IOP Publishing Environ. Res.: Climate 4 (2025) 045007 https://doi.org/10.1088/2752-5295/ae1051

ENVIRONMENTAL RESEARCH
CLIMATE

Check for updates

OPEN ACCESS

RECEIVED
28 July 2025

REVISED
30 August 2025

ACCEPTED FOR PUBLICATION
7 October 2025

PUBLISHED
17 October 2025

PAPER

Growth synchrony in white spruce across Canada and Alaska: climate or distance?

Fang Wu[1], **Junwen Jia**[1,2], **Cheng Li**[3] **and Xuefeng Cui**[1,*]

[1] State Key Laboratory of Earth Surface Processes and Hazards Risk Governance (ESPHR), Faculty of Geographical Science, Beijing Normal University, Beijing, People's Republic of China
[2] School of Earth and Environmental Sciences, Cardiff University, Cardiff, United Kingdom
[3] School of Plant Protection, Yangzhou University, Yangzhou, People's Republic of China
[*] Author to whom any correspondence should be addressed.

E-mail: xuefeng.cui@bnu.edu.cn

Keywords: growth synchrony, network analysis, MRM, geographic proximity, climate synchrony

Abstract

Boreal forests, which serve as major terrestrial carbon sinks, are experiencing rapid warming across much of their range. Spatial synchrony in tree growth is crucial for the stability and persistence of these forests. Despite its importance, the geographic patterns and drivers of tree growth synchrony in boreal forests remain underexplored. This study aims to address these gaps by investigating growth synchrony of white spruce (*Picea glauca*), a widespread boreal species of significant ecological and economic value. Using tree-ring data from 187 sites, we quantified growth synchrony with the synchronous growth change coefficient, a non-parametric index capturing consistency in year-to-year variations. We then analyzed its spatial pattern and drivers using complex network analysis and multiple regression on distance matrices (MRM). We found that white spruce growth synchrony follows a clear biogeographical pattern, decreasing from northwest to southeast. The relationship between growth synchrony and geographic distance was non-linear, deviating from the typical distance-decay pattern described by Tobler's First Law of Geography. Specifically, synchrony increased as geographic distance decreased at shorter distances, but reversed at longer distances, where more distant sites showed relatively stronger synchrony. MRM analysis showed that climate factors explained 55% of the variance in growth synchrony, with geographic proximity contributing minimally after accounting for climate (increasing to 56%). These results suggest that synchronization of climate, particularly temperature, was the primary driver of spatial synchrony in white spruce growth, while spatial proximity-related mechanisms played a limited role. Given that high synchrony can reduce population stability, we recommend prioritizing management efforts that promote asynchronous growth, especially in regions exhibiting strong synchrony (e.g. northern Northwest Territories and Yukon). These findings provide new insights into boreal forest dynamics and inform adaptive management and conservation strategies in the face of ongoing climate change.

1. Introduction

Boreal forests play a key role in the carbon cycle and climate regulation (Pan *et al* 2011). However, they are warming at nearly twice the global average rate (Post *et al* 2019) and are expected to face the largest temperature increases among forest biomes by the end of this century (Gauthier *et al* 2015). These rapid changes have already and may further strongly affect tree growth and forest stability (McDowell *et al* 2020), highlighting the need to better understand boreal forest dynamics and their underlying mechanisms.

Spatial synchrony in tree growth, the consistent fluctuation of interannual growth among spatially separated trees, offers a valuable perspective for such understanding. In ecological theory, synchrony plays a key role in shaping population dynamics, stability and persistence (Heino 1998, Liebhold *et al* 2004). While initially developed in the context of population abundances, these principles are equally applicable to growth, a vital rate of population dynamics. Growth synchrony has thus been recognized as a comprehensive indicator of environmental stress and a potential early-warning signal of declining forest resilience (Cailleret *et al* 2019, Jia *et al* 2024). Tree-ring records provide precise annual resolution and extensive spatial-temporal coverage needed to study growth synchrony (Zhao *et al* 2019). Yet despite these advantages, the spatial patterns and underlying drivers of tree growth synchrony remain comparatively understudied (Shestakova *et al* 2018).

Recent studies have shown that tree growth synchrony exhibits complex geographic patterns, largely shaped by environmental variation and population dynamics (Walter *et al* 2017, Tejedor *et al* 2020). Complex network theory offers a powerful tool for detailing such spatial complexity. By modeling correlations among constituent elements, it reveals the underlying topological structure of complex systems from a global perspective (Qiao *et al* 2019). A key strength of this method lies in its generality and robustness, as network nodes and links represent abstract properties independent of spatial and environmental constraints (Phillips 2019). Nevertheless, its application to tree growth synchrony is still in its infancy, with only a few studies to date (e.g. Astigarraga *et al* 2025).

Complex geographies of growth synchrony are typically attributed to two types of mechanisms. One is the Moran effect, arising from direct climatic influences on biological processes (Moran 1953). Another involves spatial processes, such as dispersal and disturbances mediated by shared natural enemies (Haynes *et al* 2013, Reuman *et al* 2025). These processes are often interdependent, as illustrated by spruce budworm outbreaks, which are both climate-driven and spatially contagious (Bouchard *et al* 2018). Partitioning the variance in spatial synchrony into spatial and environmental sources provides a useful framework for identifying its drivers (Hegel *et al* 2012). Multiple regression on distance matrices (MRM) is particularly suitable for this task, as it quantifies the relative contributions of predictors while accounting for dependence (Lichstein 2007). Hitherto, it has been applied mainly to spatial synchrony in other ecological processes, such as seed production (Bogdziewicz *et al* 2021), population abundance (Walter *et al* 2021), and forest-defoliating insect outbreaks (Haynes *et al* 2013). By contrast, its application to tree growth remains scarce, which is the focus of this study.

White spruce (*Picea glauca* (Moench) Voss), a dominant boreal species ranging from Newfoundland to Alaska, plays a key role in ecosystem stability by contributing to carbon storage, soil-water conservation, and habitat provision (Nienstaedt and Zasada 1990). It also holds substantial commercial value as a timber species (Hassegawa *et al* 2020). However, it has experienced growth declines in many regions since the late 20th century, mainly driven by warming and water deficits (Hynes and Hamann 2020). Taken together, these characteristics make white spruce an ideal reference species for studying growth synchrony in boreal forests.

To address these gaps, we compiled tree-ring records from the International Tree-Ring Data Bank (ITRDB) (Zhao *et al* 2019) and Canadian Forest Service Tree-Ring Data (CFS-TRenD) (Girardin *et al* 2021). We applied complex network theory to map spatial variation in white spruce (*Picea glauca* (Moench) Voss) growth synchrony and identify regions that contributed most to the overall synchrony network. Moreover, we used MRM to disentangle the causes of growth synchrony and quantify their relative importance. This study advances understanding of white spruce growth dynamics and introduces a novel framework for investigating spatial synchrony in tree growth.

2. Materials and methods

2.1. Tree-ring data

We compiled tree-ring width records of white spruce (*Picea glauca* (Moench) Voss) from two major open-access repositories (figure 1(a)): ITRDB (www.ncei.noaa.gov/pub/data/paleo/treering/; Zhao *et al* 2019) and CFS-TRenD (https://treesource.rncan.gc.ca/en/; Girardin *et al* 2021). Sites were selected based on the following criteria: (1) the radius of each sample, calculated as the sum of annual ring widths, ranges from 5–100 cm; (2) the average ring width is less than 1 cm, with over 95% of annual values also below this threshold; (3) a minimum sample replication of five trees per site; (4) continuous annual coverage from 1901 to 1996 CE. The 1996 cut-off date reflects a compromise: it captures the period of accelerated climate change beginning in the 1980s, while ensuring sufficient data for robust analysis, as tree-ring records declined sharply thereafter (figure 1(b)). The resulting dataset includes 187 sites (164 from ITRDB, 23 from CFS-TRenD), with 6890 tree-ring series and 661 440 measured growth rings.

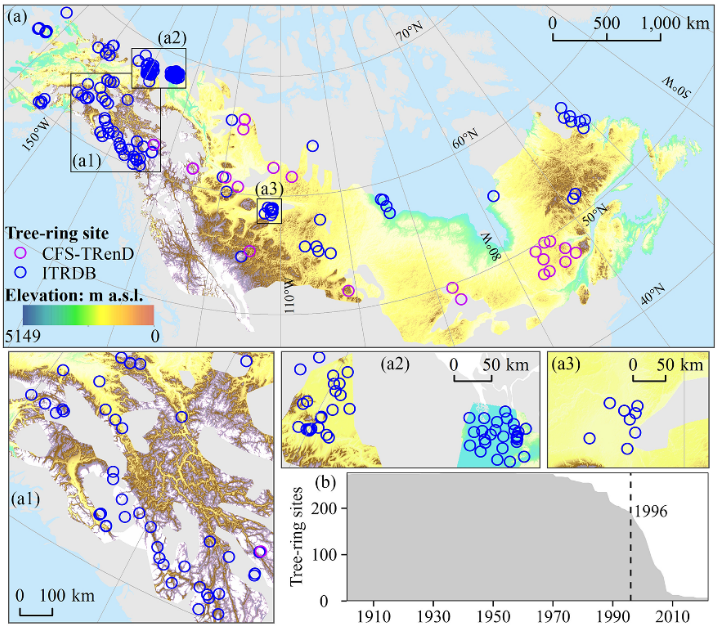

Figure 1. Spatial (a) and temporal (b) distribution of white spruce tree-ring sampling sites.

2.2. Climate data

Climate data were obtained from the CHELSAcruts dataset (Karger *et al* 2017; http://chelsa-climate.org/chelsacruts/), which provides high-resolution gridded climatic variables (∼1 km). Monthly minimum and maximum temperatures and precipitation were extracted for each tree-ring site. Seasonal mean temperature and total precipitation were then calculated for each site over the period of 1901–1996, focusing on four key periods: late winter (February–March), spring (April–May), summer (June–August), and autumn (September–November), which are known to have significant effects on white spruce growth (Griesbauer and Green 2012, Hynes and Hamann 2020).

2.3. Tree growth synchrony network

2.3.1. Tree growth chronologies

To quantify annual growth, we converted tree-ring width into basal area increment (BAI; $cm^2\ yr^{-1}$), which provides a biologically meaningful measure of wood production (LeBlanc 1993, Wu *et al* 2022). BAI is increasingly applied in dendrochronological studies as it minimizes biases introduced by data transformation and better reflects actual growth dynamics (Jiao *et al* 2015). Unlike ring width, BAI is typically less influenced by stem diameter, making it a more reliable metric for long-term growth comparisons across different tree sizes (Dial *et al* 2022). Individual BAI series were calculated from ring width measurements using the following formula, from which site-level chronologies were constructed by averaging the BAI of all sampled trees within each site:

$$\mathrm{BAI} = \pi \left(R_t^2 - R_{t-1}^2\right),$$

where R represents the tree radius at breast height (cm) for a given year, and t refers to the year in which the tree-ring was formed. BAI for individual trees was calculated using the 'bai.in()' function from R package 'dplR', and averaged into site-level BAI chronologies using Tukey's Biweight Robust Mean method (Bunn 2008).

2.3.2. Growth synchronization

Synchronous growth changes (SGC) is a non-parametric metric that quantifies growth synchrony among trees by measuring consistency in the direction of interannual changes, regardless of magnitude (Visser 2021). Unlike parametric methods, it does not assume specific data distributions, and thus avoids the need to normalize tree-ring series before comparison, preserving the integrity of the original data (Hollander *et al* 2013). Its simplicity also facilitates interpretation and reduces computational demands. SGC is an improved variant of the classical Gleichläufigkeit (GLK) index, addressing its inherent overestimation of synchrony by separating fully synchronous and semi-synchronous events (Schweingruber 1983, Buras and Wilmking 2015). This refinement makes SGC a more reliable option for applications such as clustering and dendro-provenance analysis, particularly in large dendrochronological datasets (Visser 2021). SGC was calculated as the percentage of years in which the BAI of two compared growth series showed same upward or downward trend relative to the previous year, as given by the following formula:

$$\mathrm{SGC} = \frac{n_{\mathrm{sync}}}{n_{\mathrm{ol}} - 1},$$

where n_{sync} is the number of SGCs, defined as years in which both series exhibit concurrent increases or decreases. n_{ol} denotes the number of overlapping years between series (96 years in this study). SGC coefficients were calculated with the 'sgc()' function in the 'dplR' R package (Bunn 2008, Visser 2021).

2.3.3. Construction of the tree growth synchrony network

A complex network consists of many nodes and edges, mathematically described as a graph structure $G = (V, E, W)$. Here, V represents the set of nodes, corresponding to individual tree-ring sampling sites; E is the set of edges, indicating pairwise connections between sites; and W denotes edge weights, determined by SGC coefficients quantifying growth synchrony between pairs of sites.

To detect the spatial pattern and community structures in growth synchrony, we applied a threshold filter to remove weak or spurious synchrony signals, retaining only statistically robust connections. Specifically, connections with SGC values below the significance threshold τ (set at the 0.05 level) were excluded. The resultant synchrony network structure was encoded in an adjacency matrix A, with elements defined as:

$$A_{i,j} = \begin{cases} 1 - \delta_{i,j}, & \left|\mathrm{SGC}_{i,j}\right| > \tau \\ 0, & \left|\mathrm{SGC}_{i,j}\right| \leqslant \tau \end{cases},$$

where, $\delta_{i,j}$ is the Kronecker delta, defined as $\delta_{i,j} = 0$ when $i \neq j$ and $\delta_{i,j} = 1$ otherwise. $A_{i,j} = 1$ indicates a link between site i and j, whereas $A_{i,j} = 0$ denotes the absence of a link. Synchrony network was visualized by the 'graph_from_data_frame()' function from the package 'igraph' of R (Csardi and Nepusz 2006).

2.3.4. Basic synchrony network measures

Degree centrality measures the connectivity of a node by counting the number of direct links it has with other nodes (Zhao et al 2020). In the synchrony network, higher degree centrality indicates that a site exhibits synchronous growth with more sites. For a network comprising n sites, the degree centrality D_i for site i is calculated as:

$$D_i = \sum_{j=1}^{n} \mathrm{A}_{i,j},$$

where $A_{i,j}$ is the element of the adjacency matrix. Degree centrality was computed using the 'degree()' function from R package 'igraph' (Csardi and Nepusz 2006).

Community structure refers to clusters of nodes that are densely connected internally but sparsely connected externally (Newman and Girvan 2004). Identifying these communities is essential for revealing the internal structure and functional properties of complex network (Milo et al 2002). In this study, we applied the Fast-Greedy algorithm, a widely used hierarchical method for community detection (Clauset et al 2004, Newman 2006). This algorithm follows a bottom-up detection process, initially treating each node as a singleton community and progressively merging them to optimize modularity (Kumari et al 2022). The process stops when no further aggregation can improve modularity. Community detection was performed with the 'cluster_fast_greedy()' function from the R package 'igraph' (Clauset et al 2004, Csardi and Nepusz 2006).

2.3.5. Statistical analysis of growth synchrony

To explore the association between growth synchrony and geographic distance, we employed the Mantel correlogram. This non-parametric method is particularly effective in capturing complex, non-linear spatial patterns and thus widely used to quantify how inter-site similarity varies with inter-site geographic distance (Oden and Sokal 1986, Borcard and Legendre 2012). We conducted this analysis using pre-computed pairwise growth synchrony values and corresponding geographical distances between all pairs of sites. Geographical distances were calculated as pairwise Haversine distances based on tree-ring site coordinates, using the 'distm()' function of 'geosphere' R package (Hijmans et al 2017). The resulting synchrony and distance matrices were then subjected to a Mantel test with 1000 permutations to examine the statistical significance of their correlation. This calculation was performed using the 'mgram()' function from the R package 'ecodist' (Legendre and Fortin 1989, Goslee and Urban 2007).

However, the correlogram alone cannot identify the underlying causes of growth synchrony, as it is impossible to determine the relative contributions of climate and spatial processes (Rossi *et al* 1992). To disentangle these factors, we employed MRM. It can handle diverse data types (e.g. continuous, ordinal and categorical) and support linear, nonlinear, and nonparametric relationships (Lichstein 2007, Legendre and Legendre 2012). MRM is well-suited for studying relationships between response matrix and any number of explanatory matrices, with statistical significance of each predictor and model fit assessed via permutation tests (Pandit *et al* 2016). Here, we built three models using MRM to assess the contributions of climate factors and geographic distance to growth synchrony: (1) a space-only model, using geographic proximity as the only explanatory matrix. Geographic proximity was calculated by first computing the Haversine distance d between sites, then transforming it into a similarity measure using $1 - [d/\max(d)]$. (2) A climate-only model, constructed from synchrony in temperature and precipitation variables, which are key features that may act as climatic synchronizing agents (Haynes *et al* 2013). Climate synchrony was quantified using the SGC coefficient, which reflects the directional consistency of interannual climatic fluctuations. These variables implicitly capture all time lags for key growth stages, thus not requiring explicit lag modeling. Therefore, climate variables include synchrony measures of both temperature and precipitation across four seasons, yielding 8 variables. (3) A combined model, including both climate factors and distance. All explanatory variables were standardized using the z-score method to ensure comparability. MRM analysis was performed using the 'MRM()' function of 'ecodist' R package (Legendre *et al* 1994, Goslee and Urban 2007, Lichstein 2007). Given the challenge of accounting for all relevant climatic drivers, any unmeasured factors were implicitly attributed to spatial effects (Haynes *et al* 2013, Bogdziewicz *et al* 2021).

3. Results

3.1. Spatial pattern of tree growth synchrony

Figure 2 presents a correlogram illustrating how white spruce growth synchrony varies with increasing geographic distance between sites. All instances of extremely high growth synchrony (SGC > 0.9) occurred between site pairs less than 53 km apart. The Mantel correlation coefficients (r) declined sharply at shorter distances and then leveled off beyond approximately 1100 km. Significant positive correlations were detected for the first three distance classes (up to about 700 km; $p < 0.05$), indicating that geographically proximate sites exhibited stronger synchrony in year-to-year growth variation. Beyond this distance, Mantel r gradually became negative. Significant negative correlations emerged at larger distances (947–5276 km, with $p < 0.05$; 5276 km being the maximum recorded distance between tree-ring sites in this study), albeit with very low correlation coefficients ($|r| < 0.14$). This indicates that, within this distance range, geographically closer sites tended to exhibit relative weaker synchrony in tree growth than those farther apart.

The map visualization in figure 3(a) intuitively reveals a clear biogeographical pattern in the growth synchrony of white spruce, with synchrony generally decreasing from northwest to southeast across its natural range. Using the Fast-Greedy algorithm, tree-ring sites were clustered into three distinct communities based on pairwise growth synchrony (figure 3(b)). Community A, primarily in northern Northwest Territories and Yukon, showed the highest within-community synchrony (SGC $= 0.72 \pm 0.08$ (mean $\pm$ SD), $n = 53$ sites). Community B, mostly in Alaska and northwestern Northwest Territories, exhibited moderate synchrony (0.62 ± 0.09, 74 sites). Community C, mainly in central and eastern Canada, showed the lowest synchrony (0.53 ± 0.08, 59 sites).

Additionally, in the growth synchrony network, synchrony within communities is greater than between communities (figure 3(c)). The link proportions are as follows: A–A = 92%, A–B = 15%, A–C = 4%, B–B = 53%, B–C = 3%, and C–C = 17%. By plotting each community's distribution in climate space (figure 3(d)), we found that Community A is located in areas with relatively colder and drier growing seasons compared to the other communities. Community B is found in areas with the lowest temperature and moderate precipitation, while Community C is located in areas with relatively warmer and wetter growing seasons.

3.2. Potential mechanisms driving spatial synchrony in tree growth

In the space model, we found a significant positive relationship between geographic proximity and tree growth synchrony (table 1). This model explained approximately 25% of the variance in pairwise synchrony of tree growth. In comparison, the climate model explained 55% of the variance, more than

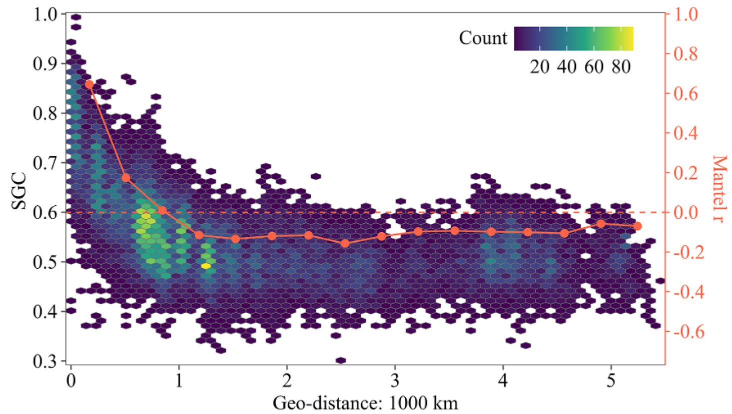

Figure 2. Relationship between growth synchrony and geographic distance across sites. The primary y-axis shows the synchronous growth changes (SGC) coefficient, and the secondary y-axis shows Mantel correlation coefficients (r). Hexagons depict the density of pairwise site comparisons with lighter colors indicating higher frequencies. Most comparisons occur at shorter distances (<1500 km), with a mean of 1737 ± 1437 km. SGC values exceeding 0.6 are considered statistically significant synchrony. The red line displays the Mantel correlogram across 20 equal-interval distance classes. Filled symbols denote significant Mantel correlations ($p < 0.05$), based on 95% bootstrap confidence intervals.

twice that of the space model. The strongest predictors of growth synchrony in the climate model, in descending order of importance, were synchrony in summer and autumn temperature, and summer precipitation. In contrast, synchrony in both autumn and spring precipitation were not significantly associated with pairwise synchrony of tree growth.

The combined model (space + climate) explained only slightly more variance in pairwise tree growth synchrony than the climate-only model (56%; table 1). Geographic proximity was the most influential explanatory variable. Among climatic variables, summer temperature synchrony remained the strongest predictor, followed by synchrony in spring temperature and summer precipitation. Synchrony in autumn temperature, and late winter, autumn and spring precipitation were not significantly related to pairwise tree growth synchrony.

4. Discussion

4.1. What are the main drivers of spatial synchrony in growth?

The study offers valuable insights into the spatial pattern of growth synchrony in white spruce and its underlying drivers. Notably, even without incorporating location or distance information in the community segmentation, tree-ring site communities still showed strong spatial clustering. Geographic proximity was positively correlated with growth synchrony, explaining about 25% of the variance. However, the relationship between growth synchrony and geographic distance in this study differs from Tobler's First Law of Geography, which states that 'near things are more related than distant things' (Tobler 1970). Instead, a non-linear distance-decay pattern emerged. Within about 700 km, growth synchrony increased as geographic distance decreased. Beyond this threshold, however, the pattern reversed, with more distant sites exhibiting relatively stronger synchrony. This complexity suggests that additional factors beyond geographic proximity shape growth synchrony.

When climate was considered alone, the explanatory power of model increased substantially to 55%, highlighting its dominant role in shaping growth synchrony. By contrast, the inclusion of geographic proximity yielded only a marginal increase (to 56%). This indicates that the observed statistical effect of proximity is largely mediated by spatially structured climate via spatial autocorrelation (Legendre and Fortin 1989). This may explain why the spatial pattern of white spruce growth synchrony deviates from a classic distance-decay relationship. Specifically, because climate synchrony decays with distance, growth synchrony arising from those fluctuations should exhibit a corresponding distance decay (Moran 1953, Koenig 2002). However, at larger scales, atmospheric circulation and teleconnection patterns can impose coherent climate anomalies across widely separated regions (Koenig 2002). When distant sites occupy the same climate domain and exhibit similar growth–climate responses, growth can also synchronize (Kug *et al* 2010). In addition, differences in the strength of climate signal in tree-ring chronologies affect growth synchrony, further complicating the synchrony-distance pattern (Fox *et al* 2011, Shestakova *et al* 2018).

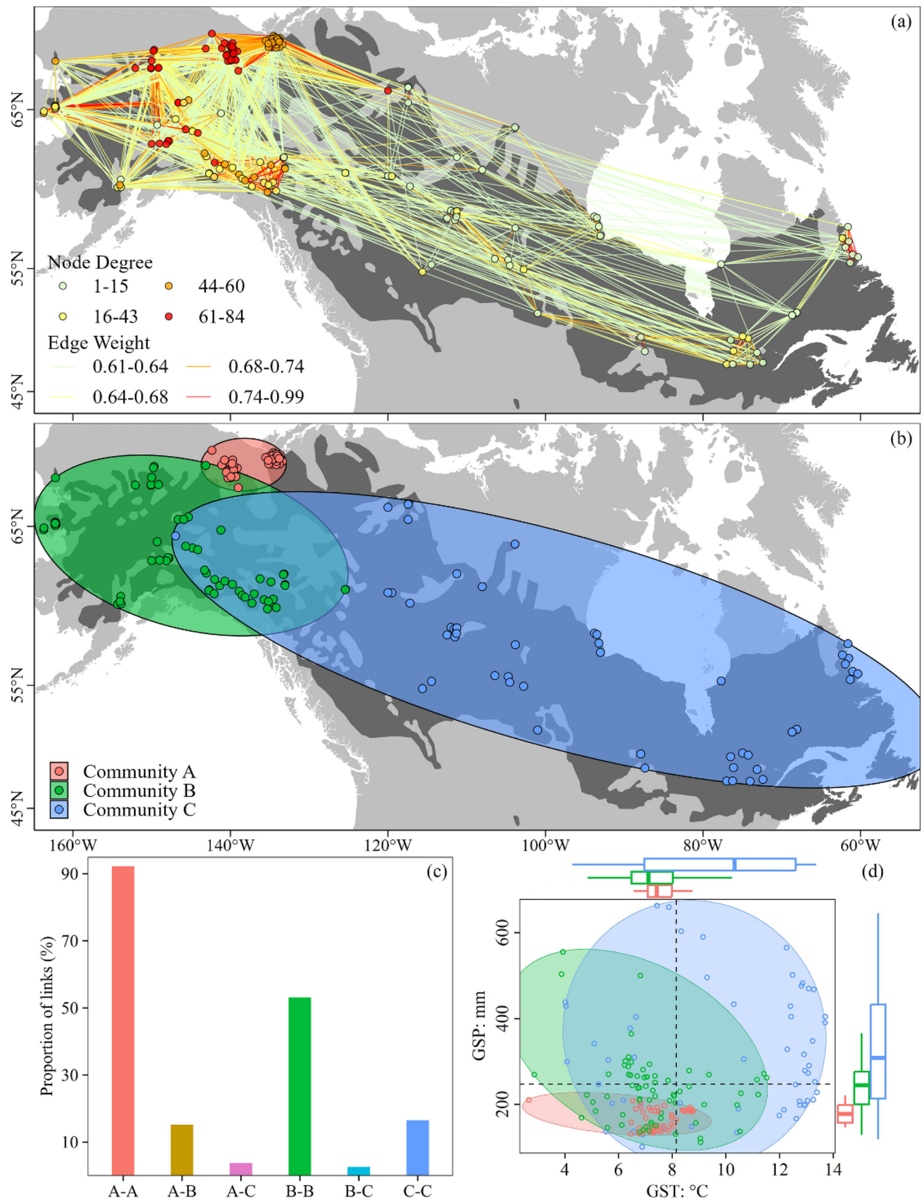

Figure 3. Growth synchrony network of white spruce. (a) Site level synchrony network, with points representing tree-ring sampling sites colored by degree centrality. Edges indicate significant pairwise synchrony ($p \leqslant 0.05$). Line color reflects the strength of synchrony, with warmer (redder) colors indicating stronger synchrony. (b) Community structure, with node colors representing community membership detected by the Fast-Greedy algorithm. (c) Probability of synchrony within and between communities. (d) Distribution of the three communities in climate space, defined by multi-year mean growing season temperature (GST) and precipitation (GSP), with colors corresponding to the communities (A–C) from the panel (b).

Notably, in the combined model, geographic proximity remained significant but showed a negative effect after accounting for climate synchrony. This result contradicts the expectation under dispersal-driven mechanisms, which predict stronger synchrony among nearby populations due to shared biotic pressures. Biotic processes like mast seeding and spruce budworm outbreaks are often considered as potential dispersal-related drivers of growth synchrony (Volney and Fleming 2000, Tumajer and Lehejček 2019). However, empirical evidence shows that their spatial synchrony is more strongly linked to broad-scale climatic variation than to dispersal per se (Peltonen *et al* 2002, LaMontagne *et al* 2020). Therefore, although the role of dispersal cannot be entirely excluded, the available evidence indicates that it is insufficient to explain the negative effect of proximity observed here. Geographically closer sites may occupy contrasting environments, such as coastal/interior or upland/lowland forests, resulting in divergent growth-climate coupling (Nicklen *et al* 2019). Similarly, stands with distinct disturbance histories (e.g. fire or insect outbreaks) may differ in stand structure and sensitivity to climate variation (Yang *et al* 2022). In such cases, populations experiencing similar environmental fluctuations may show low or even negative growth synchrony. By contrast, distant sites may share similar constraints and disturbance

Table 1. Multiple regression on distance matrices (MRM) tests for geographic proximity and climate synchrony affecting pairwise growth synchrony of white spruce.

Variable		Coefficient	R^2	Variable		Coefficient	R^2
Space-only model			0.25^{***}	Space + Climate model			0.56^{***}
Geographic proximity		0.25^{***}					
Climate-only model			0.55^{***}	Geographic proximity		-0.4^{***}	
Late winter	Precipitation	0.1^{***}		Late winter	Precipitation	0.05	
	Temperature	0.15^{***}			Temperature	0.19^{***}	
Spring	Precipitation	-0.01		Spring	Precipitation	0.03	
	Temperature	0.19^{***}			Temperature	0.28^{***}	
Summer	Precipitation	0.22^{***}		Summer	Precipitation	0.19^{***}	
	Temperature	0.44^{***}			Temperature	0.35^{***}	
Autumn	Precipitation	0.02		Autumn	Precipitation	0.03	
	Temperature	-0.28^{***}			Temperature	0.08	

Note: Coefficients are standardized to allow direct comparison between variables. Late winter: February–March, spring: April–May, summer: June-August, and autumn: September–November.

regimes, resulting in stronger synchrony (Shestakova *et al* 2016). As such, we speculate that the negative distance effect most likely reflects the combined influence of unmeasured environmental heterogeneity, disturbance legacies and dispersal-related processes.

Instead, our results highlight synchronized climate as the dominant synchronizing force across spatial scales. This finding align with previous studies (e.g. Haynes *et al* 2013), which emphasize that a climate synchronizing agent must fluctuate synchronously. In the 20th century, temperature was the primary control on boreal forest growth, affecting key physiological processes through both direct mechanisms (e.g. photosynthesis) and indirect pathways (e.g. soil thaw timing) (Fritts 2012, Babst *et al* 2019). Specifically, fluctuations in late winter temperature can affect frost hardiness and soil thaw timing, both critical for early-season water availability and the onset of growth (Makoto *et al* 2014, Dial *et al* 2022). Likewise, spring temperature synchrony likely promotes a more uniform onset of growth processes, such as budburst and cambial activity, leading to synchronized growth (Casmey *et al* 2022, Zhang *et al* 2024). Summer temperature synchrony is particularly influential, likely due to two reasons. Summer temperature strongly affects wood formation by key physiological processes, like carbon assimilation (Barber *et al* 2004). On the other hand, summer spans most of the growing season for white spruce, during which the majority of wood formation occurs (Zhang *et al* 2020). Additionally, synchronized summer precipitation also plays a key role in growth synchrony by mitigating drought stress and ensuring water availability during key growth phases.

4.2. Ecological implications

The growth synchrony network graph revealed that white spruce growth synchrony decreased from northwest to southeast. Specifically, we found that white spruce in northern Northwest Territories and Yukon showed highly synchronized growth patterns. Previous studies have shown that asynchronous growth within a species can enhance forest resilience to disturbances by reducing the likelihood of widespread decline during adverse conditions (Jia *et al* 2024, Li and He 2025). In contrast, high synchrony increases the risk of collective stress during 'bad years', making forests more vulnerable to climatic extremes (Dakos *et al* 2010). As such, management efforts in regions with high growth synchrony should prioritize fostering asynchronous growth.

Practical measures to enhance asynchrony should focus on increasing structural and compositional diversity within white spruce forests. Uneven-aged management is one effective strategy, as it promotes stand heterogeneity while reducing tree mortality and enhancing carbon sequestration by more efficient light use (Lafond *et al* 2014). Mixed-species planting can diversify climate sensitivities and expand ecological niches, thereby supporting higher biodiversity (Heidrich *et al* 2020). Furthermore, applying thinning and pollarding to individual trees can help reduce growth synchrony by alleviating inter-individual competition and promoting greater structural complexity (Sjölund and Jump 2013). The effectiveness of these measures, however, will depend on local site conditions, including species composition and existing management systems. Importantly, excessive desynchronization is not ecologically beneficial. Thus, achieving a balance between growth synchrony and response diversity is essential for maintaining the long-term health and functioning of forest ecosystems (Zhu *et al* 2025).

4.3. Limitations and future directions

We acknowledge several limitations in this study. First, tree-ring samples from the ITRDB were not strictly follow a random selection process (Zhao *et al* 2019). Since tree-ring research has historically focused on climate reconstruction and growth-climate correlations, the ITRDB samples predominantly derived from large trees in ecologically marginal areas, aimed at maximizing the climatic signal in tree-ring data (Fritts 2012). As a result, these tree-ring series may be more sensitive to climate than randomly selected trees (Klesse *et al* 2018), which could affect the generalization of our results, particularly when scaling local observations to broader geographical ranges. To mitigate the impact of 'big-tree selection', we applied the SGC coefficient to assess growth synchrony, which quantifies the directional consistency of interannual fluctuations, regardless of variation magnitude. Moreover, statistical analysis showed that the age distribution of trees in this study typically exhibited a slight positive skew (mean skewness = 0.12, median skewness = 0.14), suggesting that bias from tree size selection is unlikely to influence our conclusions. Furthermore, the strong synchrony observed among populations from distinct climate conditions and elevations implies that sampling biases related to tree size may be much smaller than other ecological factors. Nevertheless, it is still necessary to determine whether ITRDB data may overestimate or underestimate spatial synchrony in growth using a larger and more comprehensive dataset.

Another limitation is the uneven spatial distribution of sampling sites, with low density in central and eastern Canada. (i) Under-sampled regions contribute fewer short-distance pairs, typically more synchronized, which may amplify the northwest-southeast contrast without altering the declining gradient. (ii) Synchrony at a given distance varies regionally due to climatic heterogeneity. Uneven sampling may alter the weighting of pairs within distance bins, potentially shifting the synchrony-distance curve and its inflection point. Nevertheless, this does not change the overall distance-dependent pattern. (iii) As climate synchrony and growth-climate coupling vary across regions (Koenig 2002, Babst *et al* 2019), uneven sampling may affect climate's contribution in models. However, incorporating geographic proximity only slightly improves model fit, confirming the dominant role of climate despite uneven sampling. Future studies should focus on increasing spatial saturation to reduce sampling-related artefacts.

Finally, our study focused on the spatial patterns of growth synchrony and their underlying drivers, without addressing temporal dynamics. Assessing potential temporal changes in synchrony, especially in recent decades of accelerated climate change, is an important research priority. Such evaluation would require larger and more up-to-date datasets, and we consider this a valuable direction for future research.

5. Conclusions

This study advances our understanding of growth synchrony in white spruce across Canada and Alaska by identifying its key spatial pattern and the underlying drivers. We observed a distinct biogeographical gradient in growth synchrony, with synchrony decreasing from northwest to southeast across its range. The relationship between growth synchrony and geographic proximity was non-linear, with synchrony increasing at shorter distances but reversing at larger distances, deviating from the typical distance-decay pattern. Our results suggest that synchronized climate, particularly temperature, played a dominant role in shaping white spruce growth synchrony, while the influence of geographic proximity became minimal after accounting for climate effects. These results highlight the need of incorporating climatic synchronization when simulating and predicting tree growth synchrony dynamics.

Our findings have significant implications for forest management. Specifically, regions with highly synchronized growth, particularly in the northern Northwest Territories and Yukon, should be prioritized in management efforts to maintain the long-term stability and resilience of white spruce populations. In such regions, strategies that enhance structural and compositional diversity (e.g. uneven-aged management, mixed-species planting, thinning, and pollarding) can help reduce growth synchrony and thereby mitigate the risk of widespread synchronous declines. Additionally, future work should focus on expanding tree-ring samples to create a more extensive dataset and incorporating more detailed environmental and biotic observations. Such efforts will deepen our understanding of the mechanisms driving spatial synchrony in tree growth and provide more valuable insights for developing effective forest management strategies in response to climate change.

Data availability statement

All data used in this study from publicly accessible data sources. Tree-ring measurements were obtained from the CFS-TRenD (https://treesource.rncan.gc.ca/en/; Girardin *et al* 2021) and ITRDB (www.ncei.noaa.gov/pub/data/paleo/treering/; Zhao *et al* 2019). Climate datasets were obtained from the CHELSAcruts dataset (http://chelsa-climate.org/chelsacruts/).

Funding

This work was supported by the Supported by the National Natural Science Foundation of China (42301070), China Postdoctoral Science Foundation (2023M740287), and the Postdoctoral Fellowship Program of CPSF (GZB20230072).

Conflict of interest

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

Author contributions

Fang Wu 0009-0009-7367-6937
Conceptualization (equal), Methodology (lead), Writing – original draft (lead)

Junwen Jia 0000-0001-6334-1150
Validation (equal), Writing – review & editing (equal)

Cheng Li
Writing – review & editing (equal)

Xuefeng Cui 0000-0002-9617-072X
Conceptualization (equal), Project administration (lead), Writing – review & editing (lead)

References

Astigarraga J, Calatayud J, Ruiz-Benito P, Madrigal-González J, Tijerín-Triviño J, Zavala M A, Andivia E and Herrero A 2025 Forest structural diversity modulates tree growth synchrony in response to climate change *For. Ecol. Manage.* **579** 122505

Babst F, Bouriaud O, Poulter B, Trouet V, Girardin M P and Frank D C 2019 Twentieth century redistribution in climatic drivers of global tree growth *Sci. Adv.* **5** eaat4313

Barber V A, Juday G P, Finney B P and Wilmking M 2004 Reconstruction of summer temperatures in Interior Alaska from tree-ring proxies: evidence for changing synoptic climate regimes *Clim. Change* **63** 91–120

Bogdziewicz M, Hacket-Pain A, Ascoli D and Szymkowiak J 2021 Environmental variation drives continental-scale synchrony of European beech reproduction *Ecology* **102** e03384

Borcard D and Legendre P 2012 Is the Mantel correlogram powerful enough to be useful in ecological analysis? A simulation study *Ecology* **93** 1473–81

Bouchard M, Régnière J and Therrien P 2018 Bottom-up factors contribute to large-scale synchrony in spruce budworm populations *Can. J. For. Res.* **48** 277–84

Bunn A G 2008 A dendrochronology program library in R (dplR) *Dendrochronologia* **26** 115–24

Buras A and Wilmking M 2015 Correcting the calculation of Gleichläufigkeit *Dendrochronologia* **34** 29–30

Cailleret M *et al* 2019 Early-warning signals of individual tree mortality based on annual radial growth *Front. Plant Sci.* **9** 1964

Casmey M, Hamann A and Hacke U G 2022 Adaptation of white spruce to climatic risk environments in spring: implications for assisted migration *For. Ecol. Manage.* **525** 120555

Clauset A, Newman M E J and Moore C 2004 Finding community structure in very large networks *Phys. Rev. E* **70** 066111

Csardi G and Nepusz T 2006 The igraph software package for complex network research *InterJ. Complex Syst.* **1695** 1–9

Dakos V, van Nes E H, Donangelo R, Fort H and Scheffer M 2010 Spatial correlation as leading indicator of catastrophic shifts *Theor. Ecol.* **3** 163–74

Dial R J, Maher C T, Hewitt R E and Sullivan P F 2022 Sufficient conditions for rapid range expansion of a boreal conifer *Nature* **608** 546–51

Fox J W, Vasseur D A, Hausch S and Roberts J 2011 Phase locking, the Moran effect and distance decay of synchrony: experimental tests in a model system *Ecol. Lett.* **14** 163–8

Fritts H 2012 *Tree Rings and Climate* (Elsevier)

Gauthier S, Bernier P, Kuuluvainen T, Shvidenko A Z and Schepaschenko D G 2015 Boreal forest health and global change *Science* **349** 819–22

Girardin M P *et al* 2021 A national tree-ring data repository for Canadian forests (CFS-TRenD): structure, synthesis, and applications *Environ. Rev.* **29** 225–41

Goslee S C and Urban D L 2007 The ecodist package for dissimilarity-based analysis of ecological data *J. Stat. Softw.* **22** 1–19

Griesbauer H P and Green D S 2012 Geographic and temporal patterns in white spruce climate-growth relationships in Yukon, Canada *For. Ecol. Manage.* **267** 215–27

Hassegawa M, Savard M, Lenz P R N, Duchateau E, Gélinas N, Bousquet J and Achim A 2020 White spruce wood quality for lumber products: priority traits and their enhancement through tree improvement *Forestry: Int. J. For. Res.* **93** 16–37
Haynes K J, Bjørnstad O N, Allstadt A J and Liebhold A M 2013 Geographical variation in the spatial synchrony of a forest-defoliating insect: isolation of environmental and spatial drivers *Proc. R. Soc. B* **280** 20122373
Hegel T M, Verbyla D, Huettmann F and Barboza P S 2012 Spatial synchrony of recruitment in mountain-dwelling woodland caribou *Popul. Ecol.* **54** 19–30
Heidrich L *et al* 2020 Heterogeneity-diversity relationships differ between and within trophic levels in temperate forests *Nat. Ecol. Evol.* **4** 1204–12
Heino M 1998 Noise colour, synchrony and extinctions in spatially structured populations *Oikos* **83** 368–75
Hijmans R J, Williams E, Vennes C and Hijmans M R 2017 Package 'geosphere' *Spherical Trigonometry* **1** 1–45
Hollander M *et al* 2013 *Nonparametric Statistical Methods* (Wiley)
Hynes A and Hamann A 2020 Moisture deficits limit growth of white spruce in the west-central boreal forest of North America *For. Ecol. Manage.* **461** 117944
Jia H, Zheng J, Fang O, Yang J, Langzhen J-Y, Hebda R J and Zhang Q-B 2024 De-synchronization in tree growth is a strategy for maintaining forest resilience *Agric. For. Meteorol.* **359** 110292
Jiao L, Jiang Y, Zhang W-T, Wang M-C, Zhang L-N and Zhao S-D 2015 Divergent responses to climate factors in the radial growth of *Larix sibirica* in the eastern Tianshan mountains, northwest China *Trees* **29** 1673–86
Karger D N *et al* 2017 Climatologies at high resolution for the earth's land surface areas *Sci. Data* **4** 170122
Klesse S, DeRose R J, Guiterman C H, Lynch A M, O'Connor C D, Shaw J D and Evans M E K 2018 Sampling bias overestimates climate change impacts on forest growth in the southwestern United States *Nat. Commun.* **9** 5336
Koenig W D 2002 Global patterns of environmental synchrony and the Moran effect *Ecography* **25** 283–8
Kug J-S, An S-I, Ham Y-G and Kang I-S 2010 Changes in El Niño and La Niña teleconnections over North Pacific-America in the global warming simulations *Theor. Appl. Climatol.* **100** 275–82
Kumari A, Behera R K, Sahoo B and Sahoo S P 2022 Prediction of link evolution using community detection in social network *Computing* **104** 1077–98
Lafond V, Lagarrigues G, Cordonnier T and Courbaud B 2014 Uneven-aged management options to promote forest resilience for climate change adaptation: effects of group selection and harvesting intensity *Ann. For. Sci.* **71** 173–86
LaMontagne J M, Pearse I S, Greene D F and Koenig W D 2020 Mast seeding patterns are asynchronous at a continental scale *Nat. Plants* **6** 460–5
LeBlanc D C 1993 Temporal and spatial variation of oak growth-climate relationships along a pollution gradient in the midwestern United States *Can. J. For. Res.* **23** 772–82
Legendre P and Fortin M J 1989 Spatial pattern and ecological analysis *Vegetatio* **80** 107–38
Legendre P, Lapointe F-J and Casgrain P 1994 Modeling brain evolution from behavior: a permutational regression approach *Evolution* **48** 1487–99
Legendre P and Legendre L 2012 *Numerical Ecology* (Elsevier)
Li J and He F 2025 Individual asynchrony promotes population-level tree growth stability *J. Ecol.* **113** 753–62
Lichstein J W 2007 Multiple regression on distance matrices: a multivariate spatial analysis tool *Plant Ecol.* **188** 117–31
Liebhold A, Koenig W D and Bjørnstad O N 2004 Spatial synchrony in population dynamics *Annu. Rev. Ecol. Evol. Syst.* **35** 467–90
Makoto K, Kajimoto T, Koyama L, Kudo G, Shibata H, Yanai Y and Cornelissen J H C 2014 Winter climate change in plant-soil systems: summary of recent findings and future perspectives *Ecol. Res.* **29** 593–606
McDowell N G *et al* 2020 Pervasive shifts in forest dynamics in a changing world *Science* **368** eaaz9463
Milo R, Shen-Orr S, Itzkovitz S, Kashtan N, Chklovskii D and Alon U 2002 Network motifs: simple building blocks of complex networks *Science* **298** 824–7
Moran P A 1953 The statistical analysis of the Canadian lynx cycle *Aust. J. Zool.* **1** 291–8
Newman M E J 2006 Modularity and community structure in networks *Proc. Natl Acad. Sci.* **103** 8577–82
Newman M E J and Girvan M 2004 Finding and evaluating community structure in networks *Phys. Rev. E* **69** 026113
Nicklen E F, Roland C A, Csank A Z, Wilmking M, Ruess R W and Muldoon L A 2019 Stand basal area and solar radiation amplify white spruce climate sensitivity in interior Alaska: evidence from carbon isotopes and tree rings *Glob. Change Biol.* **25** 911–26
Nienstaedt H and Zasada J C 1990 Picea glauca (Moench) Voss. white spruce *Silvics of North America: Conifers* (US Department of Agriculture, Forest Service) 204–26
Oden N L and Sokal R R 1986 Directional autocorrelation: an extension of spatial correlograms to two dimensions *Syst. Zool.* **35** 608–17
Pan Y *et al* 2011 A large and persistent carbon sink in the world's forests *Science* **333** 988–93
Pandit S N, Cottenie K, Enders E C and Kolasa J 2016 The role of local and regional processes on population synchrony along the gradients of habitat specialization *Ecosphere* **7** e01217
Peltonen M, Liebhold A M, Bjørnstad O N and Williams D W 2002 Spatial synchrony in forest insect outbreaks: roles of regional stochasticity and dispersal *Ecology* **83** 3120–9
Phillips J D 2019 State factor network analysis of ecosystem response to climate change *Ecol. Complex* **40** 100789
Post E *et al* 2019 The polar regions in a 2 °C warmer world *Sci. Adv.* **5** eaaw9883
Qiao T, Shan W, Zhang M and Liu C 2019 How to facilitate knowledge diffusion in complex networks: the roles of network structure, knowledge role distribution and selection rule *Int. J. Inf. Manage.* **47** 152–67
Reuman D C *et al* 2025 Insights into spatial synchrony enabled by long-term data *Ecol. Lett.* **28** e70112
Rossi R E, Mulla D J, Journel A G and Franz E H 1992 Geostatistical tools for modeling and interpreting ecological spatial dependence *Ecol. Monogr.* **62** 277–314
Schweingruber F H 1983 *Der Jahrring. Standort, Methodik, Zeit und Klima in der Dendrochronologie* (Verlag Paul Haupt)
Shestakova T A *et al* 2016 Forests synchronize their growth in contrasting Eurasian regions in response to climate warming *Proc. Natl Acad. Sci.* **113** 662–7
Shestakova T A, Gutiérrez E and Voltas J 2018 A roadmap to disentangling ecogeographical patterns of spatial synchrony in dendrosciences *Trees-Struct. Funct.* **32** 359–70
Sjölund M J and Jump A S 2013 The benefits and hazards of exploiting vegetative regeneration for forest conservation management in a warming world *Forestry* **86** 503–13
Tejedor E *et al* 2020 A global perspective on the climate-driven growth synchrony of neighbouring trees *Glob. Ecol. Biogeogr.* **29** 1114–25
Tobler W R 1970 A computer movie simulating urban growth in the Detroit region *Econ. Geogr.* **46** 234–40

Tumajer J and Lehejček J 2019 Boreal tree-rings are influenced by temperature up to two years prior to their formation: a trade-off between growth and reproduction? *Environ. Res. Lett.* **14** 124024

Visser R M 2021 On the similarity of tree-ring patterns: assessing the influence of semi-synchronous growth changes on the Gleichläufigkeitskoeffizient for big tree-ring data sets *Archaeometry* **63** 204–15

Volney W J A and Fleming R A 2000 Climate change and impacts of boreal forest insects *Agric. Ecosyst. Environ.* **82** 283–94

Walter J A, Hallett L M, Sheppard L W, Anderson T L, Zhao L, Hobbs R J, Suding K N and Reuman D C 2021 Micro-scale geography of synchrony in a serpentine plant community *J. Ecol.* **109** 750–62

Walter J A, Sheppard L W, Anderson T L, Kastens J H, Bjørnstad O N, Liebhold A M and Reuman D C 2017 The geography of spatial synchrony *Ecol. Lett.* **20** 801–14

Wu C, Chen D, Sun X and Zhang S 2022 Contributions of competition on *Larix kaempferi* tree-ring growth were higher than long-term climate in China *Agric. For. Meteorol.* **320** 108967

Yang J, Zhang Q and Hao S 2022 Effects of fire disturbance on *Larix gmelinii* growth-climate relationship *Ecol. Indic.* **143** 109377

Zhang S, Belien E, Ren H, Rossi S and Huang J G 2020 Wood anatomy of boreal species in a warming world: a review *IForest-Biogeosci. For.* **13** 130

Zhang Y *et al* 2024 High preseason temperature variability drives convergence of xylem phenology in the Northern Hemisphere conifers *Curr. Biol.* **34** 1161–7

Zhao J, Wang Y and Deng Y 2020 Identifying influential nodes in complex networks from global perspective *Chaos Solitons Fractals* **133** 109637

Zhao S, Pederson N, D'Orangeville L, HilleRisLambers J, Boose E, Penone C, Bauer B, Jiang Y and Manzanedo R 2019 The international tree-ring data bank (ITRDB) revisited: data availability and global ecological representativity *J. Biogeogr.* **46** 355–68

Zhu L, Yuan D, Camarero J J, Cooper D J, Li M-H, Liu S, Wang X and Cherubini P 2025 Rapid escalation and release of risks to forest ecosystems triggered by warming: insights from tree growth synchrony in temperate forests *For. Ecosyst.* **13** 100336