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RESEARCH PAPER

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Pervasive effects of drought on tree growth across a wide climatic gradient in the temperate forests of the Caucasus

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Abstract

Aim: The Caucasus is a global biodiversity hotspot that includes a wide diversity of temperate forests, from xeric to mesic and rain forest. Little is known about their vulnerability to climate change. We aimed to identify the major climate constraints on tree growth.

Location: Western Caucasus of Georgia, Russia and Turkey (40–43° N, 41–43° E).

Time period: Twentieth century.

Major taxa studied: Trees, angiosperms and gymnosperms.

Methods: We used a new network of 35 tree-ring width chronologies from four angiosperm and four gymnosperm species across an elevational gradient of > 2,000 m. We used correlations to identify the major climate factors (temperature, precipitation and drought) at monthly and seasonal scales affecting tree growth and to assess whether their effects change over time. To explore common response patterns among species, we used self-organizing maps, a type of artificial neural network.

Results: Spring or summer drought reduced radial growth of most tree species, despite large differences in elevation. As expected, drought was particularly detrimental at warm, low-elevation sites. Besides drought, growth of conifers at high elevations was also limited by cold winters and summers. Important species-specific climate–growth responses were also evident. In general, climate–growth relationships were stable over time, except at some cold-limited sites, where positive responses to summer and winter temperatures have diminished over the last few decades.

Main conclusion: Growth responses to precipitation and drought among species were more similar than they were to temperature, even at humid sites, providing further evidence of drought vulnerability in mesic forests. The productivity of high-elevation conifer forests, limited by summer drought and low temperatures, will depend on the balance between temperature and precipitation. Given that climate change is expected to induce larger climatic gradients in the region, the potential reduction of forest cover at a regional scale would make the conservation of these mesic forests more essential.

KEYWORDS
climate change, climatic sensitivity, dendrochronological network, dendroclimatology, forest ecology, forest growth, gradient analysis, old-growth forest, temperate rain forest

1 | INTRODUCTION

Climate warming is expected to be detrimental for most dry forest ecosystems (Breshears et al., 2005; Gea-Izquierdo et al., 2017; Williams et al., 2013). Nevertheless, in mesic temperate forests, where abundant precipitation may buffer the effects of increasing temperature, the negative effects of drought are increasingly recognized (Allen, Breshears, & McDowell, 2015; Martin-Benito & Pederson, 2015). Although the uncertainty regarding future changes in precipitation is larger than that for temperature, a general 'wet-gets-wetter' and 'dry-gets-drier' trend is expected for many regions (Greve et al., 2014). The heterogeneous topography of mountain areas complicates projections of future climate change for these areas, particularly for precipitation. In addition, climatic extremes (e.g., severe drought, late spring frost) may cause a widespread reduction in forest productivity or increased tree decline at large spatial scales (Allen et al., 2015).

Increased forest background mortality and forest die-off induced by drought are expected to alter species composition gradually or suddenly and to induce ecotone shifts (Van Mantgem et al., 2009). Increasing variability of precipitation is expected to alter the frequency and timing of climatic extremes, such as droughts and floods. Droughts under a warmer climate can be more detrimental to trees, with mesic temperate forests probably being at higher risk than previously thought (Allen et al., 2015). A particular case of temperate forests are the temperate rain forests, which are generally diverse in terms of species composition and hold large amounts of old-growth forest and biomass (DellaSala, Alaback, Spribille, Wehrden, & Nauman, 2011). Although moister conditions and species richness in temperate rain forests might reduce their vulnerability to climatic changes (Allen et al., 2015), increasing drought may impact their dominant but less drought-tolerant species (Cavin & Jump, 2017), leading to large changes in the forests (Fensham, Fraser, MacDermott, & Firn, 2015). Furthermore, their relatively small and declining area compared with drier temperate forests and their location along mountain ranges (DellaSala et al., 2011) make understanding the sensitivity of temperate rain forests to climate a major challenge.

Colchic temperate forests thrive along extended elevational gradients at the eastern Black Sea coast and the western Caucasus (DellaSala, 2011). The region bridges between two phytogeographical regions: the Euxinian province of the Euro-Siberian region and the Hyrcanian province of the Irano-Turanian region (Browicz, 1989; DellaSala, 2011). Its location within the mid-latitudinal temperate zone, high topographical variation and proximity to the Black Sea create wide climatic gradients, from subtropical conditions at low elevations to alpine and nival conditions, resulting in high diversity of tree species and forest types. These forests transition between temperate–mesic and temperate–xeric or xeric biomes. Despite the biogeographical importance and biodiversity of the Colchic forests, little is known about how climate has influenced the development of these forests and how they might react to future climate changes.

Climate variability in the western Caucasus during the last several centuries has exceeded the ranges observed during the period of instrumental climate record (1930–2001), showing stronger droughts and wetter periods (Martin-Benito, Ummenhofer, Köse, Güner, & Pederson, 2016) and a consistent warming trend (Dolgova, 2016; Holobâcă, Pop, & Petrea, 2016). The warming of the Black Sea might be contributing to a further increase of precipitation in the wetter areas (Martin-Benito et al., 2016). Thus, better understanding the climatic constraints on tree growth in this biodiversity hotspot is crucial to analyse how these forests might respond to future changes.

Assessment of past climate–growth relationships using dendrochronological data offers the opportunity to analyse climatic effects on radial tree growth retrospectively (Fritts, 1976). Although tree growth is only one of the many processes underlying forest dynamics, it responds to climate at different time-scales, and important processes, such as mortality and competition, are closely related to growth. Annually resolved tree-ring widths result from the aggregation of the effects of environmental factors acting at intra-annual scales. The few dendrochronological studies conducted in the Caucasus (Dolgova, 2016; Holobâcă et al., 2016; Köse & Güner, 2012; Martin-Benito et al., 2016) show that growth of some species at high elevations is limited by low summer temperatures (Dolgova, 2016; Holobâcă et al., 2016; Köse & Güner, 2012). Furthermore, a widespread positive effect of spring precipitation on tree growth at lower elevations and more continental sites was observed (Köse & Güner, 2012; Martin-Benito et al., 2016). A spatially more extensive network, including many more species, is required to explore the factors limiting growth beyond the analysis of targeted trees that are presumed to be highly sensitive to climate. Such information would contribute to more accurate projections of forest development and dynamics, to improve forest growth simulations, and to development of forest management adapted to changing climate conditions. Most parts of the Western Caucasus experience higher temperatures than their central European counterparts and, in some cases, also wetter conditions (DellaSala, 2011), which could render Caucasian forests suitable models to understand how central European forests might respond to further warming.

Thus, we developed a multispecies network of tree-ring width chronologies in the western Caucasus, including gymnosperm and angiosperm species, ranging from low-elevation subtropical forests to mid-elevation productive forests and forests near the upper treeline. This is the first comprehensive dendrochronological study analysing how the growth of gymnosperms and angiosperms responds to climate along a wide elevation gradient in the Caucasus. The specific objectives of our study were as follows: (a) to analyse the growth response of tree species to monthly and seasonal climate variables; (b) to investigate the influence on growth responses of environmental conditions in relationship to elevation, latitude and longitude; and (c) to explore whether climate–growth relationships change through time and how this could influence future tree growth. Considering the number of species and wide environmental ranges covered in the network, we expect complex and diverse

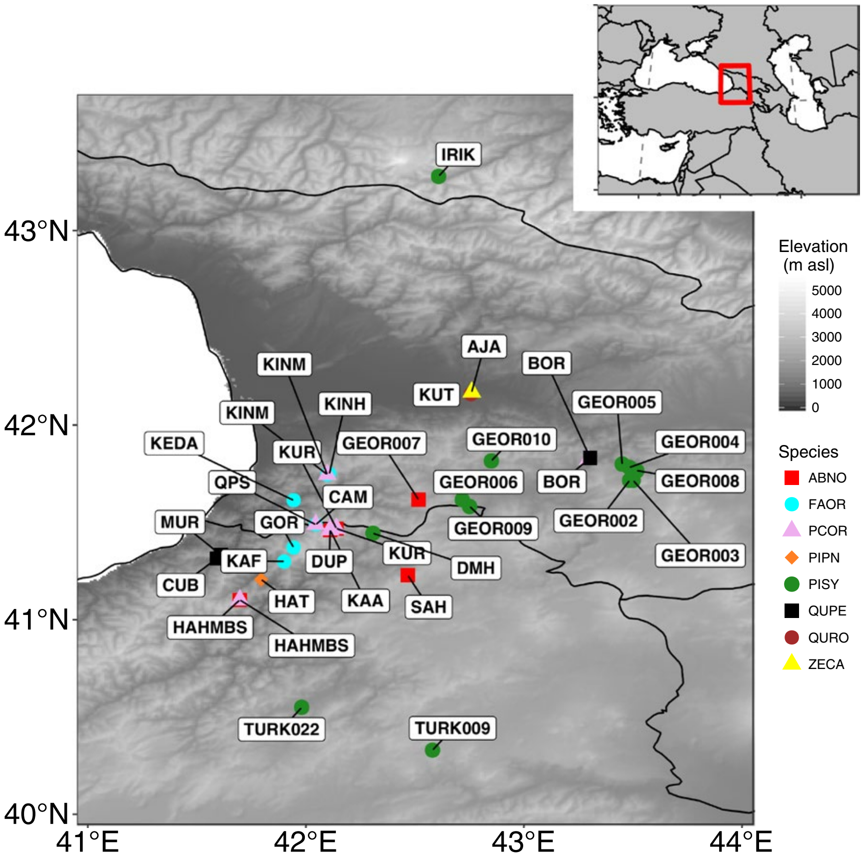

FIGURE 1 Location of collection sites in the tree-ring network. Species codes are as follows: ABNO = *Abies nordmanniana*; FAOR = *Fagus orientalis*; PCOR = *Picea orientalis*; PIPN = *Pinus pinea*; PISY = *Pinus sylvestris*; QUPE = *Quercus petraea*; QURO = *Quercus robur*; ZECA = *Zelkova carpinifolia*. For detailed site information, see Supporting Information Table S2 [Colour figure can be viewed at wileyonlinelibrary.com]

responses differing among sites and species. We hypothesize that in the most continental sites, cold and dry conditions reduce tree growth, whereas we expect low climatic constraints on growth at more coastal, warm and moist, low-elevation forests. We further expect that warming during the recent decades has reduced the effects of temperature at cold-limited sites but increased drought stress at drought-sensitive sites.

2 | MATERIALS AND METHODS

2.1 | Study area and tree species

Located in the Western Caucasus of north-eastern Turkey, western Georgia and south-western Russia (Figure 1), our study area experiences strong climatic gradients. Precipitation is higher in mountains surrounding the Black Sea (≤ 4,000 mm/year) and decreases towards the interior and south (Supporting Information Figure S1). Likewise, temperature is greatly influenced by elevation and distance from the Black Sea (Supporting Information Figure S1). Across the network sites, precipitation ranged between 560 and 2,100 mm/year, and mean annual temperature ranged between −3.8 and 13.2 °C (Supporting Information Figures S1 and S2). Although precipitation is rather well distributed throughout the year, some maxima and minima are evident. In general, late spring and early summer represent the precipitation maxima for the drier interior regions, whereas the same period represents the annual minima for the wetter areas around the Black Sea (Supporting Information Figure S2 and S3 and Table S1). Overall, the approximate corresponding Köppen climate types are as follows: (a) for the Colchic floodplains and lowlands, Cfa (warm temperate, fully humid climate with hot summers); (b) for the humid coastal low mountains, Cfb (warm temperate, fully humid climate with warm summers); and (c) for the continental interior, Dfb/Dfc (snow, fully humid climate with warm or cool summers). For details on regional climate, see the Supporting Information (Supplementary Methods).

The network consists of a total of 35 sites: nine from previous studies (Holobâcă et al., 2016; Köse & Güner, 2012; Martin-Benito et al., 2016), 11 from the international tree-ring data bank (ITRDB; https://www.ncdc.noaa.gov/data-access/paleoclimatology-data/datasets/tree-ring) and 15 newly collected sites (Supporting Information Table S2). This network included four broadleaved [*Quercus petraea* (Matt.) Liebl., *Quercus robur* L., *Fagus orientalis* Lipsky and *Zelkova carpinifolia* (Pall.) K. Koch.] and four conifer species [*Abies nordmanniana* (Steven) Spach, *Pinus sylvestris* L., *Picea orientalis* L. and *Pinus pinea* L.]. For details on regional vegetation and species in the tree-ring network, see Supporting Information (Supplementary Methods).

2.2 | Dendrochronological methods

At each of the 15 newly sampled sites and in those from Martin-Benito et al. (2016), we collected one or two increment cores per tree at breast height (1.30 m). We aimed at increasing tree replication whenever higher cores-per-tree replication was not possible (e.g., owing to conservation reasons in nature reserves; Martin-Benito & Pederson, 2015). We aimed at sampling trees of different ages and diameters at breast height (DBH), with DBH > 30 cm whenever possible, while including as many trees as possible with the features of old trees (Pederson, 2010). These sites included a wide range of forest types, from old-growth forests and forests with little evidence of anthropogenic influences to managed forests (Supporting Information Table S2).

Cores were glued onto grooved boards and sanded until annual rings were clearly visible. Cores were visually cross-dated with annual precision [i.e., each annual ring was assigned an exact calendar year of formation, using a combination of skeleton plotting (Stokes & Smiley, 1968) and the list method (Yamaguchi, 1991)]. We measured tree-ring width with a precision of 0.01 mm and statistically verified cross-dating with the program COFECHA (Holmes, 1983). In total, we used 664 trees from 35 sites and eight species, with between one and 12 sites per species (Supporting Information Table S2).

Each ring-width series was detrended using a spline function with a 50% variance cut-off equal to two-thirds of the series length after variance stabilization with an adaptive power transformation in ARSTAN (Cook, 1985). Growth indices were computed by subtracting each individual spline from each ring-width series. Each series of growth indices was first individually pre-whitened by autoregressive modelling and then, at each site and for each species, ring-width indices were combined into chronologies by using a bi-weight robust estimation of the mean. The common autoregressive properties of all series were added back to create the ARSTAN chronology, because these chronologies are considered to be more suitable for closed canopy forests with endogenous disturbances than residual or standard chronologies (Cook, 1985).

2.3 | Climate data

In much of our study area, meteorological stations are scarce, restricted to the main urban areas, and their data are of short duration, with records rarely reaching > 55–65 years in duration (Türkeş & Erlat, 2003). In addition, stations at higher elevations (*ca.* > 700 m) are extremely rare. Therefore, we used two 0.5° gridded climatic products, CRU TS 4.01 (Climatic Research Unit Time-Series version 4.01) for mean monthly temperature (https://doi.org/10/gcmcz3; Harris, Jones, Osborn, & Lister, 2014) and GPCC.v5 (Global Precipitation Climatology Centre version 5), for total monthly precipitation (Schneider et al., 2014). The GPCC.v5 dataset is well suited to represent precipitation patterns in areas where abrupt topography induces strong precipitation gradients, such as the Caucasus (Schneider et al., 2014). For every site, we used monthly temperature and precipitation from the closest grid-points for all analysis. From monthly temperature and precipitation, we calculated the multiscalar standardized precipitation and evaporation index (SPEI) to represent drought for time-scales of 1, 3, 6 and 12 months (Vicente-Serrano, Beguería, & López-Moreno, 2010) with the R package SPEI (Beguería & Vicente-Serrano, 2017). Higher (lower) values of SPEI correspond to wetter (dryer) conditions. Although minimum and maximum temperatures could be more meaningful ecologically, fewer meteorological stations providing these variables make gridded data products less reliable.

2.4 | Statistical analyses

We used different methods to explore climatic constraints of tree growth at the site and species level. First, we calculated Pearson correlation coefficients between growth index chronologies and monthly precipitation, temperature and SPEI from the previous July to the current October between 1930 and 2009 or the end of each chronology (Supporting Information Table S2). The statistical significance of these correlations was tested by bootstrapping with 1,000 resamples. Second, based on results from these correlation analyses, we calculated bootstrapped correlation coefficients at the seasonal scale for mean temperature and precipitation sums. We evaluated the stability of seasonal climate drivers of tree growth by calculating moving correlation coefficients between ring-width indices and precipitation, temperature and SPEI, with 40-year windows and 5-year offsets for each site and species. The SPEI at multi-month scales can be considered a seasonal variable. These analyses were conducted in R (R Development Core Team, 2017) using the package *treeclim* (Zang & Biondi, 2015).

We used three clustering methods to compare chronologies and their responses to climate (Martin-Benito & Pederson, 2015). First, to evaluate common growth patterns at the inter-annual to decadal scale, a principal components analysis (PCA) was performed on the chronology indices for the common period of all chronologies, 1900–1992. Second, based on PCA results, we applied a hierarchical cluster analysis with the Ward2 algorithm (Murtagh & Legendre, 2014) in the function *hclust* in R. Third, to consider the possible climate drivers behind growth patterns, we also used self-organizing maps (SOM) in the R package *Kohonen* (Wehrens & Buydens, 2007) to evaluate how the site chronologies clustered based on their monthly responses to climate. Self-organizing maps are a particular application of artificial neural networks with an increasing use in dendrochronology (Babst et al., 2013; Martin-Benito & Pederson, 2015). Self-organizing maps allow the number of resulting groups (nodes) to be controlled, as a compromise between using numerous nodes, which would result in low generalization, and few nodes, which would result in the analysis having little detail. For our analyses, we used four SOM nodes, which allowed for enough chronologies to fall within each node while retaining detail on the different types of climate–growth responses.

3 | RESULTS

3.1 | Chronology descriptions

The time span covered in the network ranged between 510 years (1498–2007) for the DUP *P. orientalis* site and 132 years (1882–2013) for the KUT *Q. robur* site (Supporting Information Table S3). Trees with ages > 300 years were found in 20 chronologies, and nine had trees > 400 years old, representing the five main species in the network (*A. nordmanniana*, *P. orientalis*, *P. sylvestris*, *F. orientalis* and *Q. petraea*). Mean interseries correlations in all chronologies were high (> .5), and > .65 in six of them, showing a strong agreement between all individual series within each chronology. All chronologies had an expressed population signal (EPS) above the .85 threshold (Wigley, Briffa, & Jones, 1984) after 1900 (Supporting Information Table S2).

The first three principal components (PCs) together accounted for 38.5% of the variability in growth (Supporting Information Figure S4). Principal component 1 explained 18.5% of the variance, PC2

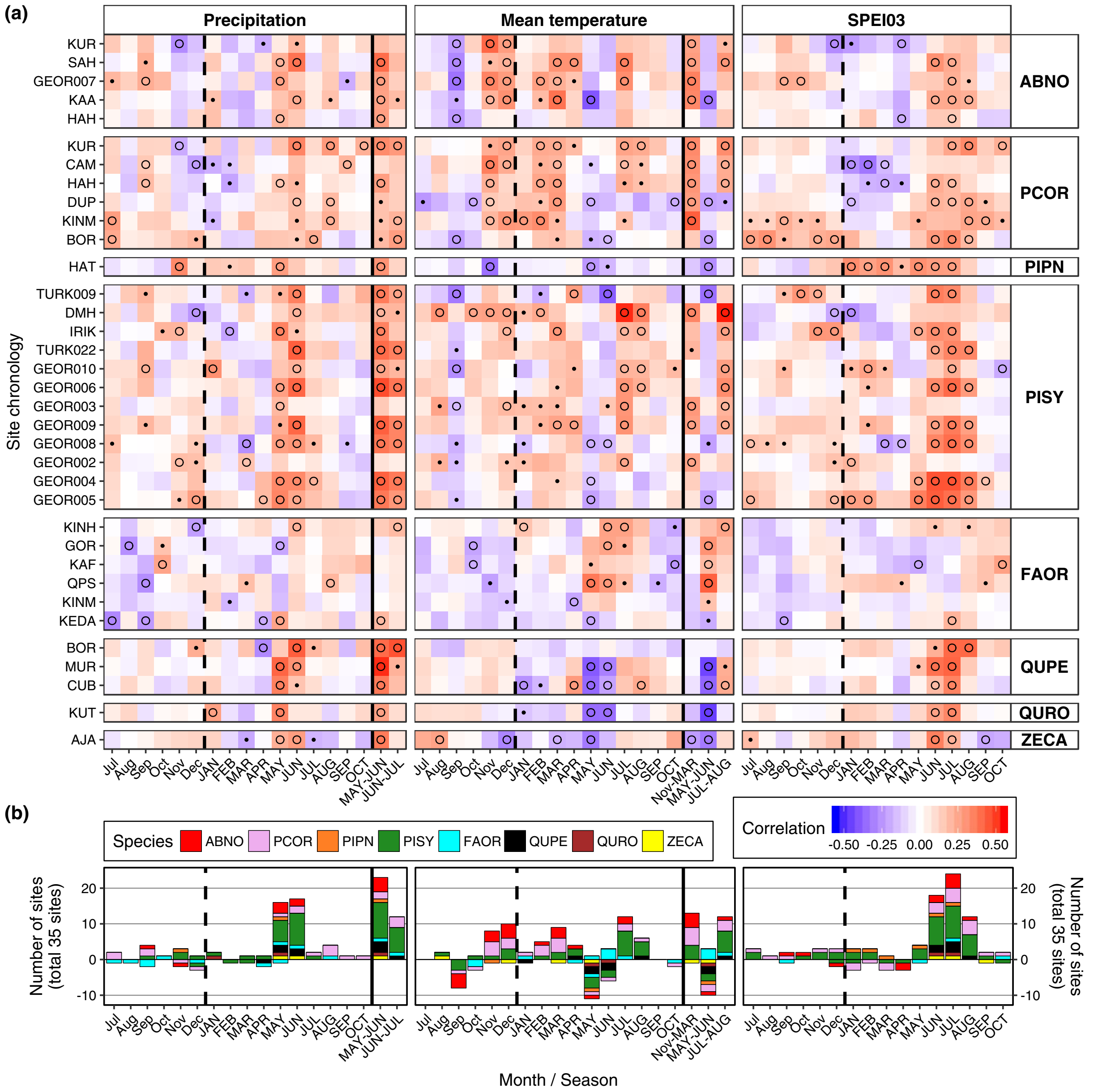

FIGURE 2 (a) Correlation coefficients between tree-ring chronologies and precipitation, mean temperature and the drought index SPEI03 (standardized precipitation and evaporation index at a 3-month scale) between previous year July (Jul) and current October (Oct) for the period between 1930 and 2009 or to the end of each series. Also, correlations with seasonal variables May–Jun and Jun–Jul for precipitation; previous November to current March, May–June and July–August for temperature. Open circles and black dots signal coefficients that are significant at $p \leq .05$ and at $p \leq .1$, respectively. Within each species, sites are ordered in decreasing elevation from top to bottom. (b) Number of sites that show monthly or seasonal correlation coefficients significant at $p \leq .05$. Positive numbers represent sites with positive coefficients for a given variable; negative numbers indicate negative coefficients. Species codes are as in Figure 1 [Colour figure can be viewed at wileyonlinelibrary.com]

10.4% and PC3 9.6%. Hierarchical clustering of these first three PCs showed three main clusters: (a) all high-elevation *F. orientalis* sites; (b) lowland sites (AJA and KUT), the low-dry mountain site HAT (*P. pinea*) and the three lowest *P. sylvestris* sites and the lowest *P. orientalis* site; and (c) all other conifer sites and *Q. petraea*.

3.2 | Monthly and seasonal climate–growth relationship

Most chronologies showed positive responses to spring–summer (May–June) or summer (June–July) precipitation, with 80% (29 of 35) of them showing a significant correlation during at least one of those months (Figure 2). The effect of precipitation during the previous September was positive for some mountain conifers (*A. nordmanniana*, *P. orientalis* and *P. sylvestris*) but significantly negative for *F. orientalis*. In general, drought index at a scale of 3 months (SPEI03) showed the strongest correlations with tree growth (Figure 2; for SPEI at other time-scales, see Supporting Information Figure S5), with these effects clearly concentrated during the summer: > 70% of all sites (i.e., all except 10 sites; five of them *F. orientalis*), showed at least a significant, positive effect of SPEI03 in June, July or August. In conifers, this drought response was common in 80% of sites (19 of 24) despite positive responses to July and August temperature in 58% of them (14 of 24). *Fagus orientalis* was the only species that displayed negative effects of May precipitation and SPEI03 on growth at some sites, although this was significant in only one chronology.

Species and sites differed more in their responses to temperature than they did in responses to precipitation and drought. Trees responded to temperature positively and/or negatively during different seasons, whereas responses to precipitation and drought index were mainly positive and concentrated in May–June and July–August, respectively (Figure 2; Supporting Information Figure S5). First, high temperature at the end of the previous growing season (September, October) reduced radial growth in conifers and broadleaf species, mainly in *A. nordmanniana* and *P. sylvestris* but also in *P. orientalis* and *F. orientalis*. Second, high temperature during the previous dormant season (November–March) promoted growth in mountain conifers (*A. nordmanniana*, *P. sylvestris* and *P. orientalis*). *Fagus orientalis* showed negative responses to temperature from October to December except at its highest site. Third, May temperature had the strongest negative effect on trees during the growing season, but its effects were species dependent. High May and June temperatures enhanced radial growth only in high-elevation *F. orientalis* sites, but high summer temperatures (July, August) had positive effects on growth of four species at 13 sites.

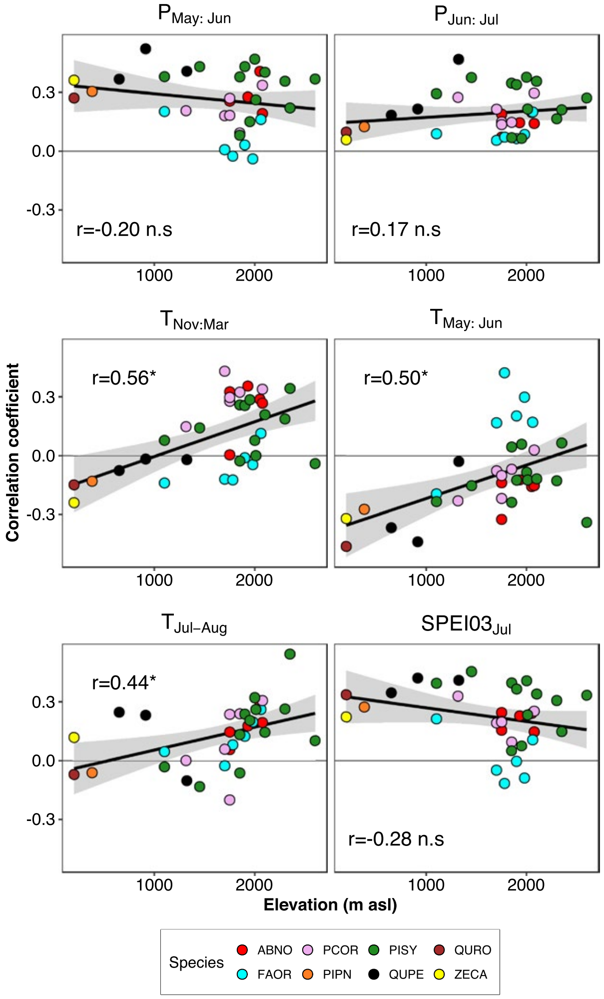

FIGURE 3 Seasonal correlations between tree-ring chronologies and climate variables and drought index SPEI03 (standardized precipitation and evaporation index at a 3-month scale) as a function of elevation. Linear models are fitted to the 35 sites independent of species. *Significant correlation at $p \leq .05$; n.s. = non-significant effects. Grey shades represent 95% confidence intervals. Species codes are as in Figure 1 [Colour figure can be viewed at wileyonlinelibrary.com]

The analysis of seasonal climate revealed similar responses but stronger correlation coefficients (Figure 2). Our results highlighted the strong positive effects of May–June precipitation ($P_{May–Jun}$) in all species and at 66% of sites, except for *F. orientalis* sites at medium-high elevation (> 1,200 m a.s.l.; Figure 3). Apart from the difference between low- and high-elevation *F. orientalis* sites, we observed no significant influence of elevation on the correlation coefficients of growth with either May–June or June–July precipitation or July SPEI03 (Figure 3). Elevation-dependent growth responses to SPEI were significant only at the beginning of the growing season in May (see Supporting Information Figure S6). Responses to the three seasonal temperature variables analysed ($T_{Nov–Mar}$, $T_{May–Jun}$ and $T_{Jul–Aug}$), however, showed a strong positive influence of elevation. Again, high-elevation *F. orientalis* sites showed a distinct response, with the highest correlations for $T_{May–Jun}$ but the lowest for $T_{Nov–Mar}$. We observed no general influence of either latitude or longitude in the growth responses to seasonal climate effects (results not shown).

3.3 | Stability of climate–growth correlations

Correlations of tree growth with precipitation, temperature and drought appeared rather stable and did not show any general and consistent temporal trend over the study period (Supporting

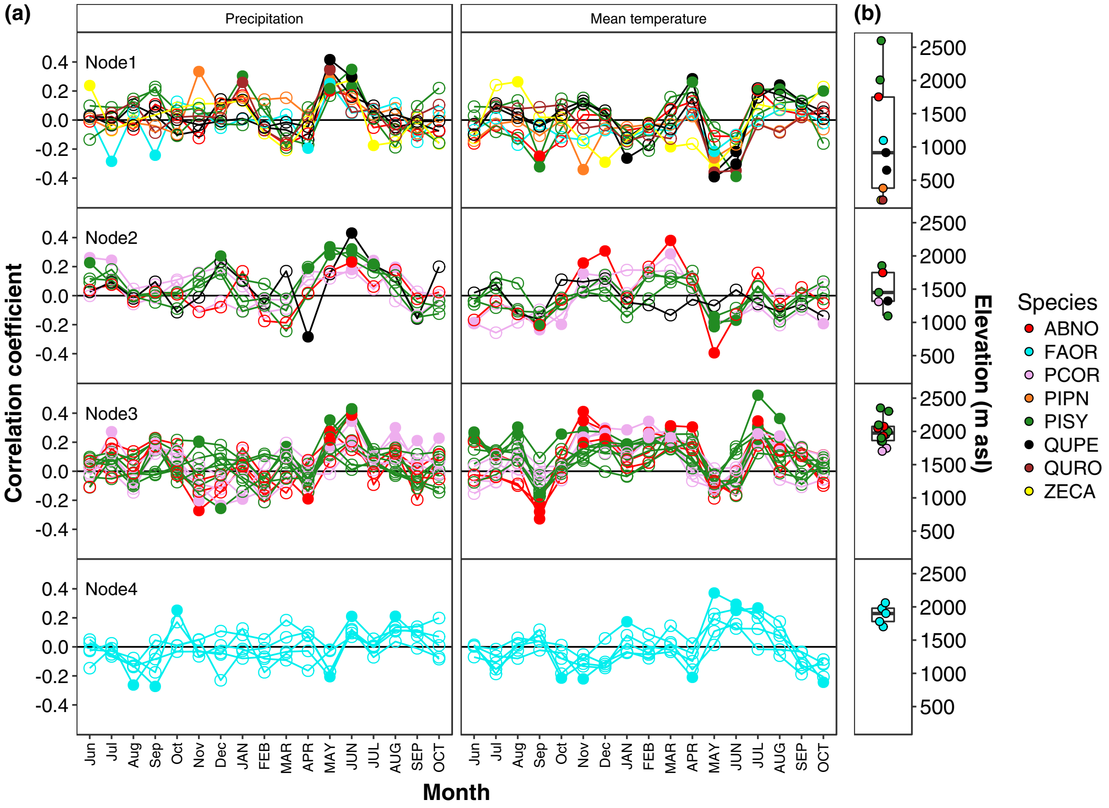

FIGURE 4 (a) Self-organizing maps based on correlation coefficients between tree-ring chronologies and precipitation and temperature. Dots represent coefficients significant at $p \le .05$. (b) Elevation of sites within each node. Species codes are as in Figure 1 [Colour figure can be viewed at wileyonlinelibrary.com]

Information Figure S7). A notable exception was the decreasing influence of $P_{\text{May–Jun}}$ and July SPEI03 at the *P. pinea* site. Likewise, the non-stationarity of temperature–growth correlations was also the exception in cases such as the following: (a) influence of $T_{\text{Nov–Mar}}$ on growth decreased at most *P. orientalis* sites; (b) a decreased influence of $T_{\text{July–Aug}}$ at the highest *P. sylvestris* sites and $T_{\text{May–Jun}}$ in *Q. petraea*; and (c) $T_{\text{Nov–Mar}}$ became increasingly negative for *Z. carpinifolia* and *Q. robur* growth while the negative influence of $T_{\text{May–Jun}}$ decreased (became less negative).

3.4 | Climatic response patterns

Our SOM analysis identified general patterns of climatic responses within the network (Figure 4). The first node was characterized by a strong positive influence of May–July precipitation and a strong response to temperature in April (positive) and May–June (negative). This first node featured the widest elevation range (200–2,600 m a.s.l.), including the lowest (*Q. robur*, *Z. carpinifolia* and *P. pinea*) and highest sites (TURK009 *P. sylvestris*) of the network and the lowest sites of *A. nordmanniana*, *Q. petraea* and *F. orientalis* (Figure 4b). The second node grouped sites with positive responses to growing season precipitation and opposite strong responses to temperature in November–March (positive) and summer (negative). The third node grouped drought-responsive sites with strong positive responses to November–April and summer temperatures, but weak to spring temperatures. This third node also showed positive effects of summer–spring precipitation, but weakly negative to winter precipitation, and included 13 conifer sites, particularly with *P. orientalis* (four out of five sites), *P. sylvestris* and *A. nordmanniana* from elevations > 1,700 m a.s.l. The fourth node was characterized by positive responses to May–July temperature and included only high-elevation *F. orientalis* sites (1,700–2,000 m a.s.l.).

4 | DISCUSSION

4.1 | Growth responses to climate across species and sites

Precipitation and drought exerted the strongest and most consistent limitation to radial growth along the elevational gradient of > 2,000 m across the western Caucasus. From the wet and warm lowlands in the west to the Colchic temperate rain forest and the cold and dry interior mountains to the east, sites of all species showed positive responses to spring–summer precipitation and summer drought index (i.e., drier conditions resulted in lower growth). These results partly contradict our main hypothesis, especially where low climatic constraints were expected on growth at more coastal, warm and moist, low-elevation forests. Most sites had their strongest response to drought during the summer (June–July) at a 3-month time-scale.

Mesic temperate sites have been reported previously to respond to drought at these relatively short time-scales, mainly < 5 months (Vicente-Serrano et al., 2013). Also in line with these previous results, the more xeric sites had longer response times, at least up to 12 months (Supporting Information Figure S5). This broad drought response across species is similar to other temperate–mesic forests (Cavin & Jump, 2017; Martin-Benito & Pederson, 2015; Rozas, Camarero, Sangüesa-Barreda, Souto, & García-González, 2015) and adds to the increasing evidence of global vulnerability of forest ecosystems to drought (Allen et al., 2015), even for short-duration water deficits. This level of vulnerability was particularly unexpected at wet locations (e.g., KEDA, *F. orientalis* site; KINM and CAM, *P. orientalis* sites) or in the floodplains of central Georgia (AJA, *Z. carpinifolia*; and KUT, *Q. robur*), because of the abundant and well-distributed precipitation in these areas. Warm spring–summers negatively affect growth mainly by increasing evapotranspiration and the water stress of trees (Breda, Huc, Granier, & Dreyer, 2006). Although the positive effect of temperature increased with elevation, the positive influence of precipitation did not decrease, suggesting that lower temperatures were not enough to compensate for reduced precipitation to alleviate drought impacts.

Species were, in some cases, more important than site in defining the growth response to drought. In mixed *Picea–Fagus* forests (i.e., QPS and CAM; KINM), growth of *P. orientalis* was reduced by spring–summer drought (positive correlation with SPEI03) and high temperatures, whereas growth of *F. orientalis* was neutral or negatively affected by higher moisture (negative correlation with SPEI03), but positively by warm temperatures. These relative climate responses and the rooting systems of close species, such as *F. sylvatica* with a deep rooting system versus *P. abies* with superficial roots (Bolte & Villanueva, 2005), suggest that *P. orientalis* could be more sensitive to drying of the upper soil layers than *F. orientalis*. Also, *P. orientalis* responded to precipitation during a longer period than *A. nordmanniana*, even in mixed stands (HAH, SAH, KAA and DUP). In this regard, *P. orientalis* behaved in a similar manner to *P. abies* at low elevations in central Europe (Altman et al., 2017; Mäkinen et al., 2002; Sidor, Popa, Vlad, & Cherubini, 2015). These results support the importance of drought for *P. orientalis*, even at elevations of *ca*. 2000 m a.s.l. and suggest that *P. orientalis* might be more drought sensitive than *A. nordmanniana*, in agreement with *P. orientalis* being more abundant in oceanic and wetter locations (Kayacik, 1955). These species-specific responses might be crucial for the future development of these forests.

Sites of *P. sylvestris* experienced stronger drought limitations than any other species except *Q. petraea*, thus supporting our hypothesis that continental sites would be particularly sensitive to dry and cold conditions. In the Caucasus, *P. sylvestris* is the most drought-tolerant mountain conifer (Barbéro, Losiel, Queézel, Richardson, & Romane, 1998), which allows it to occupy drier sites than *P. orientalis* and *A. nordmanniana*. Spring–summer precipitation and high temperatures in May–June were the strongest climatic constraints for *P. sylvestris*, which is consistent with results from other mountain areas (Lévesque, Rigling, Bugmann, Weber, & Brang, 2014). As elevation increases, the negative effects of May–June temperature give way to growth enhancement by summer temperature and to reductions of the length or strength of summer drought stress. However, the highest and most continental *P. sylvestris* site (TURK009) did not show any positive effect of warm summers, and its responses were similar to more thermophilous species, such as *Z. carpinifolia* and *Q. robur*. The range of responses of *P. sylvestris* along the network agrees with previous results for the species and highlights the high environmental plasticity of this widely distributed conifer.

Compared with other species, *Fagus orientalis* showed the most distinct response in the network. At high-elevation sites *ca*. 200–300 m below the current treeline in the Western Caucasus (Dolukhanov, 1978), growth was enhanced by May, June or July temperatures (i.e., 1 or 2 months earlier than mountain conifers at similar elevations). It was also the only species negatively affected by spring precipitation and higher moisture availability. This strong dependence of growth on spring–summer temperature is common in treeline trees (Frank & Esper, 2005) and probably reflects energy limitation on cambial and leaf phenology influenced by thicker snowpack, lower temperatures and cloud cover. Cold springs delay the onset of cambial activity and budburst (Peterson & Peterson, 1994; Rötzer, Grote, & Pretzsch, 2004), affecting wood formation dynamics and shortening the length of the growing season (Rossi et al., 2016). During cold and wet spring–summer, clouds may reduce carbon sequestration (Alton, 2008) and photosynthesis (Coulthard, Smith, & Meko, 2016; Graham, Mulkey, Kitajima, Phillips, & Wright, 2003; Stine & Huybers, 2014) even more than temperature (Hari, Hallman, Salminen, & Vappavuori, 1981). In contrast, at low elevation *F. orientalis* sites (KEDA), warmer springs contribute to drought, which may be alleviated by cloud cover (Rozas et al., 2015). The contrasting behaviour between low- and high-elevation *F. orientalis* sites has been observed for the closely related *F. sylvatica* (Cailleret & Davi, 2011; Dittmar, Zech, & Elling, 2003). The drought sensitivity of trees at 1,100 m a.s.l. and abundant rainfall being similar to other species in drier sites (Figure 4) highlights drought as a ubiquitous major limiting factor, as in temperate–mesic forests worldwide (Cavin & Jump, 2017; Martin-Benito & Pederson, 2015; Rozas et al., 2015), and suggests a wide ecological plasticity of *F. orientalis*. The climatic response of *F. orientalis* as a dominant species in the region requires greater investigation across its range.

4.2 | Influence of winter temperature on tree growth

The growth response to temperature outside the growing season was different for evergreen versus deciduous species. Warmer and drier winters enhanced tree growth in several conifers, mainly *A. nordmanniana* and *P. orientalis* (Figures 2 and 3), which is in line with results for temperate regions (Altman et al., 2017; Mäkinen et al., 2002; Martín-Benito, del Rio, & Cañellas, 2010; Pederson, Cook, Jacoby, Peteet, & Griffin, 2004; Sidor et al., 2015). In contrast to other studies (Lévesque et al., 2014), *P. sylvestris* showed a positive but weak and seldom significant influence of winter temperature.

Different processes might control how winter conditions affect tree growth. During warm winters, a reduced snowpack may increase the growing period and thus enhance tree growth for species and sites where winter precipitation is not crucial. This was the case at *P. orientalis* and *A. nordmanniana* sites, similar to *A. alba* in parts of the Alps (Rolland, 1993), although low winter temperatures pose stronger limitations for *A. nordmanniana*. However, on drier, south-facing slopes, warm and dry winters reduce snow cover and soil-water recharge and may lead to soil freezing, which increases root mortality (Groffman et al., 2001), inducing negative responses to winter temperature, as was the case in the lowest *Q. petraea* site. Warm winters allow only evergreen species to photosynthesize longer and to accumulate carbohydrates for growth (Nippert, Duursma, & Marshall, 2004; Schaberg, 2000). In contrast, in deciduous species, such as *F. orientalis*, warm winters may increase respiration, consuming carbon reserves (Haeni et al., 2017) that could not be compensated through increased photosynthesis. Finally, embolism induced by freeze–thaw cycles increases with xylem conduit size (Sperry & Sullivan, 1992), which makes ring-porous species (*Q. petraea*) more vulnerable to low temperatures than conifers and diffuse porous species (*F. orientalis*). However, frost damage in conifer xylem and needles affects tree growth during the subsequent growing season (Nippert et al., 2004), which may also be responsible for the differential response between evergreen and deciduous species.

4.3 | Implications for forest ecology and future forest development

The broadly stable climate–growth correlations did not support our general hypothesis that warming during recent decades would have increased drought stress but relaxed cold limitations at higher sites. Our results, however, have general implications for how forests in the Caucasus might respond to future climate changes. The eight species in this investigation showed a rather similar response to precipitation and drought across sites, but they diverged strongly in their response to temperature. Projections of future precipitation changes are prone to considerable uncertainty at regional scales (Greve et al., 2014). Considering the large environmental gradients in our study, changes in precipitation and temperature could induce important changes in forest growth, biomass and species composition. The winter cold limitation of *P. orientalis* has decreased in recent decades, without a simultaneous increase in other constraints at any but the lowest sites. Further warming would reduce the species major climate constraints and probably result in accelerating growth. If this trend continues, the growing season of conifers would lengthen and, probably, increase winter carbon fixation. Warming, however, could also increase respiration rates (Haeni et al., 2017) or reduce cold hardiness and increase frost damage (Schaberg, 2000) if low extreme temperatures persist despite global warming (Liu et al., 2018).

If summer temperatures increase beyond certain thresholds, their negative impacts could offset the positive effect of winter warming, especially if the increase in precipitation in wetter areas is not enough to compensate for the increased evapotranspiration. Likewise, drier areas getting drier could result in growth declines if drought increases more than winter limitations are relaxed. Late summer drought has been suggested as a cause for the decline of *A. alba* (Camarero, Bigler, Linares, & Gil-Pelegrín, 2011). In our study area, a similar decline of *A. nordmanniana* seems unlikely considering its climate sensitivity over the last decades. However, in drier areas farther away from the Black Sea coast that experience more continental climates (not studied here), the radial growth response of *A. nordmanniana* and its future development might be different.

In the nearly subtropical lowlands of Georgia, the relict *Z. carpinifolia* experienced negative effects of winter warming, possibly as a result of higher evapotranspiration or increased respiration (Haeni et al., 2017). Further winter warming might negatively affect the performance of this species. In contrast, further tropicalization (i.e., warmer and wetter conditions) might positively impact the growth of this and other broadleaved species. The stable influence of precipitation on *Q. petraea* and the relaxation of its response to summer temperature might increase growth, particularly at mid- to high elevations. Warmer spring could induce earlier growth onset of *F. orientalis* at mid- to high-elevation sites. Given that high-elevation *F. orientalis* growth showed little drought response but positive responses to spring–summer warmth, growth might accelerate in the future. Thus, these rain forests could act as potential climatic refugia in a warming world (D'Orangeville et al., 2016), particularly considering the drier areas surrounding the Western Caucasus.

Many of the sites in this study are old-growth forests, with a high abundance of > 400- year-old trees. Protection of old-growth forests is a priority for sustainable development and forestry, for maintaining the high biodiversity and structural diversity of the area, and they are prime sites for ecological monitoring. Given that it is likely that more old-growth forests exist in the Caucasus, more work is needed to improve the temporal and spatial coverage of a tree-ring network, which would also support the protection of old-growth forests in the region. Lastly, a network of climatically sensitive, old trees opens the possibility of developing new climate reconstructions for the region.

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DATA ACCESSIBILITY

Tree-ring chronologies listed as 'this work' in Supporting Information Table S2 can be provided upon request from the corresponding author. Other chronologies can be accessed from sources shown in Supporting Information Table S2.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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