



Tree growth response to recent warming of two endemic species in Northeast Asia

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Received: 23 August 2019 / Accepted: 6 April 2020 / Published online: 27 April 2020
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Abstract

The impact of climatic change on forest ecosystems has received considerable attention, but our understanding of the modulation of this impact by elevational differences and by species interaction is still limited. Here, we analyse tree-ring-based growth-climate relationships for two dominant tree species along an 800-m elevational gradient on Jeju Island, South Korea. Both species, broadleaf *Quercus mongolica* (QUMO) and coniferous *Abies koreana* (ABKO), grow at the southern end of their distributional range and they have adjacent altitudinal ranges. We use static and moving bootstrapped correlation analysis to identify the effect of recent warming on their growth. QUMO is primarily positively influenced by moisture during the previous autumn at its upper elevational distribution. Recent warming, however, has diminished this relationship, while the enhancing impact of warm and dry summer conditions on QUMO growth has increased. These recent shifts in growth-climate relationship suggest an upward migration potential for QUMO due to warming-enhanced growth at higher elevations. ABKO growth, on the contrary, is primarily reduced by high winter and summer temperatures. This negative relationship has become more explicit in recent decades, particularly at lower elevations. At the highest elevation, however, ABKO growth-temperature relationship has consistently become more positive in the most recent decades. In the elevational zone where ABKO and QUMO co-exist, warming plays a primary role in ABKO growth reduction, while QUMO growth increases and thus induces a potential upward migration of QUMO. This combined effect can lead to population decline of ABKO. Our results significantly enhance our understanding of the impact of climate warming on two interacting species and provide information necessary for adaptation strategies to preserve declining ABKO populations.

Keywords Dendroclimatology · Elevation · Endangered species · Population decline · Global warming · South Korea

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s10584-020-02718-1>) contains supplementary material, which is available to authorized users.

1 Introduction

Climate is one of the most important factors determining tree species performance (Buechling et al. 2017; Sorte et al. 2013) and distribution (Dyderski et al. 2018; Sánchez-Salguero et al. 2017b), and climatic changes can influence the geographical distribution of species (Ettinger and Hillerislambers 2017). Biogeographical research therefore benefits from the exploration of the spatiotemporal variability of the climatic boundaries for individual species (Marotzke et al. 2017).

Forest ecosystems worldwide have responded to recent climate changes and are especially sensitive to warming, decreasing precipitation, and increasing aridity, but also to warming-induced disturbances such as catastrophic winds and fires (Altman et al. 2018; Williams et al. 2013). Climatic changes affect forest structure and composition through their impacts on tree growth, with species-specific responses varying in space and time (Altman et al. 2017; Babst et al. 2013). Thus, assessing responses to climate change improves predictions of rapid climate change impacts on tree performance and potential range shifts (Babst et al. 2019; Charney et al. 2016; Franks et al. 2014). In cold and humid regions, rising temperature is generally considered to be a key driver of vegetation change as illustrated by recent tundra greening (Elmendorf et al. 2012), treeline shifts (Liang et al. 2016), and the upward migration of alpine species (Chen et al. 2011), while changing precipitation regimes and their effects on soil water balance may be more important in warm regions and at lower elevations and latitudes (Allen et al. 2015; Tumajer et al. 2017).

Current understanding of forest responses to climate change is often based on accurate, but short-term (a few decades or less) forest inventories that do not capture long-term trends (Willis and Birks 2006). To determine the impact of past climate variability and to better forecast the impact of future climate change on species and ecosystem performance, however, high-resolution proxies of long-term climate and forest ecosystem changes are needed (Hasselmann et al. 2003; Moss et al. 2010). In addition to this, responses to climatic changes are most pronounced at the edge of a species geographical distribution, where even small climatic changes may result in expansions or contractions of distributional range (Matias et al. 2017). Thus, altitudinal transects that include species-specific treelines are an extremely valuable platform for understanding climatic-driven tree growth responses under projected climatic changes (King et al. 2013).

Tree-ring-based radial growth is commonly used as a proxy to identify biological responses to climate and to investigate the temporal stability of this response (Frank et al. 2010; Treydte et al. 2006). The main advantage of such tree-ring-based approaches is that they provide long time series at high spatiotemporal resolution (Frellich 2002; Speer 2010) and thus a dynamic perspective on the evolution of the tree responses to climate and a better understanding of how trees cope with climate change (Biondi 2000; Sohar et al. 2017). We can therefore retrospectively determine the performance of individual tree species growing under different environmental conditions and compare the variability in performance of different species and the importance of such variability for the whole ecosystem (Dwyer and Laughlin 2017; Housset et al. 2016).

Potential changes in range shifts of trees, especially for dominant species, could have large impacts on biodiversity and on a variety of ecosystem services, including carbon sequestration and socio-economic factors (Cheaib et al. 2012). Most of our understanding about the impact of climatic changes on temperate forest ecosystems is based on data from North America, Europe or the Himalayas, with large regions in Asia remaining underrepresented (Zhao et al. 2019). The most diverse temperate forests on Earth, however, are located in northeast (NE) Asia (White 1983), characterized by low past human impact compared to Europe. They

represent a unique opportunity to identify tree growth responses to climate change, because in more managed ecosystems it can be difficult to distinguish the driving forces (anthropogenic versus climatic) behind recent forest changes (Améztegui et al. 2010; Clavero et al. 2011; Gehrig-Fasel et al. 2007). Due to increasing population density at the southern borders of NE Asian temperate forests in Korea, China, and Japan, a better understanding of the impact of climate changes is of high importance and will contribute to the development of adaptation and mitigation strategies to reduce the impact of future climate changes.

Here, we studied temperate forests in the Hallasan National Park (UNESCO Biosphere Reserve and World Heritage Site), Jeju Island, South Korea, where climate has changed rapidly over recent decades (Jung et al. 2002, 2011; Kim and Kim 2000; Kim and Jain 2011). Jeju Island is of specific interest because of its high biological diversity and endemism (Cerny et al. 2015; Kong and Watts 2012) thanks to the combination of three main factors: (1) it is located on a former crossroad of several plant migration routes in coastal East Asia, (2) it is located on the edge between temperate and subtropical climates, and (3) it is characterized by an altitudinal gradient ranging from sea level to nearly 2000 m a.s.l. (Dolezal et al. 2012).

We investigated two dominant tree species of Mt. Hallasan, *Quercus mongolica* (hereafter QUMO) and *Abies koreana* (hereafter ABKO). Both QUMO and ABKO are at their southern distributional limit on Jeju Island and their distribution has been affected by recent climate change (Duan et al. 2014; Choi et al. 2011; Lee et al. 2014; Yun et al. 2018). ABKO, an endemic cold relict distributed in a few alpine and subalpine zones in the Republic of Korea at between ca. 35°40' and 33°50' N, is particularly sensitive and has been listed as an endangered species by the IUCN (Kim et al. 2011). The decline of ABKO was previously identified based on short-term observations and is projected to continue into the future (Koo et al. 2017; Lim et al. 2018). QUMO, on the other hand, is expected to increase its abundance under warming climate scenario (He et al. 2005). Nevertheless, long-term information from multiple localities along the elevational gradient is missing for both species. Thus, there is substantial uncertainty in the extent that climate change will alter the growth and distribution of these two dominant species and their interaction. The objective of our study is to determine the spatiotemporal variability in the growth response to climate of these two range-adjacent dominant species using dendrochronological methods. Specifically, we aim to (1) reveal the climatic factors controlling radial growth of QUMO and ABKO and (2) determine how growth-climate relationships change across time and along an 800-m elevational gradient (1130 to 1930 m a.s.l.).

2 Materials and methods

2.1 Site description

Our study sites are located in the Hallasan National Park (153 km²) on Jeju Island (33°10'–33°34' N, 126°10'–127° E), 90 km from the southern tip of the Korean Peninsula (Fig. 1a). Hallasan National Park is situated in the centre of the island, which is dominated by an extinct volcano, Mt. Hallasan, the highest mountain of South Korea (1950 m a.s.l.) (Fig. 1c). Climate on the island is strongly affected by winter cold air masses from Siberia, and summer monsoons and tropical cyclones (typhoons) from the Pacific Ocean that bring abundant moisture and produce heavy rainfall. Precipitation ranges from about 1500 mm in coastal areas to more than 4000 mm in upland areas (Kim 2008). The mean annual temperature on the island (Jeju City meteorological station, 1945–2017) is 15.5 °C, mean January temperature is

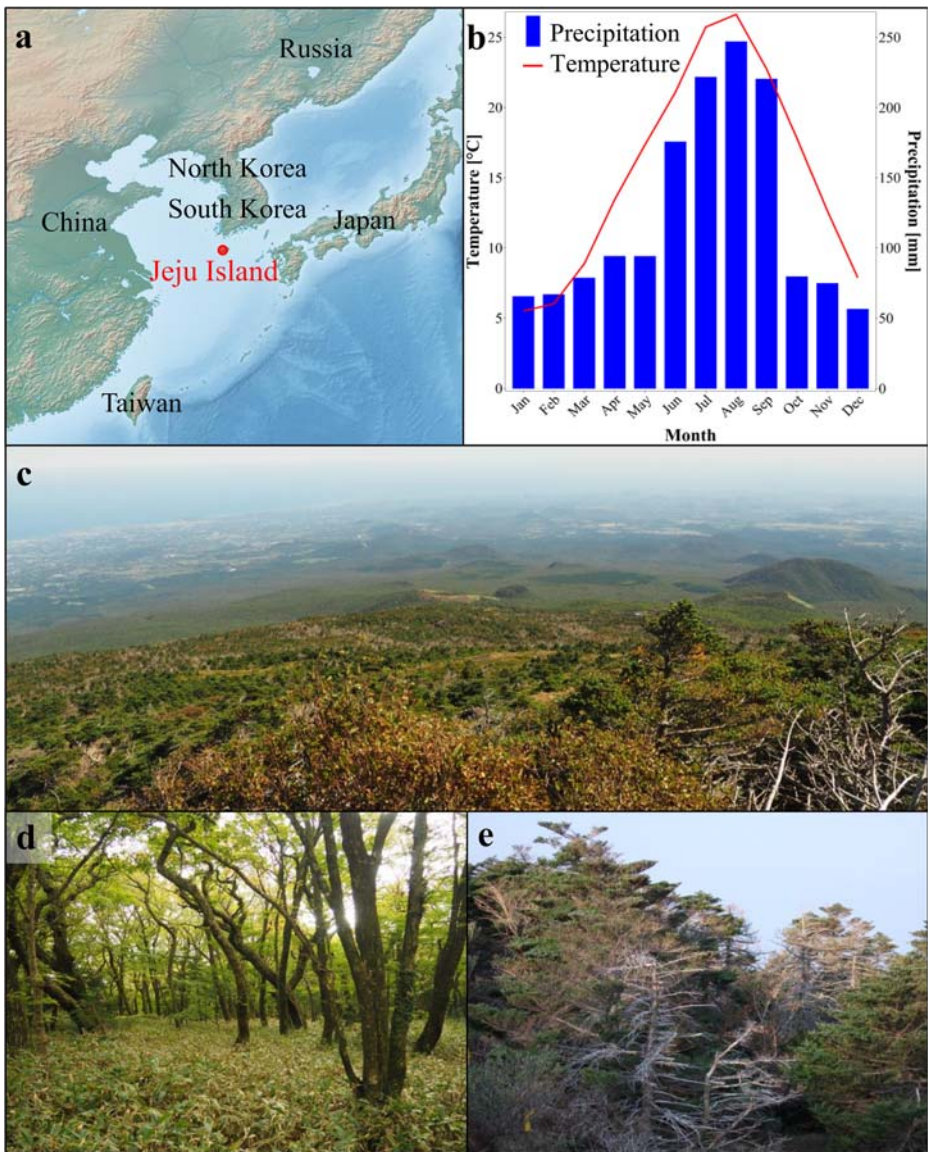


Fig. 1 **a** Location of Jeju Island, where Hallasan National Park is located, in East Asia; **b** climate diagram with mean monthly temperature and precipitation sums over the period 1945–2017 based on the data from Jeju City meteorological station; **c** landscape of Mt. Hallasan with **d** cool-temperate broadleaved forests dominated by *Quercus mongolica* occurring from ca 1100–1500 m a.s.l. and **e** mountain-temperate forests dominated by *Abies koreana* occurring from ca 1500–1900 m a.s.l.

5.5 °C, and mean August temperature is 26.6 °C (for details, see Fig. 1b). Mt. Hallasan's mean temperature lapse rate is 6.43/1000 m (s.d. = 1.78) (Hagedorn et al. 2014).

Despite the long-lasting human influence on the island, the natural forests at higher elevations are well-preserved (Yim et al. 1990) and include two forest types: (1) cool-temperate broadleaved forests (1100–1500 m a.s.l.) dominated by QUMO (Fig. 1d), with co-dominants *Carpinus tschonoskii*, *C. laxiflora*, and *Acer pseudosieboldianum* and (2)

mountain-temperate forests (1500–1900 m a.s.l.) dominated by ABKO with high occurrence of *Betula ermanii* (Kang et al. 1997; Song 1991) (Fig. 1e), with a gradual transition between these two zones (1400–1550 m a.s.l.).

We investigated the two dominant tree species of these forest types: QUMO and ABKO. Both species form annual rings with distinct boundaries and are thus suitable for dendrochronological analyses (Altman et al. 2013; Zhang et al. 2019). QUMO is a deciduous species distributed throughout the Korean Peninsula, northern Japan, northeastern China, eastern Russia, and the Sakhalin Island. ABKO is an endemic species in Korea and it is characterized as a light-demanding, fast-growing species vulnerable to wind-breakage and uprooting.

2.2 Data collection

2.2.1 Tree-ring data

We collected radial increment cores in 10 plots along an altitudinal gradient (1130–1930 m a.s.l.; Table 1) on the north-eastern slope of Mt. Hallasan continuously from 2007 to 2011, with last additional sampling done in 2017. Five plots were located in a natural forest dominated by QUMO (1130–1500 m a.s.l.) and five in a natural forest dominated by ABKO (1430–1930 m a.s.l.). All individuals (> 7 cm diameter at breast height) of the target species within each plot were sampled at breast height using 5 mm increment borers (Haglöf, Sweden). We collected one core per tree parallel to the slope to avoid reaction wood. In total, 207 QUMO trees and 183 ABKO trees were sampled (Table 1).

The cores were dried and their surface prepared for tree-ring width measurements using a core-microtome (Gartner and Nievergelt 2010) and chalk to highlight the tree-ring boundaries. Tree-ring widths were measured from pith to bark to the nearest 0.01 mm using the TimeTable measuring device and PAST5 software (www.sciem.com). We measured earlywood (EW) and latewood (LW) widths separately at the lowest and highest elevations for each species, i.e. 1130 and 1500 m a.s.l. for QUMO and 1430 and 1900 m a.s.l. for ABKO, to have extra information about intra-annual growth responses at the edges of species distributional limits.

Table 1 Basic characteristics of the individual tree-ring width chronologies (ID) of both species. Number of trees included in chronologies (no. trees), their mean age, length of period with Expressed Population Signal (EPS) > 0.85, Baillie-Pilcher's *t*-value (TBP), and Gleichläufigkeit (GLK) are shown

	ID	Altitude	No. trees	Mean age	EPS > 0.85	TBP	GLK [%]
<i>Abies koreana</i>	ABKO5	1930	31	60	1938–2010	4.76	68
	ABKO4	1750	79	42	1942–2006	5.08	68.9
	ABKO3	1620	31	73	1934–2009	6.02	70.9
	ABKO2	1550	30	59	1919–2006	5.17	67.1
	ABKO1	1430	12	55	1961–2010	5.69	68.7
<i>Quercus mongolica</i>	QUMO5	1500	27	67	1922–2010	9.33	71.3
	QUMO4	1430	45	73	1928–2010	8.61	72.5
	QUMO3	1320	82	77	1889–2010	7.7	73
	QUMO2	1230	38	154	1830–2010	11.4	73
	QUMO1	1130	15	138	1859–2007	8.89	70.6

2.2.2 Climate data

For temperature and precipitation data, we used instrumental records instead of gridded extrapolated datasets based on sparse and distant climate stations. Monthly mean temperature and precipitation data were obtained from the meteorological station in Jeju City (33.52° N, 126.53° E; 22 m a.s.l.) (Peterson and Vose 1997), which covers the period 1945–2016. However, to investigate the impact of drought on tree growth, we used the monthly $0.5^\circ \times 0.5^\circ$ -gridded Standardized Precipitation-Evapotranspiration Index (SPEI) (Vicente-Serrano et al. 2010a, b) for the grid cell 33–33.5° N and 126.5–127° E (Harris et al. 2014; www.climexp.knmi.nl). We examined growth-climate relationships based on the period of overlap (1945–2013) of the instrumental (temperature and precipitation) and gridded (SPEI) climate data. We examined the occurrence of trends in 3 months seasonal climate time series with a linear regression model. We identified a rising trend in temperature for all four seasons over the entire period (Fig. 2), but no significant trend for precipitation (Fig. S1) or SPEI (Fig. S2).

2.3 Data analysis

2.3.1 Tree-ring width data

Individual tree-ring width series were first visually cross-dated (Yamaguchi 1991) and visual cross-dating was statistically verified based on the percentage of parallel variation ($p < 0.05$, Gleichläufigkeit; see Eckstein and Bauch (1969)) and the similarity of growth patterns (Baillie-Pilcher's t value; see Baillie and Pilcher (1973)). Only well cross-dated series, i.e. series with Gleichläufigkeit $> 65\%$ and $t > 4.5$ between individual series and mean plot chronology, were used in further analyses.

To remove non-climatic age-related growth trends in the time series, a negative exponential curve or a linear model with negative or zero slope (to preserve positive trends presumably due to climate in the raw data series) was fitted to each measured series and ratios from the fitted growth curves were calculated in the software program ARSTAN (Cook and Holmes 1996).

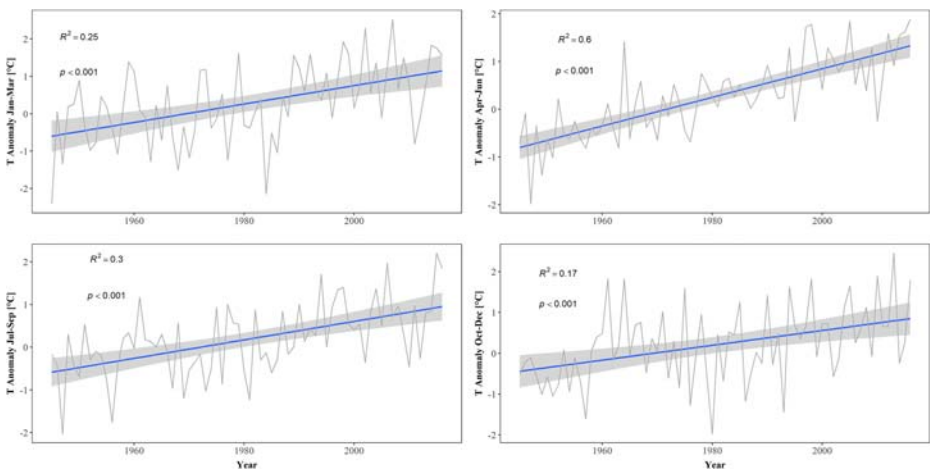


Fig. 2 Time series of mean seasonal (3-month) temperature (T) anomalies from 1945 to 2016 based on records from the meteorological station in Jeju City. All four seasons showed a significant increase in temperature. Strength of the relationships is indicated by adjusted coefficient of determination (R^2) level of significance (p), and 95% two-sided confidence interval (grey area)

The expressed population signal (EPS) was calculated with a threshold of 0.85 to estimate sample size adequacy and length of individual plot-based chronologies used in subsequent analyses (Wigley et al. 1984). A mean chronology that fulfils the required EPS selection threshold is expected to capture the climatic signal recorded in tree-ring width variation of a given population. Thus, we created ten plot chronologies based on whole tree-ring width (WTR), i.e. five for QUMO and five for ABKO (Table 1). In addition, we developed earlywood and latewood width chronologies for the uppermost and lowermost plots for both species (see data collection), i.e. four plots with eight additional chronologies. Our data set for further analysis thus includes 18 chronologies in total.

2.3.2 Dendroclimatological analysis

The relationships between the tree-ring width chronologies and the climatic variables were assessed based on bootstrapped Pearson's correlation estimates. Bootstrapped confidence intervals were used to estimate the significance ($p < 0.05$) of the correlation coefficients (Zang and Biondi 2015). We performed two bootstrapped analyses for each chronology: (1) static and (2) moving correlation function.

We calculated the static bootstrapped correlations based on the same, common time period for all 18 chronologies (1961–2006), defined by the shortest chronology. This enabled us to compare results without potential bias introduced by utilization of different length of time series. Bootstrapped correlation coefficients were calculated for monthly climate variables starting in previous year October through current September (12 months).

We fitted linear regression and polynomial regressions (of second and third degree) to identify trends in growth-climate response along the latitudinal gradient for individual species. The strength of regressions was tested using analyses of variance. However, polynomial regressions did not identify any significant trends due to the low number of sites per species to fit. Thus, we present results from linear regression only.

For the moving correlation analysis, we applied a 25-year moving window at a 1-year offset with correlation values plotted on the first year of the running correlation window. Moving correlations were calculated for 3-month seasons: winter (January–March), spring (April–June), summer (July–September), and autumn (October–December) for the period starting in 1945 until the last year of chronology (Table 1). Time-varying bootstrapped correlation functions allow us to evaluate the stationarity of dendroclimatic responses (Biondi 2000). We fitted a locally weighted scatterplot smoothing curve (Cleveland et al. 1990), which is frequently used in natural sciences to find trends in time series (Rojo et al. 2017), to highlight the long-term trend in growth responses to climate (Carrer et al. 2010; Di Filippo et al. 2007; Wasserstein et al. 2019). All dendroclimatological analyses were performed with the “treeclim” R package (Zang and Biondi 2015) and plotted with the R package “ggplot2” (Wickham 2009) in R (R Core Team 2019).

3 Results

3.1 Tree-ring width chronologies

The longest chronologies spanned the period 1830–2010 for QUMO and 1919–2006 for ABKO (Fig. 3, Table 1). In general, inter-series similarities were higher for QUMO

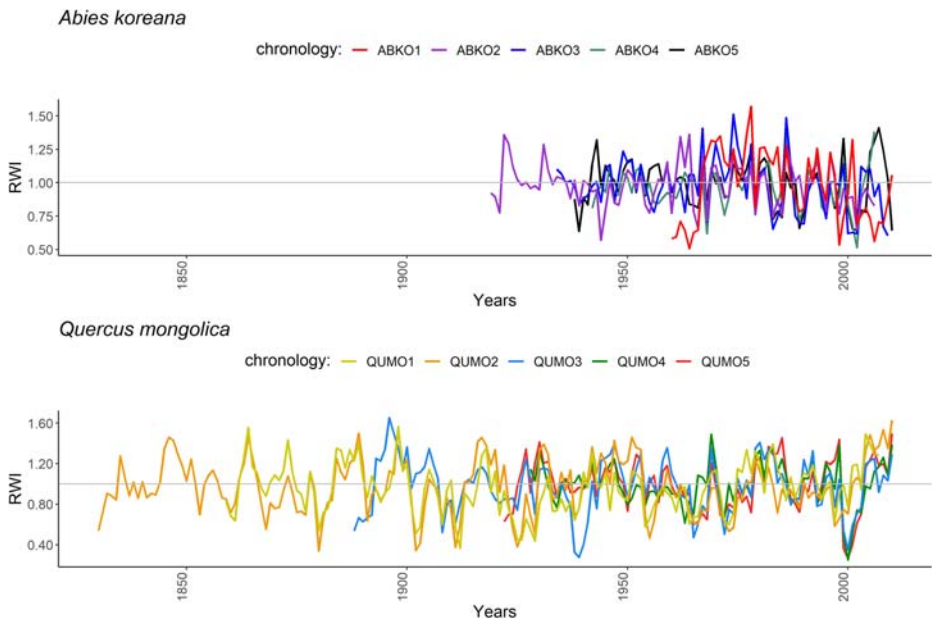


Fig. 3 Ring width index (RWI) of WTR chronologies for *Abies koreana* (ABKO) and *Quercus mongolica* (QUMO). Only parts of chronologies with the EPS > 0.85 are shown. For more information about individual chronologies, see Table 1

chronologies than for ABKO chronologies (Table 1), suggesting that QUMO chronologies have a stronger common signal than ABKO chronologies. Similarly, inter-plot correlations were higher for QUMO compared to ABKO chronologies with higher similarity at higher elevations (Table S1).

3.2 Growth-climate relationships

WTR growth of QUMO was influenced most strongly by monthly SPEI ($r = -0.23$ to $+0.38$), compared to precipitation ($r = -0.25$ to $+0.32$) and temperature ($r = -0.13$ to $+0.22$) (Fig. 4a). Growth increased significantly with higher SPEI for previous November (for elevations 1320, 1430, and 1500 m a.s.l.), previous December (1230 m a.s.l.), and current February (1320 m a.s.l.). Precipitation only influenced growth significantly at one site (1430 m a.s.l.) during previous November ($r = 0.32$, $p < 0.05$). When looking at QUMO EW and LW growth separately (Fig. S3A), we found that EW growth at the lowest elevation (1130 m a.s.l.) was negatively affected by temperature during previous November ($r = -0.21$; $p < 0.05$) and current July ($r = -0.28$; $p < 0.05$) and August ($r = -0.34$; $p < 0.05$) and positively by March precipitation ($r = 0.34$; $p < 0.05$). These results are in line with the positive relation between EW growth (1130 m a.s.l.) and SPEI in March ($r = 0.41$; $p < 0.05$) and August ($r = 0.42$; $p < 0.05$). At high elevation (1500 m a.s.l.), LW QUMO growth was significantly correlated only with previous November SPEI ($r = 0.31$; $p < 0.05$), which is in line with the results we found for WTR.

ABKO growth, in contrast, was most strongly, negatively influenced by temperature ($r = -0.39$ to $+0.08$), yet no significant correlation was found with SPEI ($r = -0.25$ to $+0.22$) (Fig. 4b). At the lowest elevation ABKO site, we found negative temperature-growth relationships throughout the year (previous November, January, February, March, August, and September). ABKO growth responded

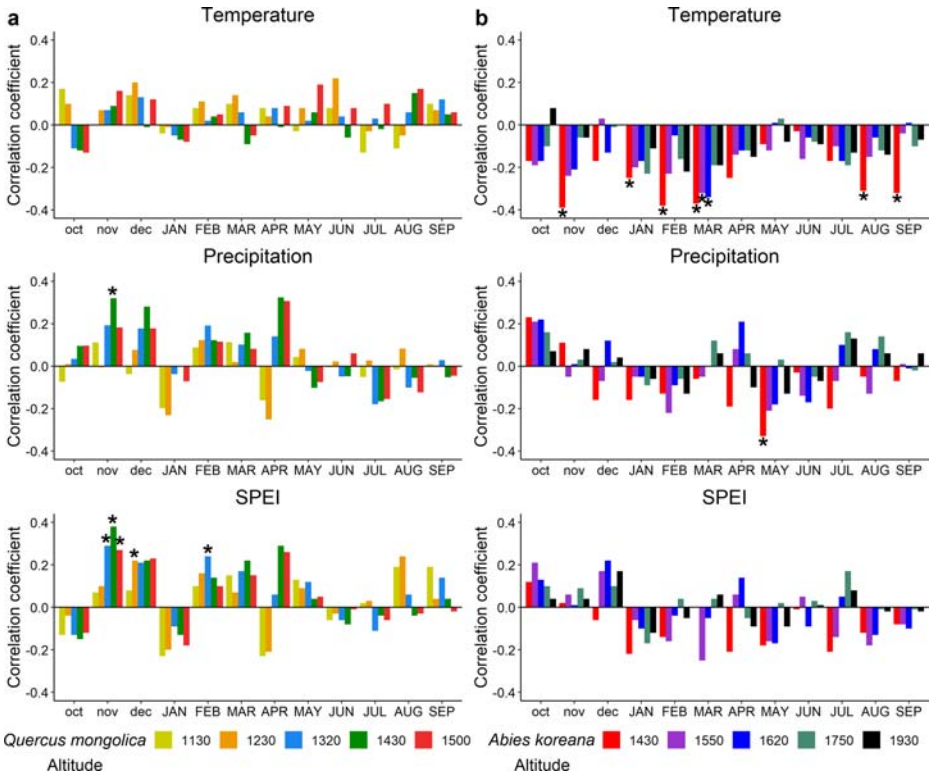


Fig. 4 Relationships between WTR indices and climate at individual sites along the altitudinal gradient for **a** QUMO and **b** ABKO. Growth responses to climate are based on bootstrapped correlations between standardized chronologies and monthly mean temperature, precipitation, and SPEI for the period 1961–2006 (EPS > 0.85 for all chronologies). Significant correlation coefficients ($p < 0.05$) are flagged by asterisk (*). Months abbreviated with lowercase letters correspond to the year prior to ring formation and uppercase letters refer to the current growth year

negatively to March temperature at three lower elevation sites (1430–1620 m a.s.l.). The negative impact of temperature on low-elevation ABKO growth was also reflected in the growth-climate relationships of the EW and LW chronologies during the same months as WTR (Fig. S3B). In addition, LW growth was negatively affected by August and September temperatures at the highest elevation site. EW at lower elevation was further negatively influenced by May precipitation ($r = -0.37$; $p < 0.05$) and by April SPEI ($r = -0.22$; $p < 0.05$).

3.3 Trends in growth-climate relationship along altitudinal gradient

We identified seven significant altitudinal trends in growth-climate relationship for QUMO (Figs. 5 and S4). The most pronounced difference in growth response along the altitudinal gradient occurred for SPEI and precipitation in April, when wet conditions were limiting QUMO growth at lower altitudes and enhancing it at higher altitudes (Figs. 5 and S4). The same relationships, but with a less pronounced trend, were identified for previous October precipitation, previous November temperature, and current August temperature (Fig. 5). The opposite trend, i.e. more positive growth-climate relationship at lower elevation sites compared to higher elevations, was identified for previous October temperature and current August SPEI (Fig. 5).

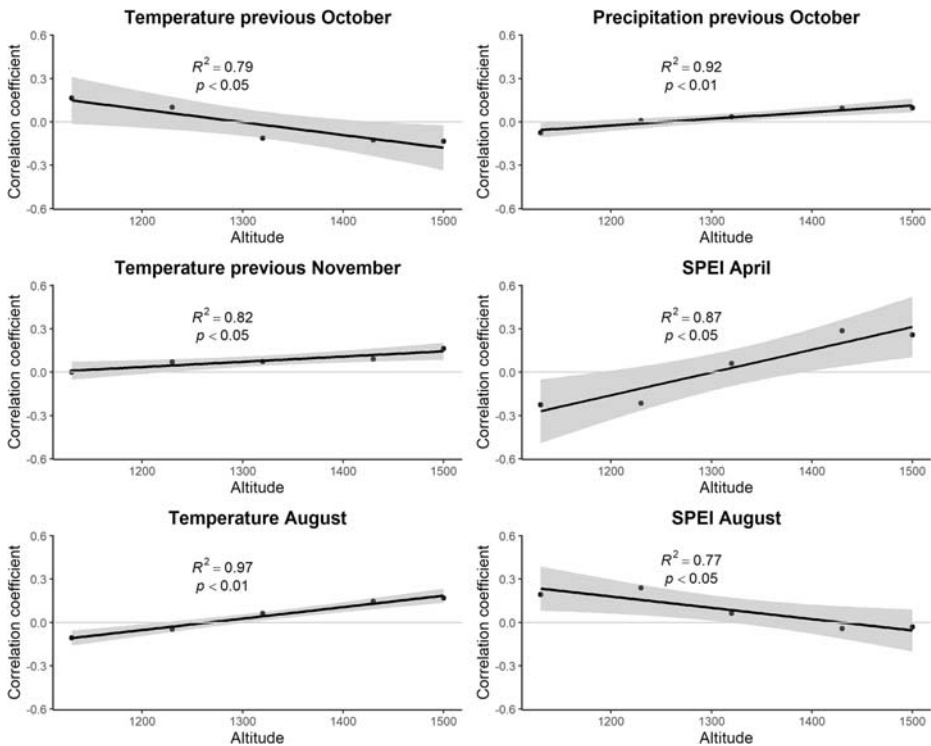


Fig. 5 Significant trends (solid lines) in relationships between WTR indices and climate along the altitudinal gradient for QUMO. Trend for April precipitation is almost identical with April SPEI (see Fig. S4). Strength of the relationships is indicated by adjusted coefficient of determination (R^2), level of significance (p), and 95% two-sided confidence interval (grey area)

For ABKO, we found four significant altitudinal trends in growth-climate relationships (Figs. 6 and S5). Growth-temperature relationships for previous October, November and current March increased with increasing altitude (Fig. 6). On the other hand, the growth-precipitation relationship for previous October slightly decreased with increasing altitude (Fig. 6).

3.4 Temporal trends in growth-climate relationships

QUMO growth-climate relationships were non-stationary and stronger at higher elevation compared to lower elevation (Figs. 7, S6, and S7). Apart from the influence of previous autumn SPEI and precipitation, which decreased steadily over time until the early 1970s, relationships with most climate parameters lacked a prevailing positive or negative trend (Figs. 7, S6, and S7). The influence of summer SPEI and precipitation on QUMO growth, however, switched from positive to negative in the 1960s, except at the lowest elevation (1130 m a.s.l.). The influence of temperature on QUMO growth peaked in the 1960s for previous autumn and current spring temperature, after which it showed a slight decrease (Fig. S7). In the most recent decades, since the 1970s, summer temperature has started to influence QUMO growth positively, especially at higher elevation (Fig. S7).

Like for QUMO, ABKO growth-climate relationships were generally strongest at higher elevations (Figs. 8, S8, and S9). At all but the highest elevation, the growth-temperature

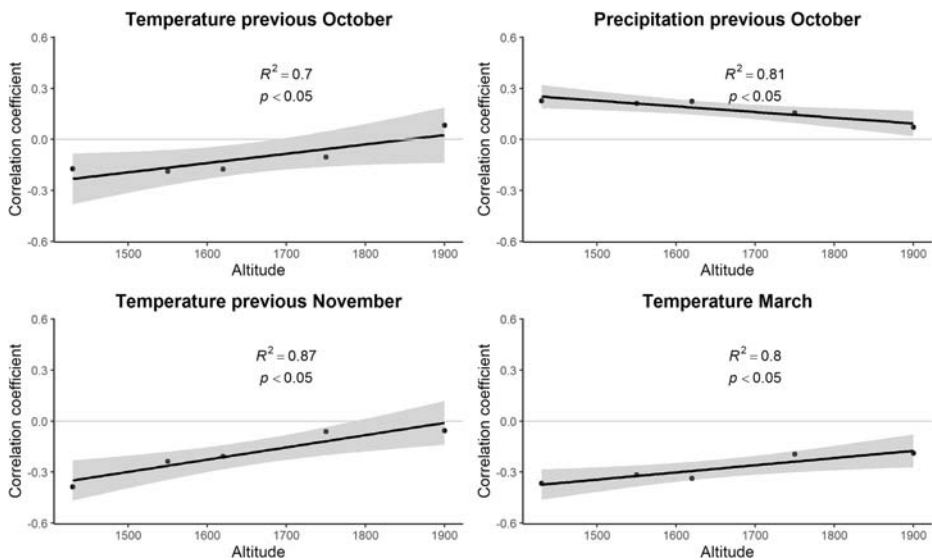


Fig. 6 Significant trends (solid lines) in relationships between WTR indices and climate along the altitudinal gradient for ABKO. Strength of the relationships is indicated by adjusted coefficient of determination (R^2), level of significance (p), and 95% two-sided confidence interval (grey area)

relationships generally showed a decreasing trend over time for all four seasons (Fig. 8). At the highest elevation, however, the influence of previous autumn temperature on ABKO growth has become more positive starting in the mid-1970s (Fig. 8). The influence of summer precipitation on ABKO growth switched from negative to positive in the 1960s at the three highest elevation sites (Fig. S8), and similarly the influence of summer SPEI on ABKO has become more positive at the middle-elevation site (1550 m a.s.l.) (Fig. S9). EW and LW growth responses to climate of both species mostly followed the trends described above for WTR growth (Figs. S10–S15).

4 Discussion

We present dendroclimatology of QUMO and ABKO that contributes to a better understanding of the response of these dominant tree species to recent climate change and of their capacity to adapt to these rapid changes in the forest types they dominate. We found distinct differences in the age structure between QUMO and ABKO. With 181 years (1830–2010) our QUMO chronology from a lower elevation (1230 m a.s.l.) site covers the longest period of all species investigated so far at Jeju Island (Kim et al. 2017; Seo et al. 2019; Zhang et al. 2019). Frequent tropical cyclones are the main disturbance agent preventing these forests from ageing, especially at exposed parts of Mt. Hallasan (Kim et al. 2017). Conifers often experience more damage than broadleaves (Yoshida and Noguchi 2009) and damage increases with altitude (Dhôte 2005; Ishizuka et al. 1997), which is also supported by the elevational gradient in our tree-age distribution (Table 1).

Due to its limited longevity and its relatively weak growth-climate relationships, ABKO has been the subject of only a few dendroclimatological studies (Koo et al. 2001; Zhang et al. 2019). Surprisingly, given its higher longevity, this is also the case for QUMO (Lyu et al.

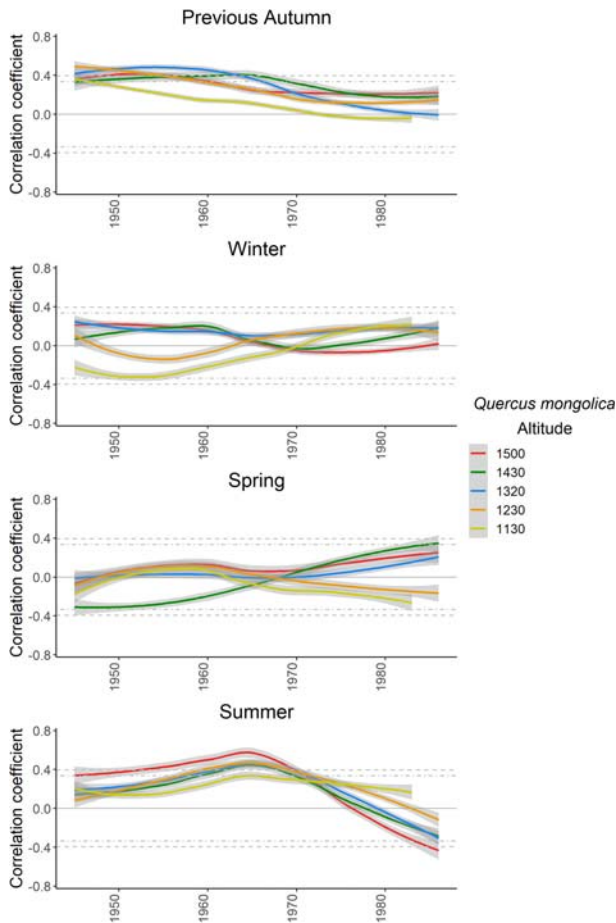


Fig. 7 Moving correlation coefficients (25-year moving window) for QUMO WTR-SPEI relationship for previous autumn (October–December), winter (January–March), spring (April–June), and summer (July–September) along the altitudinal gradient. The different length of correlations for individual chronologies was determined by $EPS > 0.85$ and/or sampling year (see Table 1). Years (x-axis) refer to the first year of the 25-year moving window. Grey area corresponds to 95% confidence interval. Dot-dash and dashed lines represent significance levels of $p = 0.1$ and $p = 0.05$, respectively

2017), even including the closely related *Quercus crispula* species (Jacoby et al. 2004; Nakatsuka et al. 2004). Unlike many other species (Chen et al. 2011), ABKO already occupies the highest elevations available in its natural fragmented distribution and cannot move higher. Thus, such species are even more vulnerable to rapid environmental changes and we should improve our understanding to introduce policy that can help prevent their strong decline or even extinction (Sax et al. 2013).

The strength of growth-climate relations, as well as their temporal trends, differed along the elevational gradient for both species. Growth-climate relationships commonly vary in time (Carrer et al. 2010), but the relatively large temporal fluctuations we found between positive and negative relationships probably contributed to the low number of statistically significant static correlation coefficients. Persistent trends or sudden shifts in growth-climate relationships, however, are reliable indicators of changing tree growth responses to climate (Di Filippo et al. 2007).

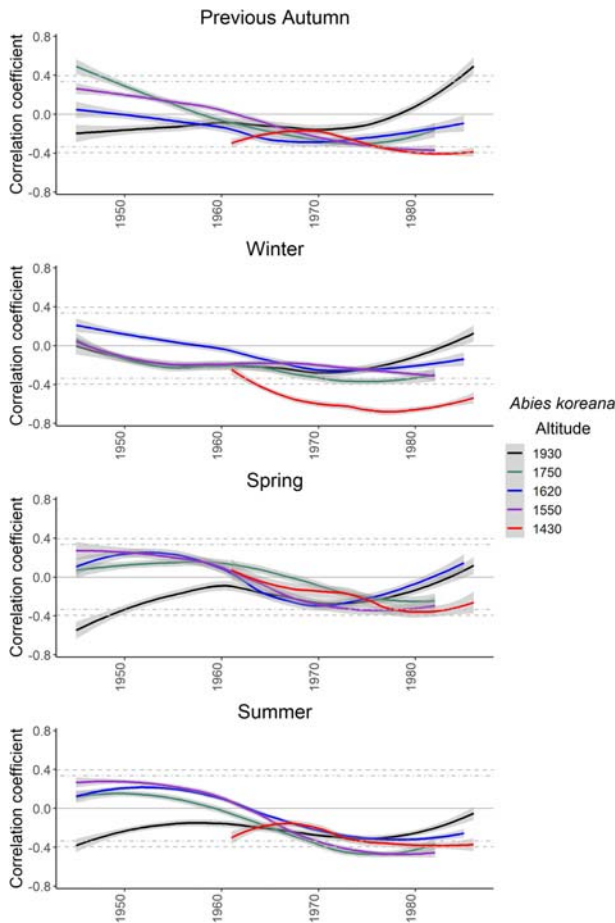


Fig. 8 Moving correlation coefficients (25-year moving window) for ABKO WTR-temperature relationship for previous autumn (October–December), winter (January–March), spring (April–June), and summer (July–September) along the altitudinal gradient. The different length of correlations for individual chronologies was determined by $EPS > 0.85$ and/or sampling year (see Table 1). Years (x-axis) refer to the first year of the 25-year moving window. Grey area corresponds to 95% confidence interval. Dot-dash and dashed lines represent significance levels of $p = 0.1$ and $p = 0.05$, respectively

Radial growth of QUMO was enhanced by wet conditions during the previous autumn at the upper part of its elevational distribution. This finding contradicts the commonly found trend that drought limitation dominates at the lower distributional limits (Alexander et al. 2018; Altman et al. 2017). Low impact of previous autumn drought on QUMO growth at its lowest distributional limit is likely caused by higher water availability there compared to higher elevations. This is due to a specific combination of outflow through porous lava from higher elevations, gentle slopes that enable longer water availability, and deeper soils that increase the amount of water that can be stored (Kim and Kim 2000; Körner 2007).

The impact of drought on QUMO growth was not stable over time. Prior to the 1970s, the previous autumn and the current summer drought conditions were primary factors limiting growth of QUMO at all elevations. These drought effects on QUMO growth, however, diminished in recent decades and remained positive only in summer at the lowest elevation.

Precipitation and SPEI did not show any long-term trends over the investigated period and we therefore suggest that temperature is the factor modulating the trend in growth response to drought (Williams et al. 2013). Late twentieth century warming might have enhanced QUMO growth by stimulating photosynthesis as previously found for other deciduous species (Way and Oren 2010) and oak in particular (Martínez-Sancho et al. 2018). However, the negative summer drought impact on QUMO growth was persistent at the lowest elevation and we expect that QUMO growth will decline under future warming as commonly identified for species at lower distribution limits (Martin-Benito et al. 2018). Differing responses of QUMO growth to autumn and summer droughts at the lowest elevation compared to higher elevations thus suggest the importance of the autumn rains for tree recovery after negative impacts of summer drought on stem biomass allocation (Vaz et al. 2010).

For subalpine ABKO, temperature was the main climatic factor controlling growth. Elevational differences in ABKO growth-temperature relationships, with stronger negative correlations at lower elevations, are in line with commonly identified patterns (Altman et al. 2017; Wang et al. 2017b). Interestingly, however, negative growth-temperature relationships dominate ABKO growth even at the highest elevations, although they were noticeably more negative at lower sites. Thus, although the commonly identified trend of increasing growth-temperature correlations with increasing altitude was identified, absence of positive growth-temperature correlation at higher altitudes is against the commonly found growth patterns. Winter temperature as a dominating factor for ABKO growth was previously identified by Koo et al. (2001). A possible explanation is that warm winter air in combination with frozen soil causes wintertime drought damage (Sevanto et al. 2006) and/or soil-frost related root injury (Kreyling 2010) and that lower elevations are more exposed to such effects. The overall dominance of negative growth-temperature relationships is in contrast with the positive influence of temperature on ABKO growth found by Zhang et al. (2019). This is particularly the case for August temperatures, which were limiting for growth at most of our sites, including LW growth at high elevation and WTR, EW, and LW growth at lower elevation, but were found to enhance growth in the Zhang et al. (2019) study. This might be explained by the fact that the study site of Zhang et al. (2019) was located on the opposite slope of Mt. Hallasan and at 1640 m a.s.l., the elevation with the weakest August temperature influence across our gradient. Such differences between studies can further be caused by different time-window lengths (1962–1998 in Koo et al. (2001), 1973–2016 in Zhang et al. (2019), 1961–2006 in this study).

The temporal trend in ABKO growth-temperature relationships varied at higher elevation sites and consistently decreased over time at the lowest elevation site. However, due to absence of older trees at the lowest elevation, we cannot exclude that this site had a similar evolution of temperature-growth relationships as higher elevation sites. At all but the highest elevation site, temperatures became increasingly important for ABKO growth over time (with the exception of spring temperatures at 1620 m a.s.l.). At the highest elevation, however, increasing temperatures since the 1970s have led to ABKO growth enhancement, not reduction, particularly in previous autumn. Temperature as an increasingly limiting factor for ABKO growth at lower elevations can be related to lower photosynthetic rates of ABKO under warmer air temperatures (Woo et al. 2008). Our findings at lower elevation are in line with negative warming effects on the growth at warm edge limits of other fir (*Abies*) species, e.g. in the Mediterranean (Sánchez-Salguero et al. 2017a), Asia (Wang et al. 2017a; Yun et al. 2018), and North America (Reich et al. 2015), and thus indicate global vulnerability of firs to warming climate.

Our results suggest that QUMO, as an early invader of disturbed areas with the ability to quickly dominate stands (Suh and Lee 1998) in combination with warming-enhanced growth at its upper distributional limit, has potential to further reduce ABKO distribution (Park et al. 2018). The only ABKO population profiting from warming temperatures is located at the peak of highest mountain of South Korea and thus lacks the option of migrating to higher elevation. In addition, QUMO and ABKO differ in their physiological adaptations to climate change, which is reflected in their growth-climate relationships. Specifically, photosynthetic rate, stomatal conductance, transpiration rate, and water use efficiency of QUMO have been documented to maintain the growth potential in the warming climate and precipitation fluctuations (Cheng et al. 2011). ABKO, on the contrary, has very limited possibilities to physiologically adapt to these climate changes as its photosynthetic rate is significantly reduced during drought, especially under full sunlight (Je et al. 2018). Furthermore, subalpine ABKO populations are most vulnerable to disturbance by tropical cyclones (Kim et al. 2017), which increases the chance for ABKO's complete extinction at Jeju Island (Yun et al. 2018). Hence, combining knowledge from various research fields (ecology, physiology, genetics, modelling, growth) to investigate ABKO decline will provide strong support for active conservation of these highly vulnerable populations (Liang et al. 2018). Targeted protection of thermal microrefugia (Koo et al. 2017) together with active management (Yun et al. 2018) focusing on heat tolerant individuals (Hwang et al. 2018) are necessary under projected climate warming (Brown and Caldeira 2017; Li et al. 2018).

5 Conclusion

Our dendroclimatological study provides insight into the radial growth variability of two interacting tree species in warming climate along an elevational transect that spans their entire vertical distributional range. Specifically, we provide new long-term evidence of a strong negative impact of recent warming on ABKO growth at the lower part of its distribution. Our findings indicate potential expansion of QUMO to higher altitudes as recent warming has enhanced QUMO growth at its higher distribution. On the contrary, increasing temperatures have led to ABKO growth reduction at all elevations, except the highest locality. Thus, combination of warming, increasing competition, and frequent tropical cyclone disturbances can lead to population decline or even extinction of ABKO at Jeju Island. Active management is necessary to mitigate impacts of projected climate changes on ABKO. We highlight the importance of multi-species studies along environmental gradients to provide evidence about the impact of climate change on forest ecosystems.

Acknowledgements We thank Eva Navratova and Tomas Plener for help with tree-ring width measurement and fieldwork.

Funding information The study was funded by research grants 17-07378S, 20-05840Y, and 17-19376S of the Czech Science Foundation, MSM200051801 of the Czech Academy of Sciences, and long-term research development project No. RVO 67985939 of the Czech Academy of Sciences. KT acknowledges funding by the Swiss National Science Foundation (SNF 200021_175888).

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