

Biome-scale heterogeneity in Scots pine drought resilience across Eurasia

Edurne Martinez del Castillo

`emdc85@gmail.com`

Johannes Gutenberg University Mainz <https://orcid.org/0000-0003-1542-2698>

Max Torbenson

Texas A&M University <https://orcid.org/0000-0003-2720-2238>

Frederick Reinig

Johannes Gutenberg University <https://orcid.org/0000-0001-6839-8340>

Emanuele Ziaco

Johannes Gutenberg University Mainz <https://orcid.org/0000-0002-0459-6927>

Roberto Serrano-Notivoli

University of Zaragoza <https://orcid.org/0000-0001-7663-1202>

Weipeng Yue

Yunnan University <https://orcid.org/0000-0001-8785-6431>

Miroslav Svoboda

Czech University of Life Sciences <https://orcid.org/0000-0003-4050-3422>

Alberto Arzac

Siberian Federal University. <https://orcid.org/0000-0002-3361-5349>

Vaclav Trembl

Charles University, Faculty of Science <https://orcid.org/0000-0001-5067-3308>

Ernst van der Maaten

TU Dresden <https://orcid.org/0000-0002-5218-6682>

Jiří Mašek

Charles University

Adomas Vitas

The State Scientific Research Institute Nature Research Centre

Marieke van der Maaten-Theunissen

Chair of Forest Growth and Woody Biomass Production, TU Dresden <https://orcid.org/0000-0002-2942-9180>

Martin Wilmking

University of Greifswald <https://orcid.org/0000-0003-4964-2402>

Andrei Popa

National Institute for Research and Development in Forestry “Marin Drăcea” <https://orcid.org/0000-0003-3953-0060>

Ionel Popa

National Institute for Research and Development in Forestry “Marin Drăcea” <https://orcid.org/0000-0003-0069-0905>

Juliane Stolz

Chair of Forest Growth and Woody Biomass Production, TU Dresden

Marcin Klisz

Dendrolab IBL, Department of Silviculture and Forest Tree Genetics, Forest Research Institute
<https://orcid.org/0000-0001-9486-6988>

Martin de Luis

University of Zaragoza <https://orcid.org/0000-0002-7585-3636>

Ernesto Tejedor

National Museum of Natural Sciences-Spanish National Research Council <https://orcid.org/0000-0001-6825-3870>

Jan Tumajer

Department of Physical Geography and Geoecology, Faculty of Science, Charles University
<https://orcid.org/0000-0002-7773-7081>

Jelena Lange

Department of Physical Geography and Geoecology, Charles University <https://orcid.org/0000-0002-7872-6667>

Alexander Kirdyanov

V.N. Sukachev Institute of Forest SB RAS, Federal Research Center <https://orcid.org/0000-0002-6797-4964>

Marcin Jakubowski

Poznań University of Life Sciences <https://orcid.org/0000-0001-6701-1482>

Jan Krejza

Global Change Research Institute of the Czech Academy of Sciences <https://orcid.org/0000-0003-2475-2111>

Sergei Mikhailov

Global Change Research Institute, Czech Academy of Sciences <https://orcid.org/0000-0002-5901-9174>

Petr Horáček

Mendel University in Brno

Maris Hordo

Estonian University of Life Sciences <https://orcid.org/0000-0002-0824-7636>

Vladimir Shishov

Siberian Federal University <https://orcid.org/0000-0001-8850-6142>

Jernej Jevšenak

Slovenian Forestry Institute <https://orcid.org/0000-0002-4811-3624>

Antonio Gazol

Instituto Pirenaico de Ecología (IPE-CSIC)

Jesús Julio Camarero

IPE (CSIC) <https://orcid.org/0000-0003-2436-2922>

Jan Esper

Johannes Gutenberg University <https://orcid.org/0000-0003-3919-014X>

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Biome-scale heterogeneity in Scots pine drought resilience across Eurasia

Edurne Martinez del Castillo ^{1*}, Max C.A. Torbenson ^{1,2}, Frederick Reinig ¹, Emanuele Ziaco ¹, Roberto Serrano-Notivoli ³, Weipeng Yue ^{4,1}, Miroslav Svoboda ⁵, Alberto Arzac ⁶, Václav Trembl ⁷, Ernst van der Maaten ⁸, Jiří Mašek ⁷, Adomas Vitas ⁹, Marieke van der Maaten-Theunissen ⁸, Martin Wilmking ¹⁰, Andrei Popa ^{11,12}, Ionel Popa ^{11,13}, Juliane Stolz ⁸, Marcin Klisz ¹⁴, Martin de Luis ³, Ernesto Tejedor ¹⁵, Jan Tumajer ⁷, Jelena Lange ^{7,10}, Alexander V. Kirdyanov ^{6,16}, Marcin Jakubowski ¹⁷, Jan Krejza ^{2,18}, Sergei Mikhailov ², Petr Horáček ², Maris Hordo ¹⁹, Vladimir Shishov ⁶, Jernej Jevšenak ²⁰, Antonio Gazol ²¹, J. Julio Camarero ²¹, Jan Esper ^{1,2}

1 Department of Geography, Johannes Gutenberg University. Mainz, Germany

2 Global Change Research Institute of the Czech Academy of Sciences (CzechGlobe). Brno, Czech Republic

3 Departamento de Geografía y Ordenación del Territorio, Instituto Universitario de Ciencias Ambientales (IUCA), Universidad de Zaragoza. Zaragoza, Spain

4 Yunnan Key Laboratory of International Rivers and Transboundary Eco-Security, Institute of International Rivers and Eco-Security, Yunnan University. Kunming, China

5 Department of Forest Ecology, Czech University of Life Sciences. Prague, Czech Republic

6 Siberian Federal University. Krasnoyarsk, Russia.

7 Department of Physical Geography and Geocology, Faculty of Science, Charles University. Prague, Czech Republic

8 Chair of Forest Growth and Woody Biomass Production, TU Dresden. Dresden, Germany

9 The State Scientific Research Institute Nature Research Centre. Vilnius, Lithuania

10 DendroGreif, Working Group Landscape Ecology and Ecosystem Dynamics, University Greifswald. Greifswald, Germany

11 National Institute for Research and Development in Forestry “Marin Drăcea”. Bucharest, Romania

12 Faculty of Silviculture and Forest Engineering, Transilvania University of Brasov. Brasov, Romania

13 Center for Mountain Economy (CE-MONT). Vatra Dornei, Romania

14 Dendrolab IBL, Department of Silviculture and Genetics, Forest Research Institute. Sekocin Stary, Poland

15 Department of Geology, National Museum of Natural Sciences-Spanish National Research Council (MNCN-CSIC). Madrid, Spain

16 V.N. Sukachev Institute of Forest SB RAS, Federal Research Center “Krasnoyarsk Science Center SB RAS”. Krasnoyarsk, Russia

17 Poznań University of Life Sciences, Faculty of Forest and Wood Technology, Department of Forest Utilisation. Poznań, Poland

18 Department of Forest Ecology, Faculty of Forestry and Wood Technology, Mendel University in Brno. Brno, Czech Republic

19 Estonian University of Life Sciences, Institute of Forestry and Engineering, Chair of Forest Management and Wood Processing Technologies. Tartu, Estonia

20 Slovenian Forestry Institute, Department for Forest and Landscape Planning and Monitoring. Ljubljana, Slovenia

21 Instituto Pirenaico de Ecología (IPE-CSIC). Zaragoza, Spain

*Corresponding author: emdc85@gmail.com

46 **Abstract**

47 The stability of global forest ecosystems is challenged by the accelerated pace of climate change,
48 raising questions about their role as future carbon reservoirs. Intensifying drought events affect
49 forest productivity and dieback at regional scales, yet how drought sensitivity and resilience
50 components vary across the full distribution of widespread tree species remains insufficiently
51 quantified. Here, we compile a pan-Eurasian network of 534 *Pinus sylvestris* tree-ring
52 chronologies spanning the species' full ecological range and quantify growth departures and
53 resilience components during the most extreme summer droughts of the past century. Drought
54 impacts diverge systematically along major climatic gradients. Growth reductions exceed 70% in
55 cold-dry and warm semi-humid regions, while cool-humid forests show muted and even positive
56 departures. Resistance is lowest under prolonged droughts in continental cold-dry interiors and
57 under short summer droughts in semi-humid lowlands, while recovery capacity is highest where
58 growth losses are most severe, reflecting local adaptations in drier regions. Despite coherent
59 biome-scale patterns, substantial site-level variability indicates that growth legacies often persist
60 beyond the event year. Nonlinear models show that resilience-climate relationships are shaped not
61 only by mean climate conditions, but also by atmospheric water demand, site-level water balance,
62 and thermal stability across climatic domains. Together, these results provide a range-wide
63 assessment of drought impacts, demonstrating how prevailing climate conditions modulates forest
64 stability and carbon sequestration capacity under intensifying climate extremes.

65 **Introduction**

66 Forests are increasingly impacted by climate extremes, with drought emerging as one of the most
67 pervasive and damaging drivers of growth decline, dieback, and mortality worldwide ¹⁻⁴. These
68 processes are critical as forest biomes constitute the main terrestrial carbon sink and strongly
69 influence climate-carbon feedbacks ⁵. Short-term deviations from this path may lead to long-
70 lasting effects in climate change mitigation estimates ⁶, threatening national and global pathways
71 towards net-zero emission goals ⁷.

72 Consequently, anticipating future forest stability under climate change and extreme events takes
73 center stage. This task requires an inter-regional understanding of how trees across large climatic
74 gradients respond to extreme dry conditions. However, large uncertainties persist as these
75 responses are mediated by spatially varying and interacting climatic, ecological, and physiological
76 processes ⁸⁻¹¹. Tree rings uniquely capture both immediate growth reductions and post-drought
77 recovery trajectories ¹², enabling the reconstruction of resilience and the quantification of drought
78 legacies over time. While numerous dendroecological studies have documented the vulnerability
79 of single species and populations at regional scales ¹³⁻¹⁷, it remains unclear whether drought
80 responses and resilience components follow consistent, climatically structured patterns across the
81 full distribution of widespread species, or where the strongest departures from historical growth-
82 climate relationships occur. Addressing this gap is critical for forecasting forest dynamics and
83 stability under intensifying drought extremes.

84 Large-scale tree-ring networks provide an opportunity to move beyond site-specific studies by
85 examining how drought sensitivity and resilience vary across climate gradients and continents ¹⁸⁻
86 ²¹. Such network approaches have demonstrated that climate-growth relationships are often
87 nonlinear, exhibiting threshold responses, asymmetric sensitivities, or shifts in limiting factors

along climatic gradients^{22–24}. For example, growth responses may change sign across moisture or temperature gradients, or display saturating or unimodal patterns that are not captured by linear correlations²³. These findings suggest that drought impacts and resilience responses may likewise vary nonlinearly across climatic space, although this possibility has not been evaluated at the scale of an entire species distribution. Consequently, distribution-wide evaluations of a single species are still lacking, leaving unresolved to what extent resilience components are associated with mean climate and how strongly these relationships depend on local conditions.

Scots pine (*Pinus sylvestris* L.) is one of the most widely distributed conifer throughout the Northern Hemisphere, extending from the Mediterranean Basin to the Arctic and from maritime sites to continental interiors²⁵. It dominates vast forested areas and is both ecologically and economically critical, occupying an exceptional range of climatic conditions²⁶. However, its response to climate varies markedly across its range, reflecting strong climatic, ecological, and physiological gradients. Some populations exhibit strong vulnerability and growth decline under water stress^{14,27}, whereas others maintain resistance or rapid recovery, suggesting tolerance in specific environments^{15,28}. The species also displays marked spatial variation in climate sensitivity^{23,29,30}, high phenotypic plasticity³¹ and contrasting productivity trends and projections across its distribution^{32–34}.

Here, we use a trans-Eurasian network of 534 tree-ring chronologies, comprising more than 14,500 trees, to assess the effects of extreme summer droughts on tree growth over the last century. Our analysis is guided by three hypotheses. First, drought sensitivity and resilience components vary systematically along large-scale climatic gradients, reflecting long-term differences in mean climate and species adaptation. Second, the relative importance of short versus multi-season droughts differs among climatic domains. Third, recovery capacity is highest in regions

historically exposed to stronger or more persistent drought stress, consistent with long-term acclimation. To evaluate these expectations, we quantify how drought sensitivity and resilience components depart from historical growth–climate relationships across the species’ range, and identify the climatic contexts in which these departures are more pronounced. We assess to what extent resilience components can be attributed to local climate conditions and how their spatial variability differs within and among climatic clusters. This approach is the first range-wide assessment of drought resilience components in *Pinus sylvestris*, providing novel insight into the climatic structure and magnitude of drought resilience across biomes, and the climatic factors associated with resilience variation under intensifying climate extremes.

Results

Biogeographic and climatic structure of the *Pinus sylvestris* network

Our network of 534 forest sites, spanning the entire distribution of *Pinus sylvestris*, extends from the Iberian Peninsula to eastern Siberia and captures the species’ full gradients in altitude and aridity (Fig. 1a; Supplementary Table 1). Our K-means clustering analysis revealed five distinct clusters based on site climatology, considering the means and seasonal variability of key climatic parameters, which represent the distinct hydroclimatic regimes (see Methods, Fig. 1b). Cluster 1 (C1) comprises cold and dry sites, with low mean temperatures and limited annual precipitation, pronounced continentality and highest aridity values across the network (Supplementary Table 2). C2 encompasses moderately warm and relatively humid regions, whereas C3 represents cool areas with the lowest isothermality and temperature diurnal range (i.e., stable daily temperature cycles despite moderate seasonal variation). C4 is defined by high precipitation and low temperature seasonality, characterizing wet sites in mostly coastal areas. In contrast, C5 encompasses warm–semi-humid regions, with warm temperatures and intermediate aridity. Together, the tree-ring

network captures the broad climatic niche of *Pinus sylvestris*, from continental cold interiors to maritime wet regions and semiarid lowlands (Supplementary Table 2).

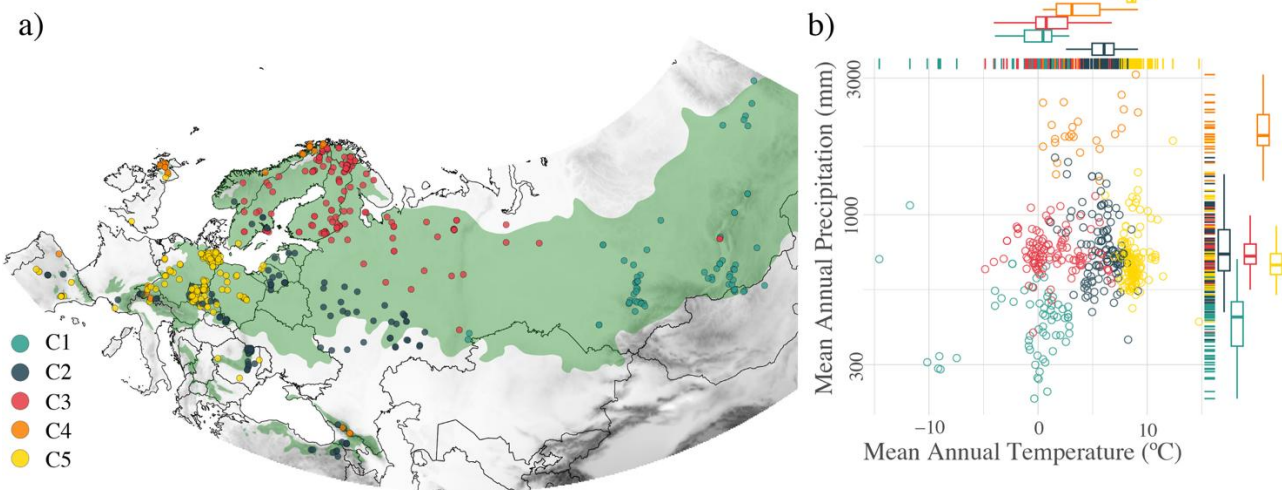


Figure 1. Pan-Eurasian *Pinus sylvestris* tree-ring network. Map (a) and climate space (b) showing the five clusters of 534 site chronologies based on temperature and precipitation variability. The clusters comprise C1 (cold-dry continental; n=65), C2 (temperate-humid; n=121), C3 (cool-humid; n=143), C4 (warm-wet maritime; n=26), and C5 (warm semi-humid; n=179). In (a), the species' spatial distribution is shown in green, with elevation represented in grayscale.

Divergent drought sensitivity and growth anomalies

Climate-growth relationships reveal strong but spatially heterogeneous drought sensitivity across sites and clusters. 40–60% of the sites in clusters C1, C2 and C5 display the expected positive association between growth and water availability (represented by the Standardized Precipitation Evapotranspiration Index, SPEI). However, a large fraction of sites shows no significant correlations between growth and SPEI, even when considering a variety of seasonal means ranging from 3 to 24 months and drought windows ending in June to September (Fig. 2a). Correlations are even negative in some regions, indicating higher growth under drier conditions. In cold northern

regions (C3 and C4), significant correlations are rare. However, when present, they indicate negative relationships with below-average water balance, with ~10% of sites exhibiting significant growth increases. Together, these patterns indicate that growth sensitivity to drought varies systematically across climatic domains, rather than following a single species-wide response.

Synchrony of drought sensitivity is quantified as the dispersion of site-level growth–climate correlations within each cluster, with lower dispersion indicating greater synchrony and higher dispersion describing more heterogeneous responses among sites (Fig. 2b). Coherence of drought responses varies significantly among climatic domains and drought temporal scales, the analysis of variance (ANOVA) reveals significant effects of climatic cluster ($F = 35.2$, $p < 0.001$), SPEI timescale ($F = 7.17$, $p < 0.001$), and their interaction ($F = 3.54$, $p < 0.001$) on the synchrony of growth–climate relationships. Clusters C1 and C2 showed increasing dispersion toward longer SPEI timescales, whereas C3, C4, and C5 exhibited the opposite pattern.

Among all sites with significant ($p < 0.01$) correlations, the length of the drought most strongly associated with tree-ring width series varies among clusters (Fig. 2c). Persisting droughts dominate in C1, including 44% of sites correlating more strongly with SPEI24, and 27% with SPEI12. In C5, 40% correlate strongest with SPEI24, whereas C2 exhibits a bimodal pattern, with equal proportions responding to both short and long droughts (37% with both SPEI03 and SPEI24). In contrast, short summer droughts prevail in C3 (48% SPEI03, 26.8% SPEI06) and in C4 (56% SPEI03). These patterns demonstrate that the species does not display a uniform drought response across its distribution range, but instead exhibits region-specific sensitivities linked to prevailing climate conditions and drought duration, consistent with contrasting growth strategies among climate domains (Fig. 2c).

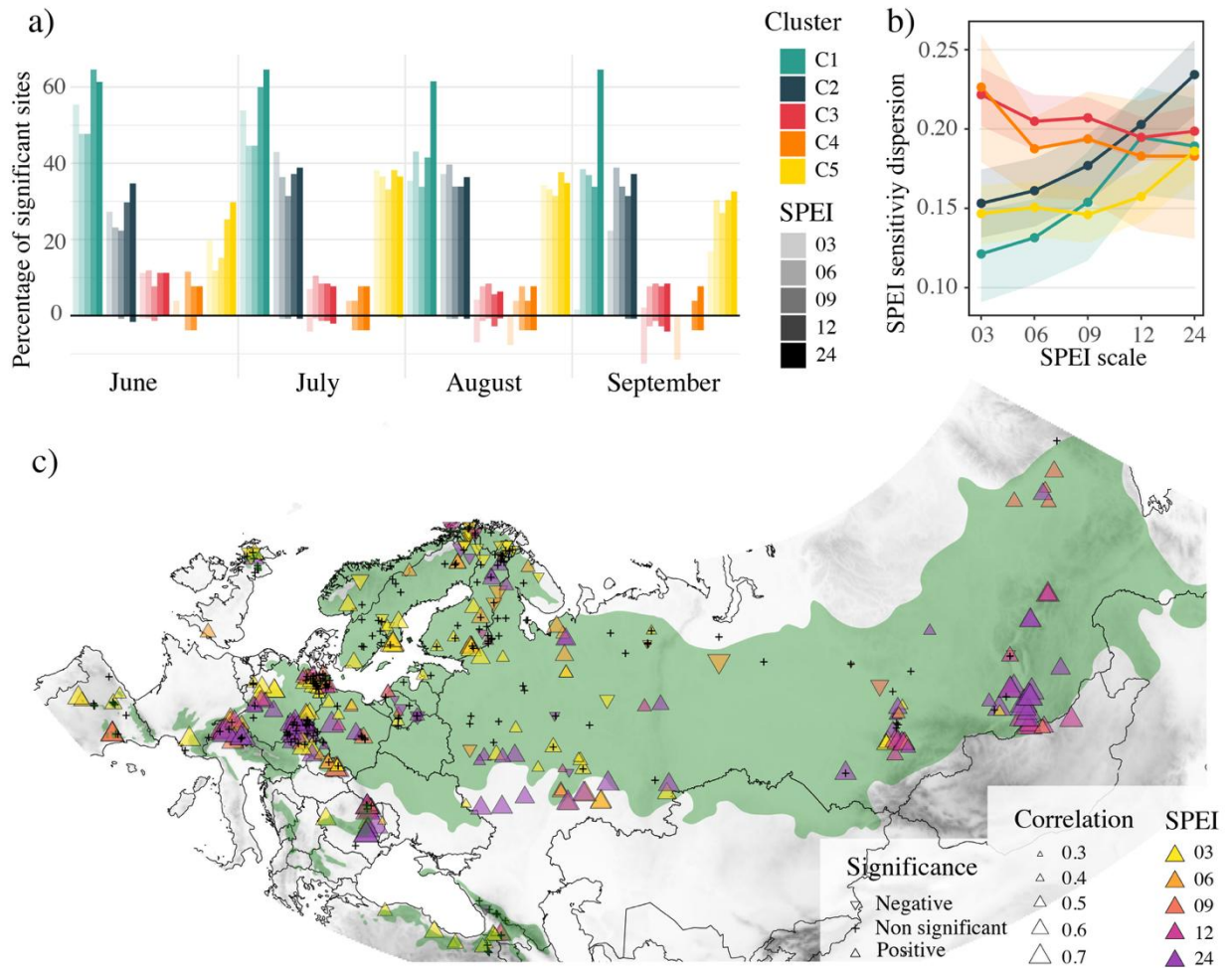


Figure 2. Spatial patterns and synchrony of drought sensitivity. Correlation coefficients between detrended growth and SPEI series. (a) Proportion of sites per cluster showing statistically significant correlations with varying SPEI series. Positive and negative values are shown above and below the zero line, respectively. (b) Synchrony of growth–climate relationships within clusters, quantified as the dispersion (standard deviation) of site-level correlations for each SPEI scale. Shaded areas represent bootstrap confidence intervals. (c) Geographic distribution of maximum correlations at each site considering SPEI 3-, 6-, 9-, 12-, and 24-month series ending between June and September. Both the strength (absolute correlation) and direction (positive or negative) are highlighted. Sites without any significant correlation are indicated with crosses. Significance is assigned at $p < 0.01$.

Growth departures during the most extreme drought vary substantially within and among clusters (Fig. 3). In C5 and C2, the mean departures converge around moderate growth reductions at approximately 20%. Nevertheless, the distributions are wide, reflecting heterogeneous site-level responses (Fig. 3a). C3 and C4 show largely stable responses, with most sites experiencing little or no change in response to extreme droughts, and only a minority displaying clear positive and negative departures. In contrast, C1 experiences severe reductions, with a mean of nearly -40% and individual site values ranging from zero to -77%, representing the 5th and 95th percentiles, respectively. This heterogeneity is also evident in the climate space (Fig. 3c), where positive growth responses to extreme dry conditions occur mainly at the cold–wet edge of the species’ distribution, contrasting with the strong negative anomalies in continental dry regions.

Year-to-year trajectories of growth departures reveal that *Pinus sylvestris* generally shows rapid recovery in the year following drought (Fig. 3b), with mean growth quickly rebounding to the baseline in subsequent years. This suggests that multi-year drought legacies in radial growth are limited in magnitude when averaged across climatic zones. The temporal response patterns are broadly similar across the clusters, but C1 still exhibits reduced growth by approximately 10% in the second post-drought year. By year +3, however, departures across all clusters converge and stabilize around zero, indicating a general return to baseline conditions. When comparing responses to short and prolonged droughts (Supplementary Figure 1), significant differences emerge. Short droughts induce sharp but transient declines, primarily affecting the dry year. More extended droughts generate persistent impacts, with growth reductions already visible in year –1 due to antecedent dry conditions, and legacies occasionally extending into subsequent years. Visual differences in growth trajectories were confirmed statistically (see Methods and Supplementary

Table 3). Despite these contrasts, recovery is rapid at the cluster scale, and growth generally converges back to baseline within a year, with sustained legacies being rare at broad spatial scales.

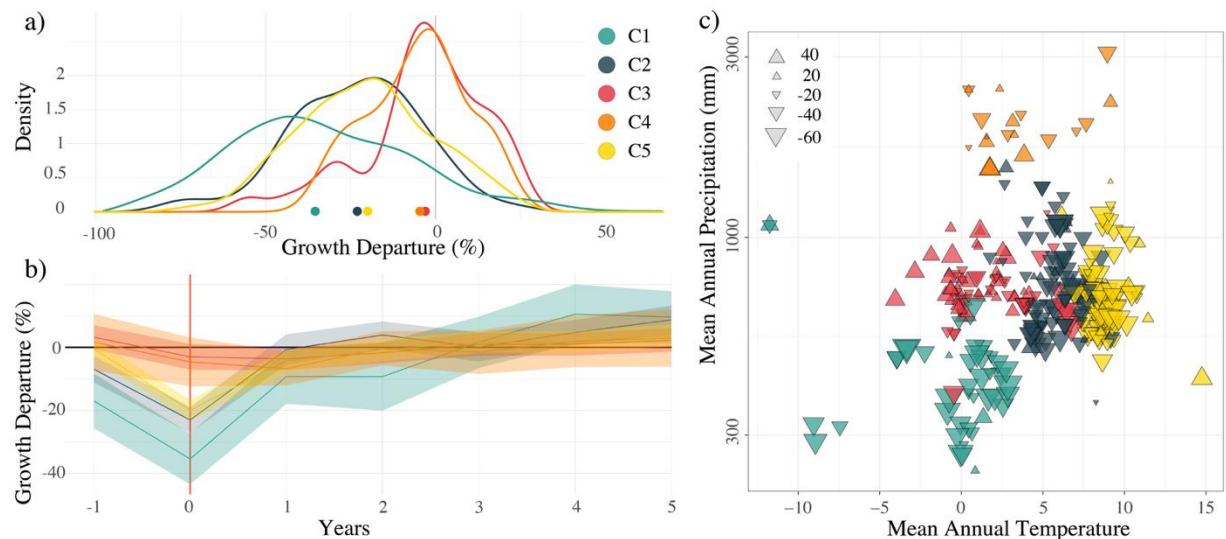
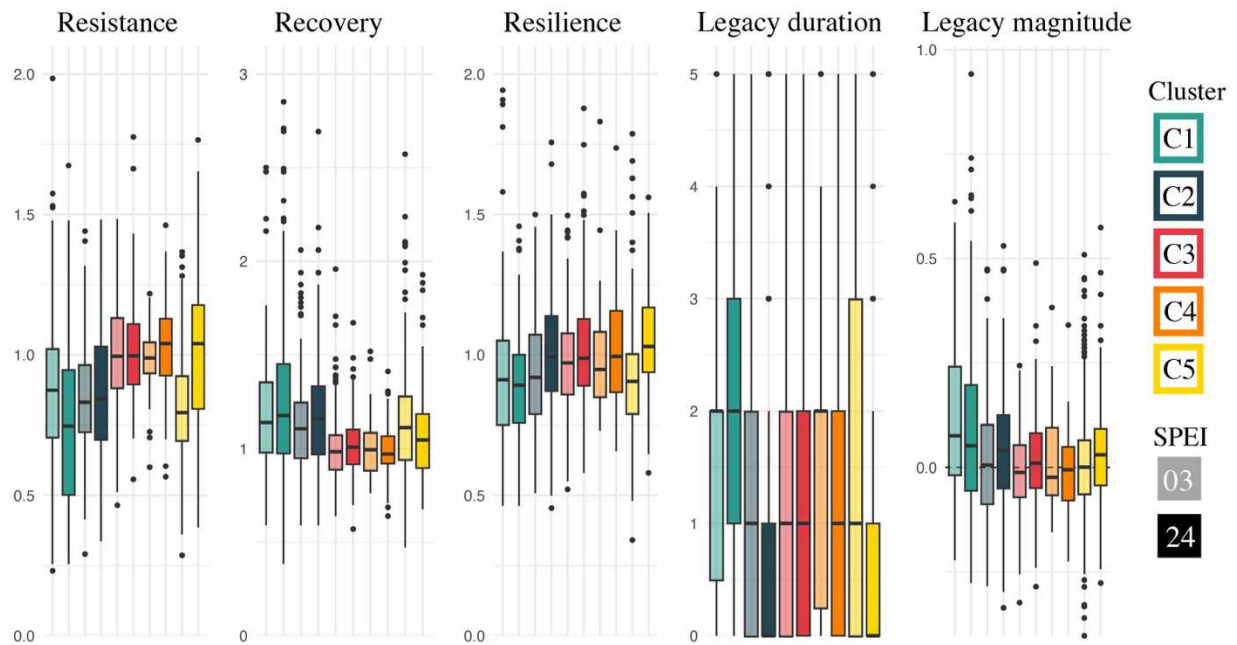


Figure 3. Growth departures under extreme dry conditions. Growth response to dry years, defined as the lowest SPEI values since 1902 CEs in each site considering in the strongest correlating season (see Methods). (a) Distribution of growth departures during drought, grouped by cluster, with dots marking cluster means. (b) Mean growth departure across clusters considering pre- and post-drought years. Shaded ribbons represent 95% confidence intervals. (c) Growth departure per site across climate space, with triangle direction indicating the sign of the growth departure (downwards = negative, upwards = positive) and size representing its magnitude in percent.

Resilience indices reveal clear contrasts between short (i.e., three-month) and prolonged (i.e., two-year) droughts, and both resistance and legacy effects vary with drought duration in a cluster-specific manner (Fig. 4). In C1, resistance is lower under prolonged droughts, whereas in C5 it declines most strongly during short droughts. In C2, resistance remains equally low under both types of droughts. By contrast, C3 and C4 maintain resistance values close to one regardless of drought length, confirming the limited impact of drought on growth in these regions. Clusters that

220 experience the most substantial growth reductions during drought (low resistance) also display the
 221 highest recovery values, particularly evident in C1, C2, and C5, where the wider range of recovery
 222 values reflects compensatory growth in some populations. In contrast, in C3 and C4, where
 223 resistance remains close to one and drought impacts are minimal, recovery values indicate little
 224 change relative to the drought year. Resilience, integrating both phases, is overall lower following
 225 short droughts, except in C1, where reductions in resistance are partly offset by enhanced recovery.
 226 Drought legacy effects further reveal differences in post-drought growth responses among clusters
 227 (Fig. 4). Legacy duration ranges from less than one year in C5 to more than two years in C1 under
 228 long droughts. Similarly, legacy magnitude is greatest in C1, particularly following prolonged
 229 droughts, whereas C3 and C4 exhibit values close to zero under both drought definitions. Clusters
 230 characterized by reduced resistance generally display longer and larger post-drought legacies,
 231 while clusters maintaining resistance values close to one show comparatively weak legacy effects.



232 **Figure 4. Drought legacy effects on growth responses among clusters.** Box plots showing the distribution of Resistance, Recovery, Resilience, Legacy duration, and Legacy magnitude for five clusters (C1, C2, C3, C4, C5) under two different SPEI values (03 and 24). The y-axis represents the value of the metric, and the x-axis represents the clusters. The legend indicates the color coding for the clusters and the different SPEI values.

Figure 4. Components of tree resilience and legacy effects under extreme droughts. Resistance, resilience, recovery, legacy duration (years), and legacy magnitude during the driest years identified by the 5th percentile of SPEI03 and SPEI24 (ending in August) for each site during the period 1906-2016. Resilience indices were calculated at the individual tree level and averaged by site. Boxplots represent the mean (horizontal line), interquartile range (IQR, box), 1.5× IQR (whiskers), and individual outliers (dots).

Climatic drivers of resilience variability

To evaluate whether site climatology is associated with differences in resilience metrics across the species' distribution, linear models (LMs) and generalized additive models (GAMs) were fitted with a climatic predictor set and site-location variables (see Methods, Supplementary Table 4). Across the entire distribution range, nonlinear models explain a greater proportion of the spatial variability in all resilience components (Table 1). Resistance show the strongest climatic associations, with adjusted R^2 values up to 0.46. Key predictors include vapor pressure deficit (vpd), soil water balance (swb), and elevation (elev), all of which display nonlinear relationships (Supplementary Figure 2). In contrast, recovery and resilience exhibit weaker and less consistent relationships with climate when analyzed globally ($R^2 < 0.3$).

Table 1. Summary of the best-performing linear (LM) and generalized additive (GAM) models explaining variability in tree resistance, resilience, and recovery to drought across *Pinus sylvestris* distribution. For each component, adjusted R^2 and AIC are reported for each model, along with F-statistics and p-values for individual predictors (0 if < 0.0001). See predictor's acronyms in Supplementary Table 4.

Component	Model	R^2	AIC	Predictor	F	p value
Resistance	GAM	0.46	-1045.99	vpd	57.23	<0.0001
				bio2	24.02	<0.0001
				elev	18.66	<0.0001

Recovery	LM	0.36	-949.88	vpd	-9.65	<0.0001
				bio8	-5.42	<0.0001
				bio2	-4.53	<0.0001
	GAM	0.28	-620.36	pet	10.71	<0.0001
				vpd	14.66	<0.0001
				bio2	10.69	<0.0001
Resilience	LM	0.23	-587.22	vpd	10.31	<0.0001
				bio18	6.04	<0.0001
				cmi	-4.68	<0.0001
	GAM	0.14	-1025.29	swb	15.32	<0.0001
				bio7	7.83	0.00029
				bio3	3.77	0.00761
	LM	0.12	-1014.76	swb	5.15	<0.0001
				elev	4.12	<0.0001
				bio2	-2.14	0.0328

Cluster-level models show that the explanatory power of site climatologies differs strongly among regions (Fig. 5), with GAMs consistently outperforming linear models. Resistance exhibits the strongest and most consistent climatic associations, with moderate R^2 values in C1, C3, and C5, while recovery and resilience are generally associated more weakly with site climatology. The exception is C4, where recovery and resistance exhibit particularly strong climate–response relationships (R^2 up to 0.86 and 0.72, respectively), underscoring the strong role of moisture availability in warm–wet sites. By contrast, C2 shows low explanatory power for all metrics, reflecting the more diffuse climatic controls in temperate–humid regions.

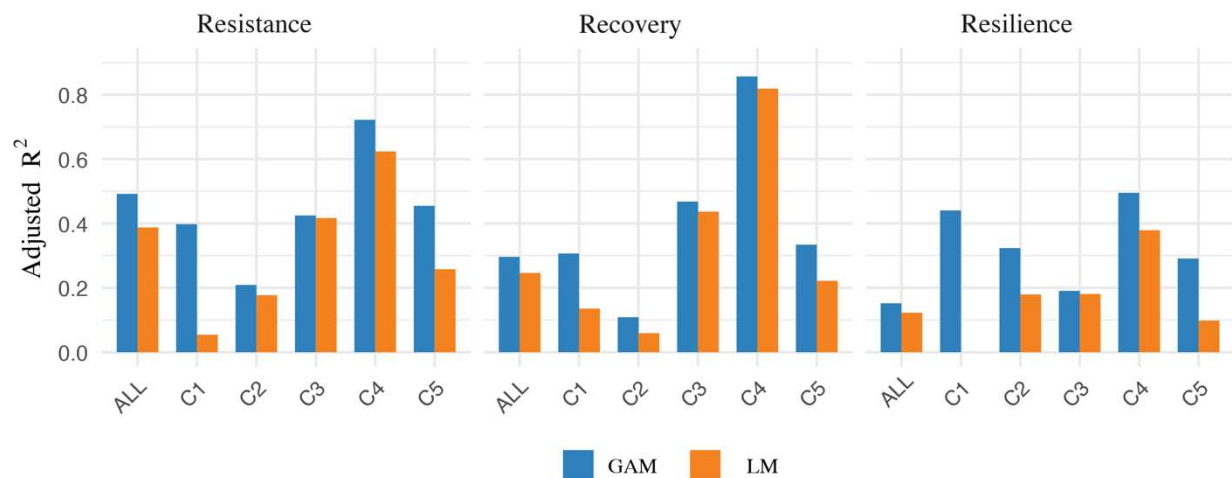


Figure 5. Model performance across clusters. Adjusted R^2 values for GAMs (blue) and LMs (orange), fitted to explain tree resistance, resilience, and recovery based on site climatology. Models were built for the strongest summer droughts at each location (5th percentile of August SPEI03 values), separately for each cluster (C1–C5) and the entire dataset (“ALL”).

The explanatory variables most frequently associated with resilience components in models with relatively high explanatory power ($R^2 > 0.4$) highlight the importance of water balance and temperature variability (Supplementary Table 5). Vapor pressure deficit, soil water balance, and precipitation seasonality (vpd, swb, and bio15, respectively) emerge as recurrent predictors across clusters, while temperature of the driest quarter, isothermality, and growing season length (bio9, bio3, and gsl, respectively) also contribute regionally. These variables consistently capture either atmospheric demand or seasonal water availability, underscoring their central role in constraining drought responses of *Pinus sylvestris* across biomes.

Discussion

The pan-Eurasian tree-ring network reveals that *Pinus sylvestris* exhibits highly heterogeneous growth responses to drought across its wide distribution range. Drought is among the most

prevalent drivers of forest dynamics, reducing growth, altering physiological functioning, and in severe cases leading to widespread mortality^{1,2,35–38}. Sensitivity varies both in magnitude and direction, with some populations showing expected growth reductions under water deficit (e.g.^{39–41}), while others remain unresponsive or even display positive anomalies. Such positive associations between growth and drier conditions often occur in cold and humid regions, where growth is primarily constrained by temperature, radiation, or excess soil moisture rather than by water availability⁴². In these contexts, moderate drying may alleviate waterlogging or coincide with warmer conditions and longer growing seasons, resulting in positive correlations with drought indices such as SPEI. This spatial divergence underscores that, despite being considered a species sensitive to extreme drought conditions in certain areas (e.g.^{14,15,28,43}), the general sensitivity of the species cannot be inferred from regional case studies²³, excluding any a priori assumptions. Moreover, the coherence of drought responses also varies across drought accumulation windows, even within similar climatic domains. In warm and drought-prone regions (C1 and C2), responses become progressively more heterogeneous as longer drought timescales were considered, whereas cold/moist northern regions (C3 and C4) exhibit comparatively greater coherence in response to multi-seasonal drought conditions. These patterns suggest that climatic constraints alone are insufficient to explain drought sensitivity, and that local factors such as site conditions, stand structure, population dynamics, and phenotypic plasticity may increasingly influence growth responses as drought duration increases²².

Large-scale tree-ring networks have been used to test how drought impacts vary across biomes and continents, revealing strong spatial heterogeneity and critical thresholds in growth decline^{30,44–46}. In case of *Pinus sylvestris*, cold–dry and warm semi-humid forests are most constrained by multi-seasonal water deficits, whereas short summer droughts dominate growth responses in cool and

301 warm–wet regions ⁴⁷. The synchrony analysis further indicates that the temporal scale at which
302 drought affects growth is not only region-specific but also differs in the degree of coherence among
303 sites within the same climatic domain. Together, these findings demonstrate that drought
304 sensitivity varies substantially across the species’ climatic range, underscoring the importance of
305 explicitly characterizing both spatial heterogeneity and coherence of drought responses when
306 interpreting large-scale patterns and informing projections of forest responses to drought and other
307 climate extremes ^{48,49}.

308 The wide variability of growth reactions underscores the complexity of *Pinus sylvestris* responses
309 to extreme droughts. The strongest growth reductions occur in cold–dry regions, where
310 populations lose up to three-quarters of their annual increment, consistent with severe hydraulic
311 constraints under high atmospheric vapor demand and low soil water storage capacity ^{50,51}. A direct
312 control of cambial activity cessation by water availability has been suggested numerous times for
313 this species ^{52–54}. Similarly, warm semi-humid sites also display pronounced growth losses,
314 confirming that drought effects are most severe at the climatic rear edges of the species distribution
315 ⁵⁵, where water limitation dominates tree performance. By contrast, cold–humid and maritime
316 regions often show muted or even positive growth departures, as reduced summer water balance
317 is associated with warmer temperatures that relieve thermal constraints on growth ^{56,57}. Positive
318 growth is the predominant response on waterlogged habitats with organic soils, such as bog pine
319 forest, where low SPEI values may reflect moderate drying that reduces waterlogging stress rather
320 than true water limitation, thereby promoting growth (e.g. ⁵⁸). This apparent contradiction
321 highlights that rear-edge populations do not always coincide with the southern geographic margins:
322 vulnerability emerges wherever drought pushes populations beyond their current functional limits,

whether in continental cold–dry interiors or warm–dry lowlands, while other margins (such as cold–wet forests) may even benefit from drier/warmer trends^{34,59}.

The use of standardized drought indices in ecological research has been debated: some authors have cautioned that standardization may obscure absolute water deficits in wet ecosystems^{60,61}, while others emphasize the value of SPEI in providing a consistent metric across regions and timescales^{37,62}. Despite these caveats, SPEI remains the most widely used index in ecological drought research and has been shown to facilitate comparability across biomes^{8,63,64}. We therefore adopted SPEI as a common baseline for identifying extreme drought events across the distribution of *Pinus sylvestris*, while acknowledging that in wet ecosystems such events may represent conditions that are unusually dry and warm relative to the local climatology rather than absolute hydrological droughts⁶⁵.

Resilience metrics reveal how drought duration and severity interact with prevailing climate conditions to shape outcomes, reinforcing our interpretation. In cold–dry regions, resilience is lowest during prolonged droughts, as multi-seasonal water deficits accumulate and constrain recovery, consistent with evidence that prolonged droughts reduce compensatory growth and sustain legacy effects^{44,66}. In warm semi-humid regions, resilience declines most under short droughts, as acute summer deficits coincide with the peak of cambial activity and induce immediate hydraulic limitations^{11,67}. In temperate–humid regions, resistance remains equally low, regardless of the length of the drought, suggesting a more general vulnerability across timescales. In contrast, cool–humid and warm–wet forests maintain resistance values close to one, consistent with their muted growth departures. Finally, clusters with the most substantial growth reductions also show the widest spread of recovery values, reflecting both mathematical scaling when resistance is low^{68,69} and genuine compensatory growth once conditions improve^{13,28}. Although

resistance and resilience varied markedly among climatic domains, legacy effects remained relatively weak, with most clusters returning to pre-drought growth levels within one to two years and only limited evidence for persistent multi-year growth suppression at the biome scale.

The rapid recovery observed at the cluster scale reflects the averaging of highly variable site-level responses, which diminishes the persistence of legacies evident in individual stands. While some sites exhibit multi-year growth reductions following drought, the overall magnitude and duration of legacy effects were generally modest, even without explicitly accounting for biological memory in tree growth dynamics⁷⁰. Nevertheless, individual sites likely experience multi-year legacies likely due to delayed restoration of hydraulic functioning, depletion of carbon reserves, or allocation trade-offs after heat and water stress^{71,72}. Local conditions such as stand structure, management, microclimate, and soil, together with genetic variation at both population and individual-tree levels, as well as tree-specific traits including life stage, and hydraulic strategies, strongly modulate resilience^{9,73}. As a result, drought impacts are often heterogeneous even within the same stand, with some individuals severely affected while neighbors remain largely unresponsive^{13,14,72,74}. This variability underscores the multidimensional nature of resilience: resistance reflects immediate hydraulic buffering, recovery depends on carbon allocation strategies, and integrated resilience emerges from the interplay of structural, physiological, and ecological processes⁷⁵.

Spatial variation in the resilience capacity of *Pinus sylvestris* is only partly explained by mean climate, with nonlinear models consistently outperforming linear approaches and underscoring the importance of threshold and unimodal responses between climate and growth^{22,76,77}. Resistance exhibits the strongest climate-response relationships at the distribution scale; yet the mean climate alone is insufficient to capture the complex pathways of drought response²³. Stronger climate–

resilience associations emerge when analyses are restricted to climatic clusters, with vapor pressure deficit emerging as a key driver, reflecting the central role of atmospheric water demand in regulating stomatal behavior and hydraulic stress^{48,78}. In fact, VPD is a primary force for transpiration, which directly impacts photosynthesis, nutrient uptake, and overall plant stress⁷⁹. Additional factors such as cloud cover influencing evaporative demand and light availability, and thermal-stability metrics (e.g., diurnal temperature range or isothermality; bio2 and bio3, respectively) further modulate the balance between carbon assimilation and water loss^{80,81}.

Despite the unprecedented spatial extent of our results, several limitations should be acknowledged. First, our analysis focuses exclusively on *Pinus sylvestris*, which, although widely distributed, is not the dominant conifer across all Eurasian regions; in some areas (e.g. Siberia) larch species prevail. Consequently, the results may not fully represent broader forest-level drought responses, and future efforts should integrate multiple species to better capture ecosystem-scale resilience patterns. Second, site coverage is spatially uneven, with denser sampling in Europe compared to Asia, and some clusters might contain some degree of pseudo-replication. Chronology length also varies among sites, leading to incomplete coverage of recent drought events in a subset of records. Additionally, differences in forest management intensity—ranging from heavily managed stands in Western Europe to largely unmanaged forests in Siberia—could contribute to the observed variability in growth responses.

Beyond these data-related limitations, some conceptual and statistical aspects of the analysis should be considered when interpreting the results. Resistance, recovery, and resilience are sensitive to the definition of drought events and reference periods, and mathematically interdependent, such that resilience partly integrates information from both resistance and recovery^{68,69}. Consequently, climatic effects detected for one component may propagate to the others, and

their associations with climate should therefore be interpreted in a relative and integrative manner rather than as fully independent signals. At the modelling level, weak residual spatial autocorrelation remained after accounting for climatic predictors, reflecting the spatial structure of both tree responses and environmental drivers. Sensitivity analyses including geographic coordinates produced only minor changes in model performance, suggesting that the identified climate–resilience relationships are not primarily driven by broad-scale geographic gradients (Supplementary Table 6). Nevertheless, climate and geography cannot be fully disentangled across the species range, and other spatially structured factors, including population history, stand structure, soil properties, management, and biotic interactions, may contribute to the observed patterns. Consequently, the reported relationships should be interpreted as climatic associations rather than strictly causal climatic effects. Despite limitations, this compilation represents the largest species-specific tree-ring network for *Pinus sylvestris* to date, encompassing its full biogeographical range and enabling robust, spatially explicit conclusions on drought resilience across Eurasia.

Taken together, our results demonstrate that the impacts of extreme droughts on *Pinus sylvestris* forests cannot be generalized across their entire distribution. Responses are strongly climate-dependent, with major legacies and severe growth reductions in rear-edge dry climates of the species' distribution, minor but variable impacts in temperate–humid and warm–wet zones, and even positive departures at cold–wet margins. The combination of climatic clustering, contrasting drought durations, and nonlinear modelling highlights the central role of prevailing climate conditions and atmospheric water demand in shaping growth responses to drought, while also revealing substantial variability among sites. Yet, substantial heterogeneity within clusters underscores the role of local factors, including genetic variation, differences in stand structure and

competition, soil water-holding capacity, and local acclimation history reflecting phenotypic adjustment to past climatic conditions, in shaping resilience outcomes. The coexistence of legacy effects, rapid recoveries, and positive anomalies within a single widespread species highlights the site-context dependence of forest stability under drought. Non-linear relationships with atmospheric demand, water balance, and thermal variability confirm that growth resilience depends not only on long-term climatic conditions but also on temporal variability and the coupled effects of energy and water fluxes. These findings build on existing evidence that forest management and modelling increasingly account for population-level variation⁸², and they underscore the need to explicitly represent site-level variability, nonlinear responses, and contrasting legacy effects when scaling drought responses across broad geographic areas. With droughts projected to intensify under climate change⁸³, monitoring and conserving vulnerable rear-edge populations while accounting for biome-scale heterogeneity will be fundamental to anticipating the future stability of Eurasian pine forests.

Methods

Tree-ring data

We assembled a pan-Eurasian network of 534 *Pinus sylvestris* sites spanning the species' full distribution from ~40° to 70° N and 5.8°W to 138° E. More than 1.3 million tree-rings from 14,787 trees were included in the analyses. The sites cover elevations from 3 to 2,500 m a.s.l. (mean 405 m) and wide climatic conditions ranging in mean annual temperatures from -14.5 to 14.8 °C (mean 4.6 °C), precipitation from 225 to 3,000 mm (mean 760 mm), and vapor pressure deficit (VPD) from 0.17 to 0.81 kPa (mean 0.39 kPa). Tree-ring width (TRW) series were obtained from the International Tree-Ring Data Bank (ITRDB) and co-author contributions to improve the representativity of site chronologies in more recent years. Crossdating followed standard

procedures with visual cross-comparisons and statistical verification⁸⁴. When multiple cores per tree were available, cores were averaged at the tree level prior to detrending. Raw TRW series were standardized by fitting a modified negative exponential curve (negative or zero slope allowed) to remove age-related growth trends. Indices were computed as ratios of observed to fitted values. Site chronologies were then developed using the arithmetic mean. No autoregressive prewhitening was applied, thus retaining low-frequency variance potentially related to long-term climate variability. Quality control excluded series with non-physical values (e.g., negative growth), spurious growth jumps (greater than two times the interquartile range 2xIQR), or extreme dispersion (TRW standard deviations falling within the upper 5% of all series). Chronology reliability was assessed using the interseries correlation ($\bar{r}$), Expressed Population Signal (EPS), mean sensitivity, sample depth (minimum of 7), and temporal coverage (covering at least 30 years of the study period). After rejecting low-quality series and chronologies, mean EPS ranged from 0.8–0.98 (mean = 0.92), $\bar{r}$ from 0.14–0.68 (mean = 0.36), and sensitivity from 0.15–0.49 (mean = 0.25), site replication from 7–123 trees (mean = 28). Site-level statistics are provided in Supplementary Table 1, and temporal coverage of the chronologies in Supplementary Figure 3.

Climate data

Monthly temperature and precipitation data were obtained from the CHELSA V2.1 database for the period 1900-2016 at 1-km spatial resolution⁸⁵. Drought conditions were quantified using the Standardized Precipitation Evapotranspiration Index (SPEI), which integrates precipitation and potential evapotranspiration to characterize climatic water balance and atmospheric demand⁸⁶. CHELSA were also used to compute potential evapotranspiration (PET) considering the Hargreaves equation⁸⁷. Drought severity was calculated as standardized anomalies of the climatic water balance (precipitation – PET) fitted to a log-logistic distribution. We computed SPEI

following the original formulation using high-resolution CHELSA climate data over 3-, 6-, 9-, 12-, and 24 months accumulation windows, for the period 1902–2016 at monthly resolution. Extreme drought years were defined as those with SPEI values below the 5th percentile of the site-specific distribution, corresponding to $\text{SPEI} \leq -1.5$. To capture short- and long-term drought signals, we used both 3- (SPEI03) and 24-month (SPEI24) windows ending in August, when summer water deficits peak across much of the species' distribution.

Site prevailing climate conditions was characterized using an extended set of bioclimatic variables (bioclim+) from the CHELSA v2.1 database^{88,89}. This dataset includes the 19 “traditional” WorldClim bioclimatic variables (bio1–bio19;⁹⁰), which summarize long term thermal and precipitation means, seasonality, and climatic extremes. In addition, bioclim+ provides indices of water availability (aridity, climatic moisture, soil water balance, potential evapotranspiration), seasonal or growing-season metrics (growing season length, growing degree days, growing season temperature and precipitation), atmospheric variables (cloud cover, relative humidity, vapor pressure deficit, net primary productivity, surface radiation, and wind speed), and categorical climate zones (Köppen–Geiger classification). Site climatology was calculated as the average value from the period 1980–2010. Together, these variables capture broad-scale gradients in temperature, precipitation, water balance, and energy input that structure species' climate niches. A full list and description of all bioclimatic variables used in the statistical models is provided in Supplementary Table 4.

The network is divided into five climatological clusters C1–C5 including 65, 121, 143, 26, and 179 sites, respectively. Patterns were identified by applying k-means clustering to standardized variables describing long-term temperature and precipitation regimes (annual precipitation, precipitation seasonality, mean diurnal temperature range, and temperature seasonality), as well as

drought-relevant site metrics (aridity index, vapor pressure deficit, growing season length). The optimal number of clusters was determined using silhouette widths, and the resulting five clusters reflect coherent climatic regions across the Eurasian distribution of the species (Supplementary Table 2).

Drought sensitivity assessment

To quantify the sensitivity of *Pinus sylvestris* growth to drought, we performed correlation analyses between detrended site chronologies and SPEI averaged over 3, 6, 9, 12, and 24 months and ending between June and September. This approach supports the identification of the varying seasons at which growth is most strongly associated with water deficits across sites. Synchrony of growth–climate relationships within climatic clusters was quantified as the dispersion of site-level correlations for each SPEI scale, using the standard deviation of site correlations. For each site and SPEI scale, the highest absolute correlation for ending months from June to September was selected to avoid pseudo-replication across overlapping accumulation windows. Uncertainty around dispersion estimates was quantified using bootstrap confidence intervals.

Tree responses to extreme droughts were characterized using growth departure and the resilience components defined by Lloret et al.,⁶⁹ calculated for each site and year. Growth departure is the relative deviation of growth during the drought year from the baseline, defined as the mean of the preceding five years. Resistance is the ability to maintain growth during drought, calculated as the ratio of growth in the drought year to pre-drought growth. Recovery is the ability to regain pre-drought growth levels, calculated as the ratio of post-drought to drought-year growth. Resilience is the capacity to recover and reach pre-drought growth, calculated as the ratio of post-drought to pre-drought growth. To quantify drought legacy effects, post-drought growth departures were evaluated during the five years following each drought event, following the general concept of

ecological memory and drought legacies proposed by Ogle et al.⁹¹ and Anderegg et al.⁷¹. Legacy duration was defined as the number of consecutive post-drought years with negative growth departures relative to the pre-drought baseline, whereas legacy magnitude was calculated as the mean growth departure across the five-year post-drought period. Pre- and post-drought periods for resilience components calculations were defined as four-year windows following the default implementation in the pointRes package ⁹², a choice that facilitates comparability with previous drought resilience studies. All indices were derived from standardized site chronologies for each extreme drought year identified from SPEI03 and SPEI24 values ending in August.

To formally test differences in growth trajectories between short (SPEI03) and prolonged (SPEI24) drought events, we fitted linear mixed-effects models including drought type (short versus prolonged), relative year (−1 to +2), and their interaction as fixed effects. Site identity and drought event were included as random effects to account for repeated measurements and non-independency among observations. A second model additionally included climatic cluster and its interactions with drought type and relative year. Significance of fixed effects was evaluated using Type III ANOVA with Satterthwaite's approximation for degrees of freedom.

Resilience modelling

To evaluate whether the spatial variability of tree resilience is associated with local climatic conditions, and to quantify the strength of these relationships, we developed a modelling framework based on linear (LMs) and generalized additive models (GAMs). This approach allowed us to quantify the strength of climate–resilience relationships and to test whether these relationships were linear or nonlinear across the species' distribution. The three response variables resistance, recovery, and resilience were modeled separately.

Prior to modeling, predictors were screened for multicollinearity, and for pairs with Pearson's correlation coefficient ($|r| > 0.80$), only the variable most strongly related to the response was retained. All predictors were centered and scaled. Predictor selection followed a greedy forward strategy, from an empty model and sequentially adding predictors that maximized improvements in explained variance and model fit (adjusted R^2), up to a maximum of three variables. This constraint was imposed to balance explanatory power and parsimony, and limit overfitting risks^{93,94}. GAMs were fitted with smoothing terms ($s(x)$) using restricted maximum likelihood with constrained smoothness (REML; $k=4$), while LMs were fitted with least-squares regression under the same selection framework.

Model fit was evaluated using adjusted R^2 and the Akaike Information Criterion (AIC), which penalizes model complexity. Models were evaluated for each response variable, climatic cluster (C1–C5) and across the full dataset. Given the explanatory focus of the analysis and the parallel evaluation of multiple response variables, climatic clusters, and modelling approaches, inference was based on the consistency of climatic effects across models rather than on isolated hypothesis tests or individual p-values.

Spatial dependence was assessed by evaluating Moran's I on model residuals. Residual spatial autocorrelation was weak but statistically significant (Moran's $I \approx 0.04$ – 0.08), with lower values for GAMs than for LMs, indicating that nonlinear climatic effects captured additional spatial structure. Given the low effect sizes and the objective of identifying broad-scale climate–resilience associations, explicit spatial correlation terms were not included. Instead, potential spatial confounding was further assessed through sensitivity analyses incorporating geographic coordinates (latitude and longitude) into the final models (Supplementary Table 6).

All analyses were performed in R⁹⁵. Tree-ring detrending and chronology development used dplR package⁹⁶. Resilience components were calculated using pointRes package⁹². SPEI time series were computed with the SPEI package⁹⁷. Forward feature selection for linear models was implemented using base R, generalized additive models were fitted using the *mgcv* package⁹⁶, and mixed-effects models were fitted using *lme4*⁹⁸. Data manipulation and visualization relied on dplyr⁹⁹ and ggplot2¹⁰⁰

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Data availability

The tree-ring data from the International Tree-Ring Data Bank (ITRDB) is openly available in <https://www.ncei.noaa.gov/products/paleoclimatology/tree-ring>. The additional tree-ring chronologies data that support the findings of this study have been deposited in Codeocean at <https://codeocean.com/capsule/6790696/tree> (doi: 10.24433/CO.6790696.v1). Climate data obtained from the CHELSA V2.1 database is available at <https://www.chelsa-climate.org/datasets>. Source Data are provided with this paper.

Code availability

Code to replicate our analyses and associated datasets are available via CodeOcean at <https://codeocean.com/capsule/6056486/tree/v1> (private link for peer review)

Author contributions

EMdC, MCAT, FR, EZ, and JE conceived and designed the study. EMdC gathered, shaped, and cleaned the data, performed the statistical analyses with input from MCAT and FR, and wrote the original manuscript. WY, JJ, AG, JJC, and JE contributed to the discussion and interpretation. MS, AA, VT, EvdM, JM, AV, MvdMT, MW, AP, IP, JS, MK, MdL, ET, JT, JL, AVK, MJ, JK, SM, PH, MH, and JE provided tree-ring datasets and contributed feedback and comments throughout the analysis and writing processes. All authors discussed the results and approved the final version of the manuscript.

Competing interests

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

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