] Enhanced monitoring *via* Sentinel-2A/2B and Himawari-8 satellites can improve predictions, supporting climate-resilient forest management to sustain the hydrological balance under warming scenarios.[41]

4. Key contributions of reviewed studies

This study highlights a significant contribution of phenological research across scientific, environmental, and societal domains. Recent studies have moved beyond descriptive observations to provide mechanistic insights, advanced modelling frameworks, and applications that inform management and climate adaptation strategies.[13,131] Together, these findings demonstrate how phenology serves as a bridge between fundamental ecological processes and practical solutions, while also underscoring a broader shift toward integrative, multi-scale approaches. Integrating species-specific responses, climate projections, and advanced methodologies may enhance predictive understanding of forest ecosystems in a changing climate.

4.1 Scientific advancements

The reviewed studies significantly expand the theoretical and empirical foundation of phenology. A key contribution is the development of novel models and methodologies, such as process-based models for autumn foliage phenology, the PhenoFlex model for dormancy dynamics, and space-for-time substitution methods to address data gaps in long-term trends.[54,132] For instance, several papers introduce innovative tools like drone-based monitoring linked to functional traits,[58,133] remote sensing validation for conifer photosynthesis phenology,[41,134] and coupled models integrating phenology with pathology under climate change.[37,135] These advancements improve model reliability, reproducibility (open-source R packages like chillR),[132] and the quantification of species-specific sensitivities, including thresholds for pollen viability, nutrient resorption, and chilling requirements.[68,136,137] Integrating genetics, remote sensing, and machine learning methods, such as Random Forest and boosted regression trees, may help researchers move towards understanding phenological response to changing climatic variability. This integration has refined ecological theory by identifying how extreme events affect different phenophases and by advancing our understanding of processes such as carbon allocation, reproductive success, and nutrient cycling (34 109). Collectively, the findings highlight a methodological shift toward mechanistic, data-intensive approaches that yield more robust, scalable, and nuanced insights into species responses to climate change.

4.2 Environmental implications

Phenological research informs ecosystem vulnerability and resilience under climate change.[6,138] Contributions emphasize predictive assessments, such as quantifying shifts in reproductive timing, seed production, and growing seasons, which highlight increased risks, including late-spring freezes, phenological mismatches with pollinators or frugivores, and reduced chilling in warmer winters. For example, evidence from oak masting, olive pollination mismatches, and tropical fruiting dynamics aids in forecasting regeneration success, biodiversity loss, and carbon cycling disruptions in temperate, tropical, and alpine forests.[79,118] Beyond species-level responses, research has examined ecosystem processes, including hydrological dynamics, urbanization effects, and habitat fragmentation.[139–141] Studies demonstrate resilience mechanisms, such as non-structural carbohydrate buffering against extremes, trait-based niche differentiation in dry forests, and microbial mediation of climate adaptation.[29,142] Integrating multi-method data may improve ecological forecasting for carbon sequestration, nutrient dynamics, and habitat shifts, identifying vulnerable regions like rear-edge Mediterranean populations or Himalayan montane zones.[38,122] Broader environmental benefits include support for conservation biology, such as species-specific data for threatened trees (*Pericopsis elata*, *Euterpe edulis*) and bioindicators like *Delonix regia* for urban climate impacts.[107,113,143] These insights underscore the importance of holistic models that account for compound stressors, facilitating biodiversity preservation, forest composition predictions, and sustainable land-use in climate-sensitive ecosystems.

4.3 Societal relevance

The practical applications of phenological findings extend to management, policy, and community benefits, promoting climate-resilient practices. In forestry and agriculture, studies provide actionable guidance, such as optimal seed collection timing for restoration, irrigation strategies saving up to 48% water in olive orchards, and provenance selection for climate-adapted reforestation, like in the case of Bulgarian beech for Europe.[79,144] Tools like automated imagery for bloom forecasting and scalable drone methods support precision forestry, reducing labor while enhancing health monitoring and genomic breeding.[97]

The review informs adaptation strategies, including urban greening for heat mitigation, assisted migration for species at risk (*Pinus strobus*), and pest management during outbreaks.[23,104] Linking phenology to ecosystem services such as timber production, tourism,[53] and food security may aid policymakers in developing climate-smart policies, carbon markets, and conservation planning.[145,146] Public engagement is fostered through accessible data sources (video archives from events like the Tour of Flanders) and bioindicators that visualize climate change impacts.[122] In resource-dependent communities, contributions support livelihood strategies, like community-based reforestation with high-value timber species or wildlife management for frugivore-dependent ecosystems in tropical Africa.[74] Ultimately, by empowering data-deficient regions with substitution methods and open-source tools, the literature democratizes phenological knowledge, enhancing global efforts toward sustainable development and resilience.

5. Identified research gaps and future directions

This synthesis revealed several persistent knowledge gaps that hinder a comprehensive understanding of phenological processes, particularly in the context of climate change, environmental drivers, and ecological interactions. These gaps span methodological limitations, mechanistic insights, modelling deficiencies, and the need for expanded temporal, spatial, and taxonomic coverage. Below are the identified gaps, synthesized and categorized into key themes to highlight priorities for future research.

5.1 Gaps in environmental drivers

A dominant theme across studies is the incomplete understanding of phenological shifts and their variability. For instance, there is a lack of clarity on the role of environmental drivers in regulating phenology continent-wide, including variability in phenological shifts across African regions and the unclear influence of photoperiod, precipitation, and other meteorological factors. Specific gaps include the limited mechanistic understanding of how blue light regulates spring bud burst in deciduous trees, the interaction between drought and photoperiod in warming climates, and the role of non-temperature stressors like defoliation or solar-wind energy flux in synchronizing tropical tree reproduction with events like El-Nino.[51,103] Additionally, the influence of non-atmospheric variables remains underexplored, particularly in tropical and alpine systems where temperature variations are minimal.

5.2 Modeling and predictive limitations

Phenological models are frequently criticized for their generalizations and lack of flexibility. Gaps include the inability of process-based models to capture the non-linear, interactive effects of multiple drivers (temperature, water, light, and biotic factors), the need for integrative approaches using machine learning to enhance accuracy in autumn phenology dynamics, and the failure to separate winter and spring warming effects.[56] Traditional models often ignore photoperiod regulation, leading to overestimated ecosystem responses to warming, and lack uncertainty estimates or validation across diverse environments, cultivars, or future scenarios.[119] There is also a need for refined models that incorporate chilling, forcing, and biotic factors, along with dynamic fitness targets, to predict adaptation and plasticity under shifting climates.

5.3 Species-specific, trait-based, and genetic responses

The literature highlights a scarcity of species-level analyses and mechanistic insights into trait variation. Gaps encompass a limited understanding of how functional traits (specific leaf area and non-structural carbohydrates) drive phenological differences, the role of intraspecific genetic variation in responses to climatic gradients, and transgenerational influences (parental temperature effects) on phenology.[83] Species-specific gaps include unclear responses in threatened tropical trees, conifers, alpine species, and cultivars such as apples and olives, as well as differential sensitivities among closely related species. A broader exploration is needed to understand how traits relate to tree health, resilience, and population dynamics, including the effects of urbanization, fragmentation, and interactions with soil microbiomes.

5.4 Methodological and data limitations

Data scarcity and methodological constraints are recurrent issues. There is a lack of long-term, multi-site, and geographically diverse datasets, especially in tropical Africa, Australia, dry forests, and urban settings, with the underutilization of unconventional sources, such as video archives or citizen science. Phenological monitoring tools face challenges, including camera sensitivity to lighting conditions, the need to validate remote sensing methods (such as CubeSats, drones, and satellites) across various species and scales, and the development of automated systems for conifers or multi-peak patterns. The digitization of historical data is incomplete, and methods often fail to capture belowground processes, intra-population variation, or shifts in phenophases from flowering to fruiting.[60,93]

5.5 Regional and management implications

Region-specific gaps are evident, such as the lack of reproductive phenology data for tropical trees in Africa or Madagascar, long-term studies in Australian temperate rainforests, or adaptive strategies for non-Mediterranean climates like Uruguay.[79] Management-related voids include optimal silvicultural practices like spacing for plantations, phenology-based strategies for rubber yield or forestry, and the integration of phenological variability into conservation planning, assisted migration, or urban species selection.[113] Broader geographic coverage is needed to assess resilience in fragmented tropical landscapes, arid systems, or elevations, alongside the applicability of findings to global-scale analyses.

Addressing these gaps requires interdisciplinary approaches, including expanding long-term monitoring networks, using advanced modeling techniques, and integrating genetic, physiological, and ecological data. Future research should prioritize multi-factor experiments, broader validation across ecosystems, and the development of scalable tools to inform climate-resilient management and conservation strategies.

5.6 Integration of phenology with climate dynamic global vegetation modelling

A significant research gap highlighted in this review is the limited incorporation of species-specific phenological processes into dynamic global vegetation models (DGVMs). Although DGVMs are widely employed to simulate vegetation dynamics, biogeochemical fluxes, and vegetation-climate feedbacks, most existing models rely on simplified or biome-level representations of phenology. These generalizations fail to capture the heterogeneity documented across our synthesis of 145 studies. For instance, our Sankey diagram and bubble-plot analyses revealed that temperature was the most frequently analyzed driver (71% of studies), predominantly in temperate and boreal regions of Europe and North America.[147,148] However, precipitation and drought were more frequently examined in tropical and subtropical systems.[72,149] Such divergent sensitivities underscore the inadequacy of "one-size-fits-all" phenology parameterizations within DGVMs.

The omission of realistic phenological variability limits DGVMs' ability to capture critical processes, including the onset and duration of the growing season, seasonal photosynthetic carbon assimilation, and water cycling. This is particularly problematic in temperate regions where earlier leaf-out extends the growing season,[14] while in drought-prone ecosystems, delayed leaf flushing or flowering may shorten it substantially.[57] Without accounting for such regions and species-specific dynamics, DGVMs risk misrepresenting vegetation-climate interactions, leading to biased estimates of terrestrial carbon budgets, evapotranspiration, and climate feedbacks. Moreover, mismatches between phenology and ecological interactions, such as earlier flowering coinciding with late frost risk5 or shifts in flowering relative to pollinator activity[33] remain poorly represented in current models.

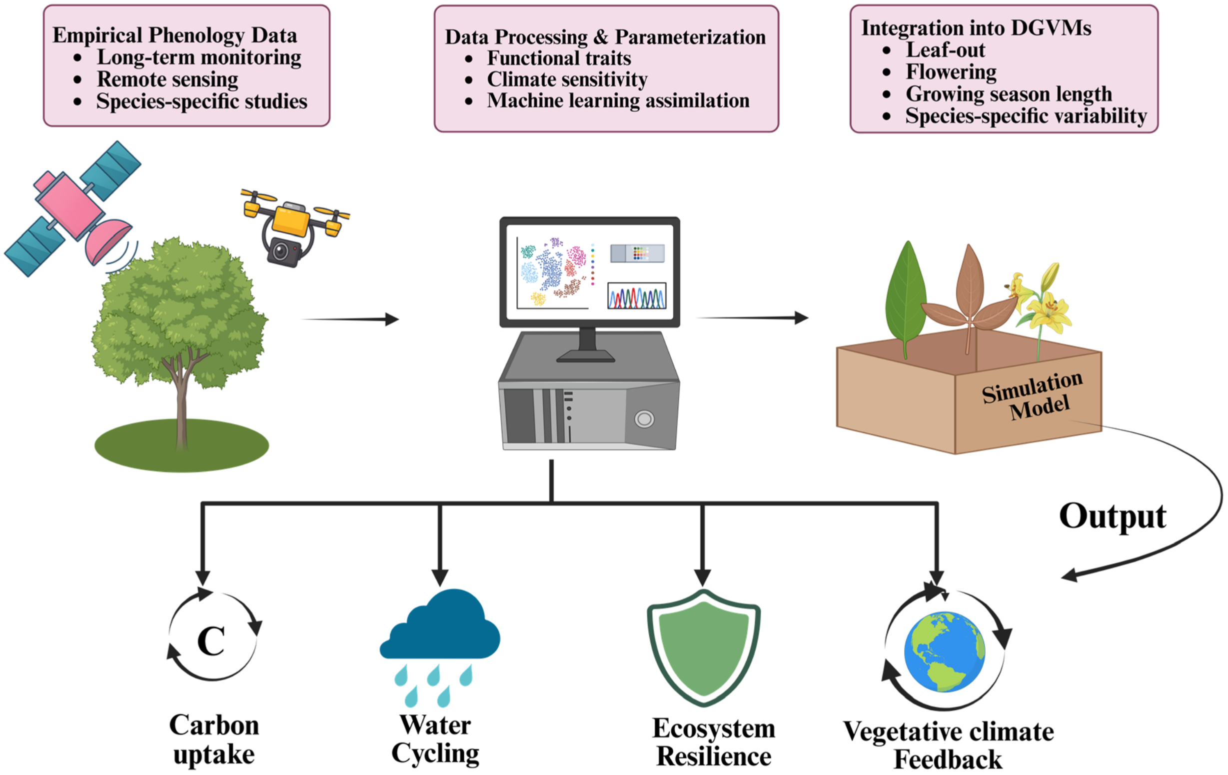

Fig. 9 Conceptual framework illustrating the integration of species-specific phenological data into dynamic global vegetation models (DGVMs). Empirical observations, climatic drivers, and remote sensing data inform phenology modules that simulate species-level responses. These modules are then linked to DGVM processes such as carbon assimilation, water cycling, and disturbance dynamics, ultimately producing outputs that improve forecasts of ecosystem functioning and resilience under climate change (created using https://www.biorender.com/).

To address this, future work should prioritize linking empirical phenological datasets to DGVM frameworks. The synthesis shows substantial evidence from long-term ground-based monitoring in temperate systems[10,150] and increasing use of remote sensing,[86,151] both of which could be leveraged to parameterize and validate phenology modules. Incorporating machine learning and data assimilation techniques offers promising avenues for translating heterogeneous phenological records, including those from understudied tropical regions[152] model-ready parameters. Importantly, integrating plant functional traits into DGVM phenology schemes could allow more realistic simulations of interspecific and intraspecific variability in phenological responses. The conceptual framework for such integration is summarized in Fig. 9. This flowchart illustrates the process of linking empirical observations (*e.g.*, budburst, flowering, and leaf senescence), climate drivers (temperature, precipitation, photoperiod, and soil moisture), and remote sensing products with model parameterization and calibration. Embedding these data streams into DGVMs would enable models to move beyond static assumptions about growing-season dynamics and better represent the functional diversity of phenological responses across biomes.

Ultimately, coupling phenological shifts with processes such as carbon uptake, evapotranspiration, albedo regulation, and disturbance regimes in DGVMs is critical for improving forecasts of ecosystem functioning and resilience under future climate scenarios. Such integration will bridge the gap between species-level responses documented in this review and the large-scale projections required for Earth system modelling.[148,153]

6. Limitations

The findings of this systematic review should be considered in light of several key factors. Similar to other large-scale syntheses of phenological research,[151,154,155] our syntheses included entirely peer-reviewed empirical studies, thereby excluding theses, reports, conference proceedings, and other forms of grey literature. This exclusion potentially omits valuable long-term observational data, particularly from forestry departments, botanical gardens, and citizen science initiatives, which often remain unpublished in peer-reviewed journals. The search strategy was limited to English-language publications, leading to an underrepresentation of studies conducted in non-English-speaking regions. This bias could be especially significant for tropical and Southern Hemisphere countries, where locally published work in regional languages may contain valuable insights into phenology. Future reviews should aim to incorporate non-English literature and region-specific databases to capture a more balanced global perspective. Finally, most of the studies included examined single or limited climatic drivers, such as temperature and precipitation. In contrast, interactive or indirect drivers, such as soil moisture and extreme weather events, were less frequently assessed. Incorporating such multi-factorial approaches in future research will be crucial for building more ecologically realistic predictions of phenological responses under complex climate scenarios.

7. Conclusion

This review synthesizes global evidence on climate-driven changes in tree phenology and highlights their ecological consequences across temperate, boreal, tropical, and subtropical biomes. Phenological responses are strongly climate-dependent but vary among species and ecosystems. In temperate and boreal forests, rising temperature is the dominant driver of phenophases such as budburst, leafing, and flowering, with *Betula* and *Quercus* species consistently showing advancement under warming. In contrast, phenology in tropical and subtropical forests is primarily regulated by precipitation and hydrological seasonality, with species such as *Acacia* responding to both rainfall and temperature, while drought-sensitive taxa (*Geoffroea spinosa* and *Shorea siamensis*) exhibit delayed phenophases under water stress or altered light regimes. These patterns underscore fundamental biome-specific controls, where thermal thresholds dominate at higher latitudes and water availability governs phenology in the tropics.

Shifts in phenology have far-reaching ecological implications. Earlier spring events increase vulnerability to late frost damage, while delayed autumn senescence can exacerbate water stress, particularly in drought-prone regions. Phenological mismatches with pollinators, herbivores, and frugivores are increasingly reported, leading to cascading effects on biodiversity and ecosystem functioning. Carbon and water cycling are also substantially affected, as extended growing seasons alter ecosystem respiration, carbon sequestration efficiency, and evapotranspiration dynamics, with contrasting responses across elevations and climatic zones. Recent advances in remote sensing, phenocams, UAVs, and process-based modeling have significantly improved the detection and scaling of phenological patterns. Nevertheless, major gaps remain, particularly in tropical and subtropical regions, where observational data are sparse. Current dynamic global vegetation models often rely on simplified phenological schemes that inadequately represent species-specific responses, limiting the accuracy of projections for carbon budgets, water fluxes, and climate feedbacks. Greater integration of plant functional traits, genetic variability, and belowground processes is needed to develop more mechanistic and predictive frameworks.

Overall, tree phenology emerges as a sensitive and integrative indicator of climate change, linking atmospheric drivers with ecosystem processes. Strengthening phenological monitoring and incorporating its insights into forest management can support climate-smart strategies, including adaptive reforestation, provenance selection, and ecosystem conservation. Addressing existing knowledge gaps will be critical for improving model reliability and safeguarding forest ecosystem services under accelerating climate change.

Author contributions

Karuna Gusain (K. G.): literature review, data collection, writing – original draft. Kajal Gautam (K. G.): literature review, suggestions, writing and editing manuscript. M. B.: literature review, suggestions, writing and editing manuscript. H. S.: supervision, project administration, review and editing, laboratory and infrastructure support. M. S.: suggestions, review and editing. S. B.: suggestions, review and editing.

Conflicts of interest

The authors declare that there are no conflicts of interest regarding the publication of this review paper.

Data availability

The supporting data has been provided as part of the supplementary information (SI). Supplementary information: the calculation for World map coordinates, Temporal trend supplementary, Sankey supplementary, Fisher z 1, Fisher z 2 mentioned in this manuscript. See DOI: https://doi.org/10.1039/d5va00292c.

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