NEMORAL EUROPEAN BEECH AND OAK FORESTS UNDER CLIMATE CHANGE

A "space for time approach" investigating a climate warming driven shift from mesic beech forests towards thermophilic oak forests in Central Europe explored at the climatic beech–oak ecotone in western Romania

Dissertation

for the award of the degree
"**Doctor rerum naturalium**"
of the Georg-August-Universität Göttingen

within the doctoral program Biodiversity and Ecology
of the Georg-August-University School of Science (GAUSS)

doi:10.53846/goediss-9885

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Göttingen, 2022

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Date of the oral examination: 23/06/2022

Summary

Global warming and increasing drought severity are exposing temperate forests to higher stress levels, challenging forest management in the 21st century. With a projected warming by 2–3 K until 2070, silvicultural adaptation measures and natural succession might lead to the replacement of European beech forests by thermophilic oak forests in drought- and heat-affected regions of Central Europe. According to RCP scenarios (RCP2.6, RCP4.5 and RCP8.5), parts of western Romania, where beech naturally occurs at its dry-warm distribution limit, are climatically analogue to predictions for large regions of Central Europe. In a "space for time approach" we investigate impacts on ecosystem carbon storage and tree vitality for a climatically driven shift in forest structure. Therefore, we systematically sampled soils and forests over natural beech–oak ecotones, quantifying storage changes in above ground biomass carbon (AGC) and soil organic carbon (SOC) between beech (*Fagus sylvatica*) dominated forests and oak (*Quercus petraea, Q. frainetto, Q. cerris*) dominated forests. Precise predictions of climate change impacts on forests also require a better species-specific and site-specific understanding of how tree growth and tree climate relationships are affected. We assessed tree vitality in these beech–oak ecotones, by analyzing tree-ring records and investigating long-term growth-trends, resilience of radial growth to drought, growth climate sensitivity, spatiotemporal patterns of climatic sensitivity and growth synchronicity for beech populations, the three oak species and silver linden (*Tilia tomentosa)*, a further dominant species.

Our results show that a climate-warming related replacement of beech by oak forests in the course of natural forest succession or silvicultural decisions may considerably reduce ecosystem carbon storage of central European woodlands. From the cooler, more humid beech forests to the warmer, more xeric oak forests, which are 1–2 K warmer, AGC and SOC pools decrease by about 22 % (40 Mg C ha^{-1}) and 20 % (17 Mg C ha^{-1}), respectively. Tree-growth-climate analysis show, that radial growth of all species is positively influenced by summer precipitation and low drought intensity, and negatively by high summer temperatures. Basal area increment (BAI) of beech and linden declined in the last 10–20 years in coherence with climate warming and a deterioration of the summer water balance, while the three oak species maintained stable growth rates, though at lower BAI levels, suggesting a negative relationship between mean BAI and drought resistance among the five species. Spatiotemporal patterns of climatic sensitivity show that the importance of summer precipitation increased after the onset of climate warming (~ 1980), while other climate factors in spring and summer became less important. Accordingly, growth synchronicity, as a measure of common climatic stress among

tree individuals, increased or remained constant for the drought sensitive beech and linden and decreased in the past decades for the oak species. The differences in growth synchrony during recent climate warming indicate a better drought adaption of oak species, a conclusion which is supported by the results for the long-term growth dynamics, showing enhanced BAI for oak in comparison to beech and linden in the last decades.

Our results demonstrate that choosing stress-tolerant oaks instead of more productive timber species such as beech is a relatively safe option for Central European forestry in a warmer climate. However, if drought- and heat-affected beech forests in Central Europe are replaced by thermophilic oak forests in future, this will lead to carbon losses of ~ 50–60 Mg ha^{-1}, thus reducing ecosystem carbon storage substantially.

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CHAPTER I

GENERAL INTRODUCTION

1 General Introduction

1.1 Climate change and the RCP scenarios

Rising atmospheric concentrations of climate relevant greenhouse gases, which are primarily water vapor (H_2O), carbon dioxide (CO_2), methane (CH_4), nitrous oxide (N_2O), and ozone (O_3) are the main drivers for climate change. Following the latest report from the Intergovernmental Panel on Climate Change (IPCC, 2021), anthropogenic activities have increased the atmospheric concentration of CO_2 by approximately 50 %, from 280 ppm to 419 ppm in 2021, and consequently has the mean global surface temperature risen by 1.09 °C in comparison to pre-industrial levels (reference year 1850). At the ongoing rate, even if CO_2 emissions would be globally reduced, temperatures will still surpass the in the Paris Agreement declared critical threshold of a 1.5 °C within the next decades (IPCC, 2021). The effects of these changes are being seen worldwide through increasing intensities of storms, flooding, extended drought periods, weather anomalies or other extreme weather events and their devastating impacts are affecting ecosystems and society (Haines et al., 2006; Kornhuber et al., 2019; Lesk et al., 2016; Lindroth et al., 2009; Mitchell et al., 2016; Wenz and Levermann, 2016). In central Europe climate change has already manifested itself in form of a higher frequency and severity in drought spells and heat waves in the last decades, e. g. in the years 2003, 2015 and 2018–2020 and the way things are developing, these conditions will maintain or increase in future (Barriopedro et al., 2011; Büntgen et al., 2021; García-Herrera et al., 2010; IPCC, 2021; Schönwiese et al., 2005; Schuldt et al., 2020).

For a prediction of future climates scientists developed the Representative Concentration Pathways scenarios (RCP), which were first published in the IPCC's 5th Assessment Report (IPCC, 2013), thus replacing the preceding Special Report on Emissions Scenarios (SRES). The four developed climate models (RCP2.6, RCP4.5, RCP6, and RCP8.5) represent a large set of probabilistic scenarios and are currently the most acknowledged models for a future climate. The term “concentration pathways” describes the model’s implications of greenhouse gas concentrations and radiative forcing as parameters, differing to the earlier SRES climate scenarios, which are mainly based on socioeconomic trends. Hence the RCP climate projections use radiative forcing (in W/m^2) and different predicted emission concentrations from 1850 (pre-industrial levels) to 2100 as well as socioeconomic and demographic trends to model climates (IPCC, 2021). Roughly described the moderate RCP 2.6 scenario represents a radiative forcing of 2.6 W/m^2 for the year 2100 and assumes that the world population increases to 9 billion but also includes climate protection measures put in place to lower anthropogenic emissions. The intermediate RCP 4.5 and RCP 6.0 presume a continual rise in greenhouse gas emissions in the next decades followed by a gradual decline (steady development) thereafter. The assumption of RCP 8.5 is that society continues to increase emissions and that the population climbs up to 12 billion by 2100. In the context of current developments in international decision making, population trends and growing economies, RCP 2.6 is an unlikely scenario and we are currently moving towards a RCP 4.5, 6.0 or even the 8.5 scenario (IPCC, 2021).

1.2 Forests and the effects of climate change

The role of forests as carbon sinks and their potential to mitigate climate change impacts has gained great attention in the past decades (IPCC, 2021; Nabuurs et al., 2015). About one third of the Earth's land area is covered by forests, which store around 45% of the terrestrial carbon (Bonan, 2008). Forests absorb CO_2 from the atmosphere through photosynthesis and store it in above- and belowground biomass or through decomposition of necromass as soil organic carbon. However, forests also emit CO_2 into the atmosphere through cell respiration and the net carbon balance for e.g. European forests was calculated at an annual rate of about 100 Tg (Luyssaert et al., 2010), making them long-term carbon sinks. In temperate forests, tree biomass generally represents the largest C pool (Knohl et al., 2003; Lal, 2005; Seedre et al., 2015) and the biggest part is stored aboveground, while coarse and fine roots represent a lower percentage (Kalyn and Van Rees, 2006; Vogt et al., 1996). Forest biomass is influenced by tree species, stand structure and stand age (Glatthorn et al., 2018; Leuschner and Ellenberg, 2017), where with increasing age biomass usually is accumulated (Pregitzer and Euskirchen, 2004). In managed forests these factors frequently underly silvicultural decision making, which strongly influences the sequestration potential of a forest (Borrass et al., 2017; Spathelf et al., 2018). Equally important for C accumulation are forest site characteristics such as climate, soil fertility and moisture, which can be stimulating or limiting factors (Babst et al., 2013; Gustafson et al., 2017; Oren et al., 2001). The effects of climate change on forest ecosystems and their carbon stocks are not always evident and while it is assumed that a higher frequency of drought periods will augment tree mortalities in Central Europe (Schuldt et al., 2020; Walker et al., 2021), rising temperatures, increased CO_2-levels and longer growing seasons can also stimulate tree growth. For example, in temperate European forests that are not limited by water, forest productivity and thus carbon sequestration, is expected to increase due to climate change effects (Gutsch et al., 2016; Lindner et al., 2010). Contrarily again, higher risks of extreme weather events such as storms extended droughts and ensuing wildfires are predicted to trigger carbon releases into the atmosphere (Lindroth et al., 2009; Vautard et al., 2019).

Forests play an important role in the global water cycle and also here, the effects of climate change are highly debated and at times controversial (Ellison et al., 2012; Luo et al., 2018). When precipitation infiltrates the forest ground either as direct throughfall, stemflow or following crown interception, it is absorbed by the vegetation and returned to the atmosphere through transpiration. The forest streamflow or water balance is determined by the precipitation amount, the loss through evapotranspiration (sum of transpiration and evaporation after interception with crown, stem or forest floor) and the change in water storage (Roberts, 2009). Forests store water and thus control flooding or flood routing, a function which can be lost when soils are fully saturated during or after extreme rainfall events (Eisenbies et al., 2007; Scherrer et al., 2007). This again affects forest soils as increased streamflow and flooding cause erosion (Fuhrer et al., 2006) with high impacts notably in poorly managed forests (Grace, 2004; Luo et al., 2018). Further projected impacts on the forest water cycle include lower soil moisture and reduced groundwater recharge or streamflow (Eckhardt and Ulbrich, 2003; Fuhrer et al., 2006; Reich et al., 2018). Carbon and nutrient dynamics of soils also depend on climate as the decomposition of organic matter is limited by temperature and water availability. Soil C stocks may either decrease due to accelerated decomposition and increased fire events or augment because of increased plant-derived C accumulation in the soil (Davidson and Janssens, 2006; Walker et al., 2021). Other expected climate change effects on forest ecosystems are declines or shifts in biodiversity (Mooney et al., 2009; VanDerWal et al., 2013) where species distribution adapts to warmer temperatures by retreating poleward or to higher elevations whilst again other species will benefit from climate warming with extended distribution ranges (Boisvert-Marsh et al., 2014; Chen et al., 2011; Hickling et al., 2006; Sittaro et al., 2017).

1.3 Beech and oak, two key species in deciduous forests of Central Europe

European Beech (*Fagus sylvatica* L.) is a mesophytic broadleaf tree endemic to Europe, which ecologically is the most important natural tree species. Its biology and ecology are well known, and it is characterized as occurring across a wide range of soil conditions and having a distribution range that is largely limited by climate (Fang and Lechowicz, 2006; Huntley et al., 1989; Leuschner and Ellenberg, 2017). Its vast distribution range in Europe is explained by an oceanic climate, where warm water from the Gulf Stream is carried with the North Atlantic Current towards the European continent creating warm and moist air masses. Westerly winds then carry these marine air masses far into the continent, which is facilitated by the lowland characteristics of western Europe. This produces a humid, temperate climate with cool winters and warm wet summers favouring beech domination. By nature, Germany would be 90% forested, of which about 67% would be occupied by beech-dominated forests (Bohn et al., 2000). Beech is very shade-tolerant and dominance in forests results in a reduction of light levels in the understory favouring its natural regeneration (Bolte, 2016). It is not particularly soil-sensitive and grows on a wide variety of soils, however it prefers moderately fertile soils which are lightly acidic or basic (pH 3.5–8.5). However, even highly acidic conditions are tolerated, provided that the mineral soil contact is guaranteed and there is no excessively thick raw humus cover. It therefore has no real nutrient deficiency limit (Leuschner and Ellenberg, 2017; Walthert et al., 2013). It grows well where the root system can easily penetrate into the soil and optimal growth is in humid mesic conditions with soft soils on calcareous or volcanic parent material. On the contrary, it does not flourish on sites that are regularly flooded, waterlogged or on compacted soils (Geßler et al., 2007; Packham et al., 2012). Despite its flexibility and broad climatic amplitude, beech depends on moderate temperatures and sufficient humidity. It is sensitive to drought, hot summers, very cold winters, and late frosts making it more vulnerable to water stress when compared to oaks and other coniferous species (Granier et al., 2007; Kasper et al., 2022; Leuschner and Ellenberg, 2017; Paule, 1995). Its thermal optimum is -1°C monthly mean for the coldest month of January and up to +18°C for the warmest month of July (Bohn et al., 2000; Huntley et al., 1989). Beech is widespread across Europe and can be found from Sicily in the South to Bergen in southern Norway. Longitudinally, its range is from the Cantabrian Mountains in the West to the Carpathians and Balkan Mountains in the East (Figure 1). At the southern and south-eastern part of its range it is normally present at higher altitudes (Bohn et al., 2000; Houston Durrant et al., 2016; Packham et al., 2012). High summer temperatures, drought and water availability are limiting factors for the distribution of beech in southern Europe, but continentality and frost also limits its range in north-eastern and eastern regions (Fang and Lechowicz, 2006).

Sessile oak (*Quercus petraea* (Mattuschka) Liebl.) is a large, deciduous tree native to most of Europe which is also one of the most economically and ecologically important species. It occurs at many sites as a main component of temperate deciduous mixed forests with a large ecological amplitude, sometimes also dominating forests at low and mid elevations (Bohn et al., 2000; Leuschner and Ellenberg, 2017). Sessile oak has a good re-sprouting ability, coppicing easily and deep taproots allow good access to water thus giving it structural stability against windthrow and a droughts resistance (Jones, 1959; Praciak et al., 2013). Sessile oak sprouts leaves relatively late in the year (Apr–May), what also makes it tolerant to late frost, unless temperatures are very low (Praciak et al., 2013). The canopy of the light-demanding tree permits light to pass through, promoting regeneration of many tree species and enriching forest diversity (Leuschner and Ellenberg, 2017). Its main competitor in deciduous forests of Europe is beech, in the presence of which it usually is unable to dominate on mesic stands. Therefore, sessile oak typically dominates on semi-dry or dry to warm soils, which are often slightly acidic, e.g. two-layer soils of loose sand on hardened clay, or shallow and rocky soils as on hill tops or slopes (Jones, 1959; Praciak et al., 2013). It often occurs with hornbeam (*Carpinus betulus*) and other deciduous tree species and is then assigned to the *Carpinion betuli* alliance (oak-hornbeam forests) replacing beech when out of its ecological range (Leuschner and Ellenberg, 2017). Sessile oak occurs across most of Europe, extending northwards to southern Scandinavia and southwards to the northern Iberian Peninsula, South Italy and eastwards to the Balkan Peninsula and Turkey (Bohn et al., 2000; Eaton et al., 2016) (Figure 1). At the southern and south-eastern range limits sessile oak can mix and even hybridize with other drought-tolerant *Quercus* species from the Mediterranean or Pannonian zone, such as *Q. pubescens*, *Q. frainetto* and *Q. cerris* (Eaton et al., 2016) thus forming thermophilic oak forests of the order *Quercetalia pubescenti-petraeae* or similar.

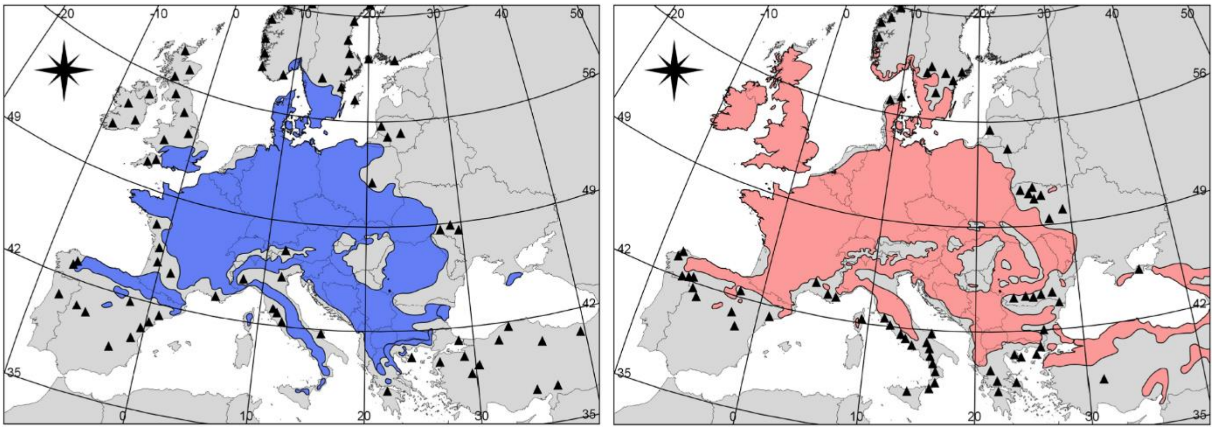

Figure 1: Distribution map of beech (in blue, left panel) and sessile oak (in red, right panel) over Europe, based the Euforgen data base (www.euforgen.org). Black triangles mark locations of natural, isolated populations or introduced populations (distribution maps created by Jan Kasper).

1.4 Beech and oak in near-natural forests in Germany today

European beech and sessile oak are two major forest tree species in temperate Europe and often form mixed stands with similar distribution ranges (Figure 1). As climatic conditions in Europe are predicted to rise and become more arid, changing competition dynamics between beech and oak are likely to favour oak, when climatic thresholds for beech are surpassed. Generally, oak forests (*Quercetalia robori-petraeae* and *Quercetalia pubescenti-petraeae*) are expected to replace beech forests (*Luzulo-Fagion* and *Fagetalia sylvaticae*) on warmer and drier sites and on a forest management level, beech forests are already being discussed to be supplemented or substituted by oak species to adapt to climate change risk (Dolos et al., 2016; Mette et al., 2013; Pretzsch et al., 2013; Schmidt, 2009).

To map the distance of the current distribution range for beech and sessile oak to the climatic distribution edge (rear edge / warm pole and leading edge / cold pole) in natural forest reserves in Germany, marginality indices were calculated. These indices specify the distance of a tree species to its niche edge, relating the probability of occurrence at a site to a standard threshold (Heinrichs et al., 2016; Mellert et al., 2016). Originally, in calculating marginality (as applied in Heinrichs et al. 2016), negative index values indicate climatic conditions within the niche (core and extended range zones), while positive values indicate conditions outside of the niche (occasional or no-occurrence zones). A further development of this index by Mellert et al. (2016) is based on the level of probability indicating the species distance to its "rear edge", where calculations are based on generalized additive models using climatic predictors (from WorldClim Version 1 data (Hijmans et al., 2005)) such as mean precipitation, mean summer temperature (Jun–Aug), min. temperature in January and the Ellenberg Climate Quotient (EQ) to calculate the probability of occurrence. A uniform default threshold of occurrence (Probability of occurrence = 0.5) is achieved via truncation weighting (Barbet-Massin et al., 2012). For details of calculation method see Mellert et al. (2016). Following this method, the marginality index for various points in German natural forests for beech and sessile oak are presented in Figure 2 (calculated by K.H. Mellert for the NEMKLIM project). The max. of the marginality index is at 2, which is reached for the occurrence of a species at the cold pole of the distribution (leading edge). Here, climatic conditions are not in the optimal range for the tree species but are expected to move toward optimal when climate warming is taken into account. For occurrences in the optimal range, the margin index is close to 1. If the occurrence of a species is in areas that face the "rear edge", they are < 1. Following Austin and Van Niel (2011) the marginality values < 1 can be interpreted as: 1–0.7 optimal; 0.7–0.4 intermediate; 0.4–0.1 marginal "rear edge" and < 0.1 occurrences unlikely to absent. From Figure 2 it becomes clear that few “leading edge” beech forests remain (mainly in mountainous regions) and most beech sites in Central Germany are at their “optimal” range (≤ 1) of occurrence while beech stands towards north-eastern Germany are already at their intermediate (≤ 0.7) range. Contrarily for sessile oak no stands were at marginality indices below “intermediate” (> 0.7) and a clear threshold at the “leading edge” is observable. This shows that “climate buffers” for beech forest occurring at the “leading edge” in Germany are low and ongoing temperature rise is likely going to lead to declining habitat suitability.

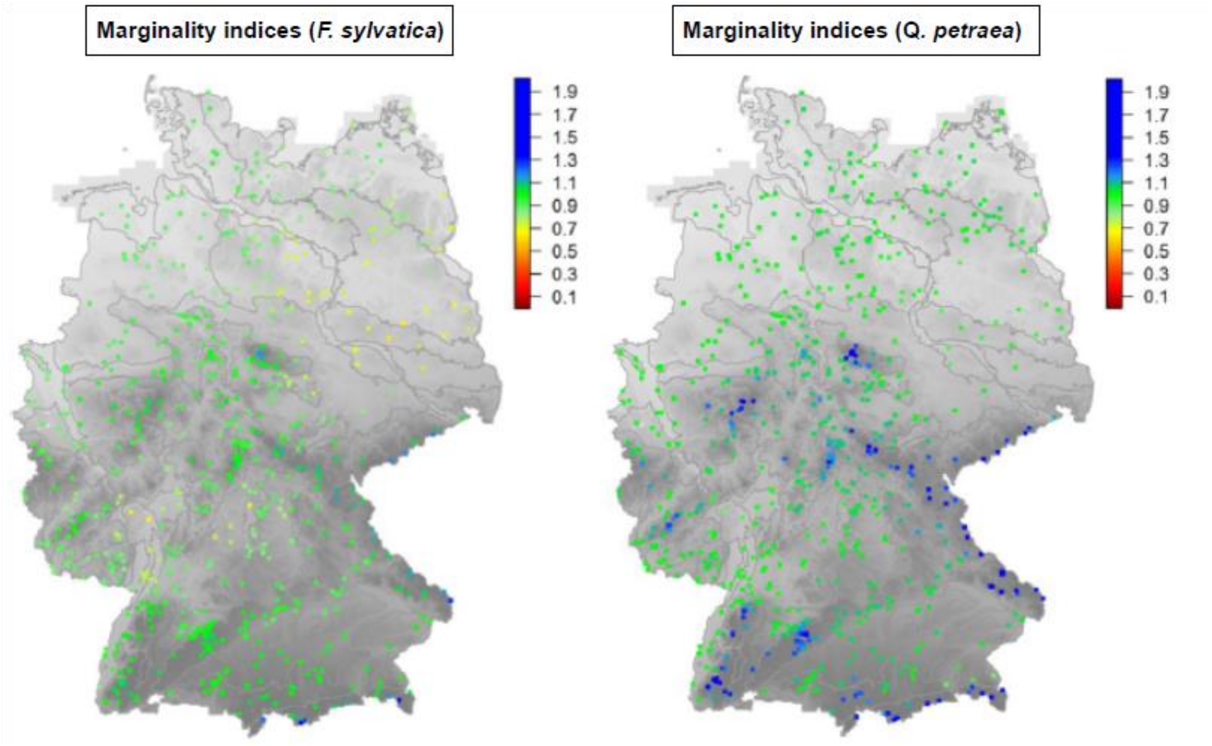

Figure 2: Marginality indices (calculated by K.H. Mellert for the NEMKLIM project) based on generalized additive models (details in Mellert et al. (2016)) for various points in German natural forest reserves for beech (left graphic) and sessile oak (right graphic). The maximum of the marginality index is at a value of 2 [dark blue] which is reached for a species at the cold pole of the distribution. For occurrences in the optimal range, the margin index is > 1 [also dark blue]. Following the classification of Austin and Van Niel (2011) if the occurrences is facing the "Rear Edge" (marginality values < 1) they can be interpreted as follows: 1–0.7 optimal [green in the map]; 0.7–0.4 intermediate [yellow–orange]; 0.4–0.1 marginal "rear edge" [red]; < 0.1 [dark red] occurrences unlikely to absent (distribution maps created by K.H. Mellert).

1.5 A possible future climate for Central Europe

While long-term weather records and changing environment show that climate change is reality, future scenarios for forest ecosystems are difficult to predict or model. This is where the possibility of a space-for-time approach (Pickett, 1989) comes into play. The idea is to look at forests exhibiting analogue climatic conditions, predicted for reference regions. Despite limitations such as differences in forest management legacies, species pools, continentality or day length (Leuschner and Ellenberg, 2017; Meusel and Jager, 1992; Willner et al., 2009), a look at forests in corresponding analogue climates can provide valuable information on climate stability of native tree species and show alternatives for future silviculture.

To find climate analogue forest sites, Kölling and Zimmermann (2014) performed a principal component analysis (PCA) representing Europe in a multidimensional space as a function of three climate variables considered biologically informative for tree growth. The variables for the three axes of the PCA were: mean January temperature, mean summer temperature (June–August) and mean growing season precipitation (May–September). In their analysis a projected increase or decrease of these input variables at a certain location shifts the position in the ordination space to locations where these conditions are currently found. Kölling and Zimmermann (2014) used three climate change scenarios (RCP 2.6, RCP 4.5 and RCP 8.5) for climate projections, simulating mean temperature, for the reference period 1961–1990, to rise between 1.3 and 3.3 °C for the future reference period 2061–2080. Starting from the climate region of Kitzingen (in Central Germany) and assuming the climates for beech forest there will change towards milder winters and warmer summers – reflecting increased early-season transpiration and late-season dryness on summer – southwestern France was identified as a climate analogue region (details see Kölling and Zimmermann (2014). For the NEMKLIM project, Kölling applied the same selection query for climate analogue regions corresponding to a beech forest (German national forest inventory point 19288) near Göttingen (Central Germany) with the results depicted Figure 3.

The PCA-predicted warming scenarios show climate analogue regions towards the South (milder winters and warmer summers), towards the South-West (milder winters and decreasing summer precipitation) and towards the South-East (warmer summers, decreasing summer precipitation combined with cold winters). Concerning the climate warming projected for winters in Central Germany, the reference region of southern France used by Kölling and Zimmermann (2014) is probably better reproduced by the more oceanic climate. However, the continental cold winters and hot summers in south-eastern Europe (e.g. western Romania) account better for extreme weather events such as late spring frosts, extreme droughts and heat, which are also predicted to increase (Kodra et al., 2011; Salinger, 2005; Schär et al., 2004; Schönwiese et al., 2005). This increase in extreme events is likely to restrict the distribution of frost-sensitive species (Liu et al., 2018; Ma et al., 2019) and the more continental south-eastern climates represent a natural distribution limit, thus may also simulate a better scenario for Central Germany concerning viable species pools.

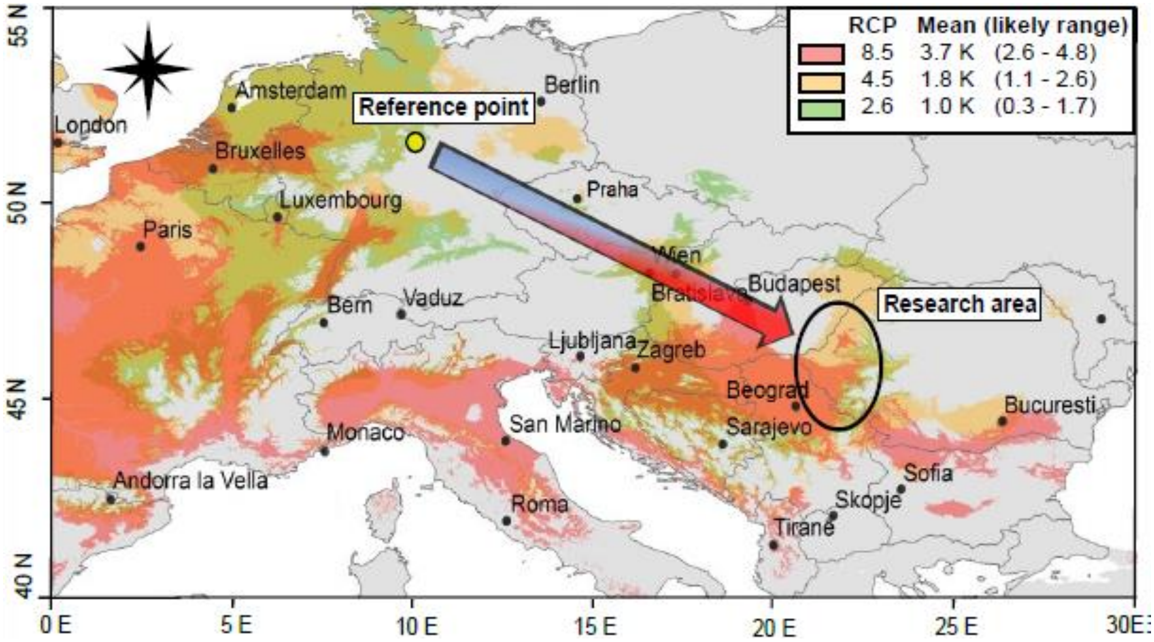

Figure 3: Climate warming projections for a beech forest reference point (German national forest inventory point 19288) in the centre of the distribution range of European beech (Central Germany). The red-, orange- and green-coloured regions of Europe are climate analogue for the climate in 50 years according to the IPCC (2013) scenarios: RCP 2.6, 4.5 and 8.5. They were identified following a principal component analysis representing Europe as a function of mean January temperature, mean summer temperature (June–August) and mean growing season precipitation (May–September). The projected values for these climate variables were matched within the ordination space with locations in Europe currently having these conditions. Depicted are the mean temperature increase (likely range) in Kelvin as well as the location of the study transects in western Romania, where A and B are located within the climate scenario RCP 2.6 and C is within the range of scenario RCP 4.5 (calculations and mapping done for the NEMKLIM project by C. Kölling, unpublished). For details on methodology, see Kölling and Zimmermann (2014).

For a "fine tuning" of our "space for time" approach, we subsequently looked for sites within the research area (Figure 3), where elevation gradients induce a natural climatically driven shift from beech to oak forests (beech–oak ecotone), serving as "in-the-field"-models for predicted shifts in species dominance. Therefore, the Ellenberg Quotient (EQ) (Ellenberg, 1963) was used, which is calculated by dividing the July temperature ($T07$) by annual average precipitation (Pav).

$$EQ = T\,07/Pav * 1000$$

The EQ was initially derived from phytosociological relevés, where forests had developed without strong human disturbance and results showed that beech dominates for EQ < 20, whereas the oak share tends to increase for EQ 20–30 and oak dominance is expected for an EQ > 30 (Ellenberg, 1963). These EQ values as a rough orientation for climatic thresholds of beech and oak have been confirmed (Dolos et al., 2016; Mellert et al., 2016), as well as their utility as proxies for predicting beech and oak dominance (Czúcz et al., 2011; Mette et al., 2013; Stojanović et al., 2013).

The climate analogue research area in western Romania exposed EQ > 20, except for restricted areas at high altitudes (Figure 4). The results show that the western lowlands and the lower mountain fringes receive too much warmth from the Pannonian Plain (EQ > 30), excluding them, but the deciduous forests at the foothills of the Apuseni Mountains and the south-western Carpathians, extending from submontane/montane elevation downwards, were suitable (Figure 4). At these sites the EQ transitions over elevation from values around 20 to values around 30 and greater, thus shifting climates from beech to oak favouring. Exemplary conditions were found in the Zarand Mountain range (Muntii Zarandului), at the western foothills of the Southern Carpathian Mountain chain (Muntii Pioana Ruscai), both in westernmost Romania and at the foot of the southern Banat Mountains (Muntii Semenic Almăj) in south-western Romania. The study transects were respectively located in the county Arad (Milova) transect A (46.1° N/21.8° E) and in the county Caraș-Severin (Maciova) transect B (45.5° N/22.2° E) both north-east and south-east of Timisoara and the county Orsova (Eşelniţa) transect C (44.7° N/22.3° E) close to river Danube (Figure 4).

To ensure comparability between sites all transects depicting the elevation gradients were demarcated on hill crests, mounting from South to North, so that hill flanks predominantly have an East-South-West slope orientation (Figure A1–3 in the Appendix). The study sites were delineated within a 250 m buffer range around transects that started in the semi-mountainous range from beech dominated forests at higher elevation (> 600 m a.s.l) and then declined towards the planar-colline oak forests of the warm temperate climate of the western lowlands and foothills (< 350 m a.s.l) (Doniță, 1992) (see Chapter 1.6). To verify that the climate shift at the elevation transects correspond with current and future climates for beech in Central Germany, we computed the modified Ellenberg Quotient (EQm) which, as ratio between mean summer (Jun–Aug) temperature (MST) and mean summer (Jun–Aug) precipitation (MSP), focuses on the climatic growth limiting summer period (Bréda et al., 2006; Hohnwald et al., 2020; Mellert et al., 2016).

$$EQm = MST/MSP \times 1000$$

Results were compared with a study by Walentowski et al. (2017) using the "Franconian Plateau" as reference region, in which the EQm was calculated from WorldClim 1.4, with a 30 arcsec resolution (Hijmans et al., 2005) for current climates (reference period 1951–2000) and projected future climates (reference period 2061–2080). Walentowski et al. (2017) calculated future climates using means of 63 climate scenarios from 19 global climate models (GCMs) for four RCP scenarios (RCP 2.6, RCP 4.5, RCP 6.0 and RCP 8.5), however for the NEMKLIM project only RCP 2.6, RCP 4.5 and RCP 8.5 were used (Table 1, with details of methodology in Walentowski et al. (2017)).

Table 1: Current and projected temperature and precipitation data as well as the modified Ellenberg Quotient for the Franconian Plateau (Worldclim 1.4, with 30 arcsec resolution, Hijmans et al. 2005). "Current" represents the periodic average of 1950–2000, and for RCP 2.6, 4.5, and 8.5 a periodic average of 2061–2080 for 15, 19, 12 and 17 atmospheric-oceanic global circulation models respectively, were averaged. Original table and details of methodology in Walentowski et al. (2017).

Climate variables		**Current**	**RCP2.6**	**RCP4.5**	**RCP8.5**
Annual Mean Temperature	°C	8.4	10.4	11.2	12.5
Mean Temperature of Warmest Quarter (MST)	°C	16.8	19.1	20.2	21.8
Annual Precipitation	mm	678	713	703	704
Precipitation of Warmest Quarter (MST)	mm	211	215	198	190
Modified Ellenberg Quotient (EQm)		**EQm<80**	**80<EQm<89**	**89<EQm<102**	**EQm>102**

Figure 5 shows the distribution of current and projected summer climates for a beech forest on the "Franconian Plateau" within our study region and for the elevation transects in this doctoral study. Also shown in Figure 5 are occurrence data for beech from the Romanian National Forest Inventory (NFI) for 1218 plots (data provided by the National Institute for Research and Development in Forestry "Marin Dracea"). The NFI data shows that beech is dominant for current climates on the "Franconian Plateau" (EQm < 80), still occurs for predicted RCP 2.6 climates and becomes scarce to not present for scenarios RCP 4.5 and RCP 8.5 (which are currently the most realistic).

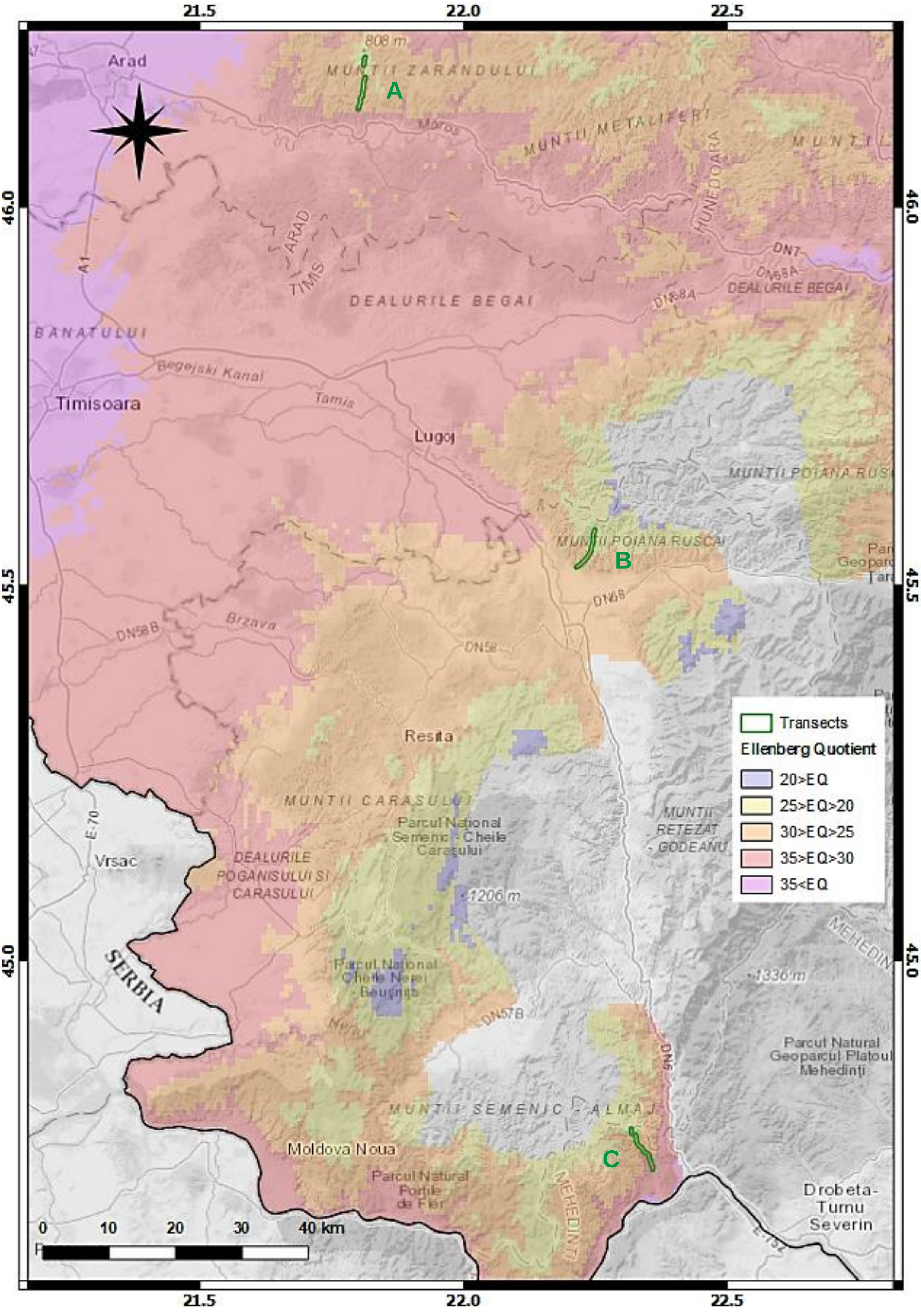

Figure 4: Map of the research area in western Romania (see Figure 3) used for selection of the three study transects (A, B, C). The colour gradient marks the calculated Ellenberg Quotient (EQ) based on WorldClim Version 2 data (Fick and Hijmans, 2017). Transects A and B are located within EQ values 20–30 and C is within the range of 20–35 (EQ distribution map created by Jan Kasper).

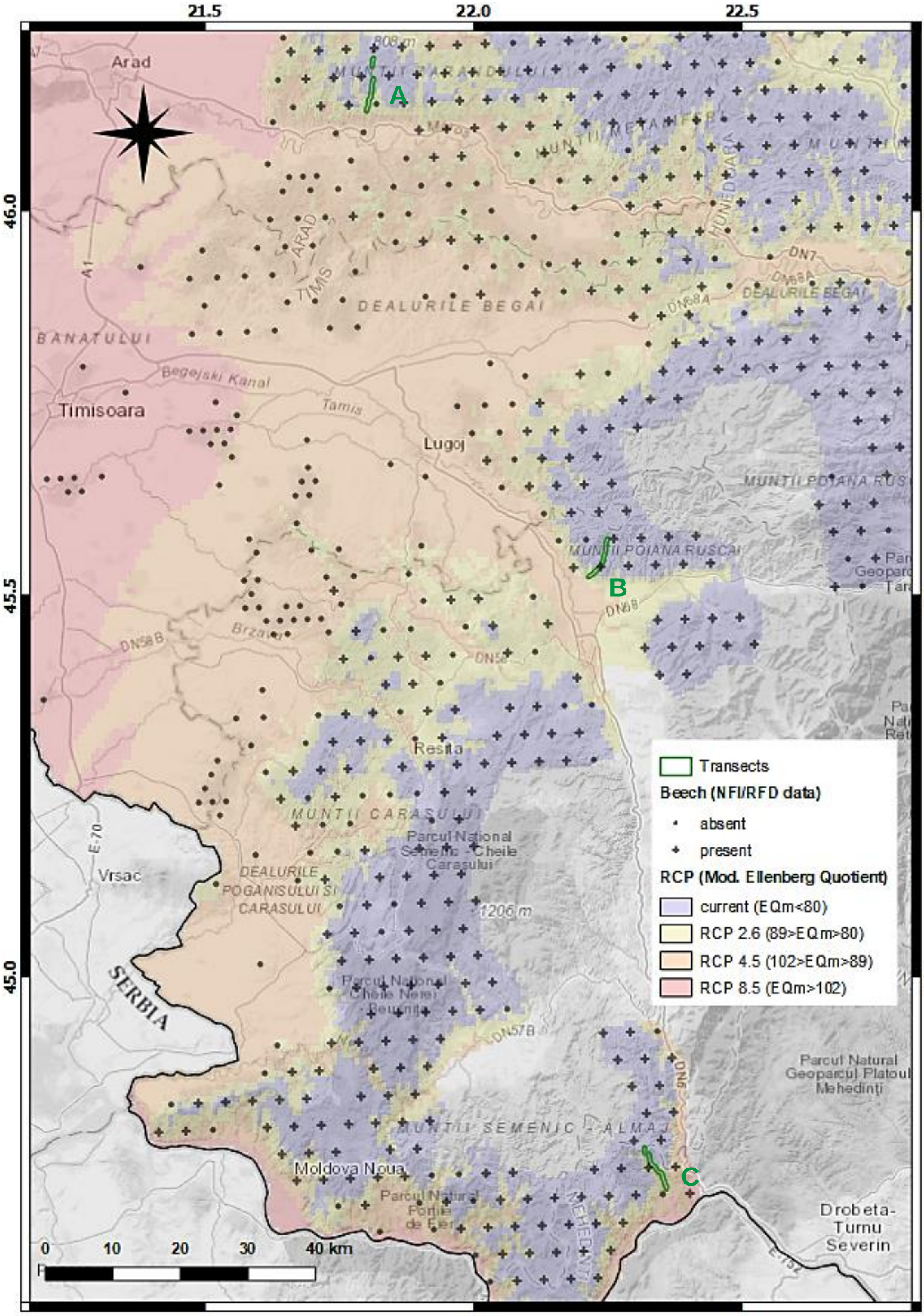

Figure 5. Map of the research area in western Romania (see Figure 3) with the three study transects (A, B, C). Record points of the Romanian National Forest Inventory (1218 plots) map the occurrence of beech forests. The colour gradient marks different modified Ellenberg Quotient (EQm) calculated for a reference beech forest on the "Franconian Plateau" for the current (period 1961–1990) and predicted (period 2061–2080) climates, using the RCP scenarios: RCP 2.6, RCP 4.5, and RCP 8.5 and data from WorldClim 1.4 (Hijmans et al. 2005). Transects A and B are located within the climate scenario RCP 2.6 and C is within the range of scenario RCP 4.5 (EQm distribution map created by Jan Kasper and details of methodology and reference site in Walentowski et al. (2017)).

1.6 Study area characteristics

Climate

The climate of Romania can be subdivided into subcontinental with warm and humid climatic influences from the West and continental with cold and dry influences from the East (Frey and Lösch, 2010). Our study sites have a typical climate for mixed deciduous beech and oak forests (Cfa–Cfb according to Köppen and Geiger) of the western lowland (Fischer, 2003; Horvat et al., 1974). According to the Chelsa v1.2 Climate data (Karger et al., 2017), the mean annual temperature for the period from 1979–2013 is in Milova 10.8 °C, in Maciova 11.1 °C and in Eşelniţa 11.9 °C and the annual mean precipitation (Pm) is 690 mm, 791 mm and 598 mm, respectively (Table 2, bottom end of transects). For all sites monthly precipitation is lowest in winter (January–February) and highest in June, where it is followed by a hot period with low rainfalls, similar to a Mediterranean climate. July and August are the hottest months and winters are cold with the lowest temperature in January resulting in a high annual temperature range (Table 2), typical for a continental climate. Annual rainfall is reduced over elevation with a lapse rate assumed to be + 45 mm year^{-1}/100 m and temperature with a lapse rate of about − 0.5 K/100 m (Maruşca, 2017). Particularly, the mean summer temperature (MST) is closely correlated with elevation (Table 2) and influences tree species distribution (Hohnwald et al., 2020; Primicia et al., 2015). Over the last 60 years temperatures (here MST) has risen markedly on all transects, whereas precipitation (here MSP) shows no clear changes (Table A1 in the Appendix).

Physical Geography

Geographically, Romania lies between central and south-eastern Europe and belongs to the central Europe geobotanical zone covering the biogeographic regions Pannonian, Continental, Alpine, Steppic and Black Sea defined by the European Environment Agency (Frey and Lösch, 2010; Walentowski et al., 2015). Western and Central Romania can be subdivided into the geographic units: Eastern Carpathians, Southern Carpathians, Apuseni Mountains, Dobrogea, Skythian platform, Moesian platform and the Transylvanian Basin (Burchfiel, 1976; Walentowski et al., 2015). The study site A (Milova) is in the Southern Apuseni Mountains, which have their boundary along the Mures Valley and rise out of the loess-covered Pannonian Plains forming separated hills with steep valleys. The region around Milova is on the foothills of the Apuseni Mountain range and lies at the fringes of the Pannonian Basin in the Zarand Mountains, with Mesozoic sedimentary rocks as main parent material (Walentowski et al., 2015). The Southern Carpathians extend to the West, neighbouring with the Eastern Carpathians and then bend South to the Danube River. The northern boundary is defined by the Transylvanian Basin, the Southern Apuseni Mountains and the Pannonian Basin. The Southern Carpathians consist of a complex overthrust of tectonic plates from West to East (Walentowski et al., 2015), where the western foothills form the geological basis for transect B (Maciova) and the southern foothills the basis for transect C (Eşelniţa). Maciova (B) is on the Getic allochthon tectonic plate (Burchfiel, 1976) formed by alternating sediment layers of sandy, conglomerate molasse of marls, sandy marls, siliceous limestone and mudstone. Eşelniţa is located at the Danubian tectonic plate and consists of carbonate shale and sandstone which is covered by marl and mudstone. A detailed description of the geology and biogeography of the study regions is available in Walentowski et al. (2015).

Soil

All sites had mesotrophic soil conditions basing on silicate parent material which were crystalline sand- and mudstone in the case of A and B and marl- and limestone in the case of Transect C. However, parent material was barely reached during soil sampling as the soil forming layer was dominantly a leached, post-glacial loess or loam layer covering the bedrock. Soil rooting layers were evolved on all sites with min. depths of 70 cm (= max. profile depth) before reaching the parental rock. Soil texture for all soils ranged from soil fraction sizes sandy–silt to silty–loam and derived potential available water capacity (pAWC in %) ranged from a min. of 23% and a max. of 35%. All soils were within the silicate buffer range and pH levels were slightly–moderately acidic (pH 4.60–5.27). Soils were generally classified as Cambisols (German soil classification “Braunerden”) and in some rare cases as Luvisols (German soil classification “Parabraunerden”). Results pooled per forest type in each transect are depicted in Table A5 (in the Appendix). A full overview on the methodology and all soil analysis results is in Kasper et al. (2021) (see Chapter 2) and for more information on the classification of soil types and soil profile documentation the reader is referred to the B. Sc. thesis’s from Gröning (2019) and Loris (2019).

Table 2: Location of the three transects with longitude (Long.) and latitude (Lat.), elevation (Elev.) and climatic characteristics of the highest (top end) and lowest (bottom end) plots (see Figures A1–A3 in the Appendix). The highest elevation plots are located in typical beech forests, the lowest plots in typical oak forests and are in proximity to the transect localities. Given are for a reference period (1979–2013) the annual mean temperature (Tm), temperature of the warmest month (Tmax), temperature of the coldest month (Tmin), mean temperature of warmest quarter (MST), mean annual precipitation (Pm), precipitation of the wettest month (Pmax), precipitation of the driest month (Pmin), and precipitation of the warmest quarter (MSP) according to the CHELSA v1.2 climate data (Karger et al., 2017).

Transect (locality)	Transect position	Long.	Lat.	Elev. m	Tm C°	Tmax C°	Tmin C°	MST C°	Pm mm yr^{-1}	Pmax mm	Pmin mm	MSP mm
A	Top end	21.8135	46.1973	759	7.9	23.4	-6.5	18.2	892	125	48	254
(Milova)	Bottom end	21.8022	46.1290	216	10.8	26.5	-6.5	21.2	690	132	52	248
B	Top end	22.2460	45.5749	719	8.2	23.8	-7.1	18.6	951	100	54	216
(Maciova)	Bottom end	22.2116	45.5248	256	11.1	26.9	-4.0	21.7	791	81	41	157
C	Top end	22.3188	44.7754	907	7.8	23.6	-3.8	18.3	844	106	45	201
(Eşelniţa)	Bottom end	22.3578	44.7173	147	11.9	28.0	-3.5	22.6	598	69	40	137

Forest stand history

Similar forest management legacies were important on all sites. The stand age span was 60+ years in the dominant canopy layer except for one *T. tomentosa* stand for transect B (Kasper et al., 2022) (see Chapter 3). For all three transects, occasional wood-cutting and coppicing had been conducted before the 1960s at low intensities. Since then, the forests were transferred to state-ownership and supervised by local forest authorities according to management plans, and previously coppiced stands were allowed to grow into high forests (Öder et al., 2021). The legacy of former coppicing in form of the presence of multi-stemmed trees is still visible in most stands. They were managed according to common Romanian silvicultural schemes, in which stands are lightly to moderately thinned (5–15% of stand volume) from the pole-wood stage up to an age three quarters of the harvest age (Nicolescu, 2018). Salvage and sanitary loggings were also irregularly conducted at low intensity (< 5% of stand volume). Records of the local forest authorities demonstrate that no major harvest operations have occurred in the last 20 years at all sites (Öder et al., 2021).

Forest vegetation

In western Romania mesic beech forests occur in humid climate at elevations above 500/600 m a.s.l. They are dominated by beech (usually *Festuco drymeiae-Fagetum* / alliance *Symphyto cordati-Fagion*) with occasional species such as *Acer platanoides*, *Acer pseudoplatanos*, *Carpinus betulus* and *Prunus avium* occurring in the dominant tree layer. Pure beech forests are gradually replaced by mesic mixed beech-hornbeam and hornbeam-oak forests (*Carpino-*

Fagetum and *Lathyro hallersteinii-Carpinetum* / alliance *Lathyro hallersteinii-Carpinion*) with decreasing elevation. Next to *Q. petraea* and *F. sylvatica*, *Tilia tomentosa, C. betulus* and different *Acer spp.* determine the main canopy layer and heat indicator species such as *Sorbus torminalis* and *Acer campestris* start to become present (Bohn et al., 2000; Coldea et al., 2015; Doniță, 1992; Indreica et al., 2017; Kasper et al., 2021). Numerous variations of classifying the social groups in the mixed forest zone exist and are quite divergent (Oberdorfer, 1992). Towards the colline belt these mixed forests give way to thermophilic oak forests (< 300/400 m) characterized by different oak species in the dominant canopy layer and *C. betulus, A. campestris* and *S. torminalis* in the under-story. In comparison to western Europe, Pannonian oak species such as Turkey oak (*Q. cerris*) and Hungarian Oak (*Q. frainetto*) are frequently present (Figure 6) forming the Pannonian-Balkan Turkey oak forests (*Potentillo micranthae-Quercetum dalechampii* / alliance *Quercion confertae*) (Doniță, 1992; Heinrichs et al., 2016; Indreica et al., 2017; Kasper et al., 2021; Walentowski et al., 2015).

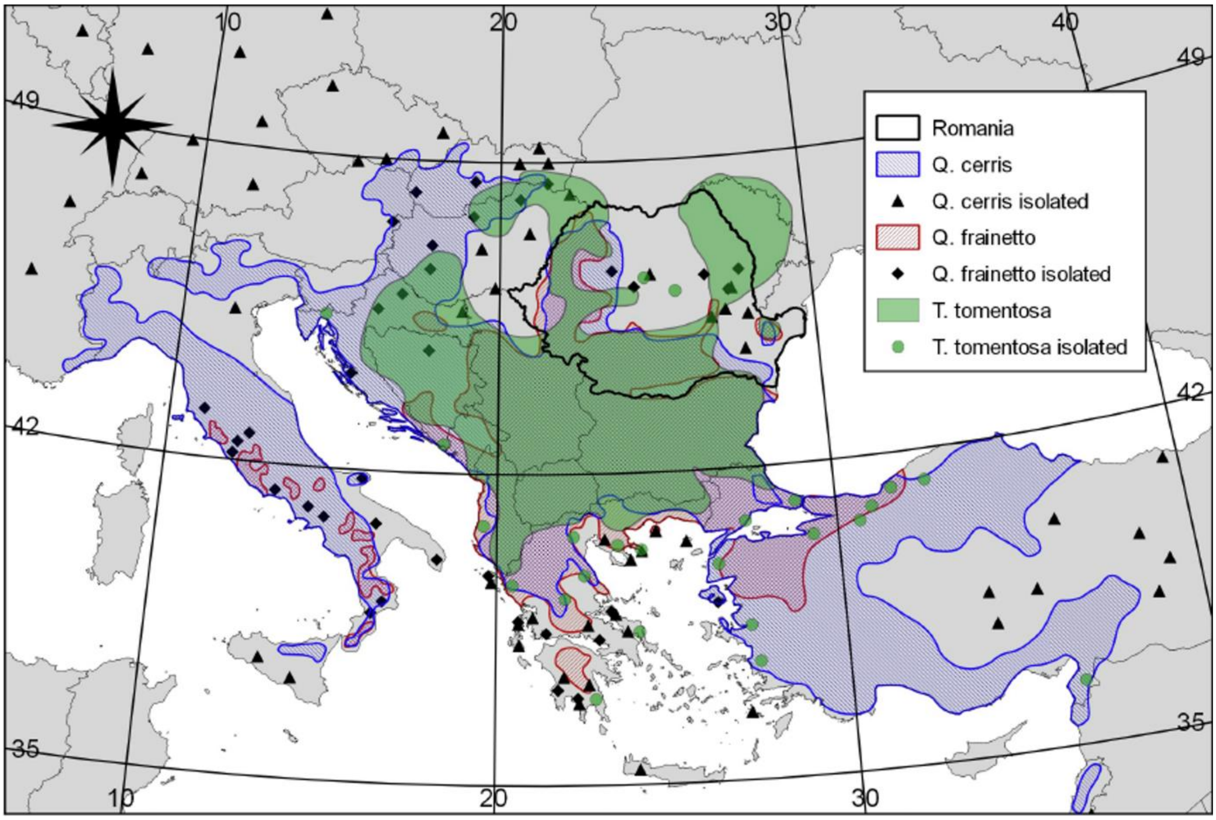

Figure 6: Distribution map of Turkey Oak (*Q. cerris*), Hungarian Oak (*Q. frainetto*) and Silver Lime (*T. tomentosa*) over south-eastern Europe, based the Euforgen data base (www.euforgen.org) (distribution maps created by Jan Kasper).

At this elevation beech forests are found only extra-zonally on northern slopes or in valleys with higher humidity, representing "rear edge" populations, while plains and slopes with southern exposition are covered by thermophilic oak forests (Doniță, 1992; Lenoir et al., 2013; Maclean et al., 2015). *T. tomentosa* as a species of the south-east European flora (Figure 6) also plaid an important role in the forests of the study region. Frequently encountered in the mixed beech-hornbeam and hornbeam-oak forest zone, the species also formed pure stands which are thought to be a result of timber extraction in the distant past as *T. tomentosa* is able to rapidly colonize forest gaps (Dinic et al., 1999; Radoglou et al., 2009).

1.7 Project framework and data collection

Project framework

The thesis was conducted in the framework of the NEMKLIM project (https://blogs.hawk-hhg.de/nemklim) as module 4 “Tree Vitality Analysis” and investigates climatically induced transitional zones from beech to oak dominated forests at natural beech–oak ecotones over elevation. The field work took place in the summers of 2018 and 2019 and compromised the collection of a wide range of data. Focus was the analysis of dendrological cores, to identify climate change impacts on the dominant tree species in the beech–oak ecotone. The dendrological analysis on all transects was supported by environmental data acquisition through forest inventories and soil sampling.

Forest inventories

Objectives of the inventories were information on species composition, identification of forest types, information on stand vitality as well as forest- and tree population structures. Furthermore, geographical characteristics and forest management legacies were assessed. The inventory design was systematic sampling with circular, nested area plots for all trees with a diameter at breast height (DBH) ≥ 7 cm. Sample plots were distributed according to a square grid (200 x 200) with a north-south orientation and a random starting point (Figure A1–A3 in the Appendix). Table A2 (in the Appendix) depicts the transect lengths (m), inventory area sizes (ha), samples sizes (n) and sample intensities (%) for the three inventory sites. Details of the forest inventory methods and results are described in Kasper et al. (2021) (see Chapter 2) and in the B. Sc. thesis’s from Rümping (2019) and Schmidt (2020).

Dendrological sampling

The vegetation gradients on the three transects reflected the altitudinal zonation of forest communities in western Romania, which was verified by the results of the forest inventories (Kasper et al., 2021) (see Chapter 2). Five dominant tree species of the four identified forest types in the beech–oak ecotone (see Tables A2–A3 in the Appendix) were selected for dendrochronological study, e. g. *F. sylvatica* as the dominant species of the moist mesic beech forests, *Q. petraea, Q. frainetto* and *Q. cerris* as the dominant species of the subhumid-thermophilic oak forests, and *F. sylvatica, Q. petraea* and *T. tomentosa* as a typical element of the subhumid mixed beech-oak-hornbeam forests in the transition zone. In addition, north-facing *F. sylvatica* stands were sampled at colline elevation as “rear-edge” xeric beech forests, which exist within the thermophilic oak forest zone in pockets of moister microclimates. In total we thus sampled five species and, in case of *F. sylvatica*, two site types. Here for in May–June 2018 and 2019, 30–60 wood cores per forest type and transect were collected, resulting in 92–153 cores per tree species. All selected trees were dominant trees of the upper canopy within most cases > 40 cm DBH, which were free of signs of pathogen attack, pre-senescent leaf abscission, canopy dieback, or other damage. For every cored tree, we recorded the DBH, height and stem coordinates (means of height and DBH). As tree cores were sampled after the beginning of the growing season, the last half-year ring was omitted from analysis and tree ring series collectively ended in 2017. Details of the tree ring analysis methods and results are described in (Kasper et al., 2022) (see Chapter 3)

Soil sampling

Soil samples were taken approximately every 50 m–100 m in altitude following the transect crest (Figure A1–A3 in the Appendix). For transects A and B, 13 samples were taken along the transect with a southern slope exposition and additionally 3 samples were taken on xeric beech forests outside from the transects with northern slope orientation. For transect C, due to its higher elevation, 15 sample plots were taken along the transect with a southern slope exposition and 3 with northern slope orientation for xeric beech forests (in this case they were located on the transects). Details of the soil analysis methods and results are described in Kasper et al. (2021) (see Chapter 2) and in the B. Sc. theses from Gröning (2019) and Loris (2019).

1.8 Hypotheses and research questions

Discrete hypotheses and research questions guiding this doctoral study were:

Chapter 2:

H1) Tree species diversity increases with the transition from beech to oak dominance, as beech dominance suppresses light and warmth-loving species.

H2) The aboveground biomass C storage decreases from beech to oak dominance, as drought-affected forests accumulate less biomass.

H3) Soil organic carbon (SOC) storage decreases from beech to oak dominance, as higher temperatures favour mineralization.

H4) The C stock decrease in biomass is primarily a tree species effect, while the decrease in SOC is mainly a climatic (elevation) effect.

Chapter 3:

Q1) Which climatic factors (precipitation, temperature, or climatic aridity) are the dominant limiting factors of radial growth in beech, linden and oak in the natural beech–oak ecotone?

Q2) Do long-term trends in radial growth differ between mesic and xeric (rear-edge) beech stands as well as between beech, linden and oak species?

Q3) What relationship exists between long-term radial growth trends and trends in summer temperature, summer precipitation and climatic water balance in the five species, and what are climatic thresholds for growth decline?

Q4) Do the five species differ in their growth response to severe 20th century summer droughts?

Chapter 4:

Q1) How do beech, silver linden and the three oak species differ in their climate sensitivity of growth?

Q2) Did the climate sensitivity of the five species change from the mid-20th century to the period with pronounced warming since the 1980s?

Q3) Do the five species differ in their between-population growth synchronicity and how did the recent warming affect the synchronicity?

Q4) Do mesic and xeric (rear-edge) beech populations differ in their climate sensitivity and synchronicity of climate stress response?

In a “time for space approach” and with these hypotheses guiding the research, the overall goal of this doctoral study was to deliver results from an “in the field” model depicting possible scenarios and effects of climate warming for Central European beech forests regarding their distribution ranges, vitality, carbon sequestration function and economic productivity in the future.

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1.10 Appendix

Tables

Table A1: Averages calculated for mean summer temperature (MST) in °C and mean summer precipitation (MSP) in mm, from the extracted CHELSAcruts climate data timeseries for the periods 1960–1979, 1980–1999 and 2000–2016 (Karger et al., 2017).

	Transect A			**Transect B**			**Transect C**			**Mean (A+B+C)**		
Period	**60–79**	**80–99**	**00–16**	**60–79**	**80–99**	**00–16**	**60–79**	**80–99**	**00–16**	**60–79**	**80–99**	**00–16**
MST	18.6	19.0	20.4	18.9	19.4	20.8	19.5	20.0	21.4	19.0	19.5	20.9
MSP	232.4	216.8	229.9	281.6	259.8	274.0	187.0	170.2	180.9	233.7	215.6	228.3

Table A2: Transect length, inventoried forest area, number of inventory plots, sampling intensity (plot area per forest area in %), and total sampled areas in the three transects (A–C). All plots had a size of 314.2 m2.

Transect	**Length [m]**	**Area [ha]**	**Plots [n]**	**Samp. int. [%]**	**Samp. area [m^2]**
A	6694	357.7	90	0.79	28278 m^2
B	6696	352.5	90	0.79	28278 m^2
C	7465	405.0	100	0.76	31416 m^2

Table A3: Basal area in percent of stand total (BA_{rel}), stem density (N_{tot}), mean DBH, mean tree height (H), basal area in absolute figures ($BA_{tot;}$) for each tree species averaged over all plots for transects A–C. Given are also the number of inventory plots (size = 314.2 m^2) per transect (n). Coniferous species (*Larix decidua*, *Pinus spp*. and *Picea abies*) and other rarely encountered broadleaf tree species (*Acer tataricum*, *Q. robur*, *Salix spp.*, *T. cordata*) were categorized into the classes Other coniferous or Other deciduous.

	Transect A (n=90)					**Transect B (n=90)**					**Transect C (n=100)**				
	BA_{rel}	**N_{tot}**	**DBH**	**H**	**BA_{tot}**	**BA_{rel}**	**N_{tot}**	**DBH**	**H**	**BA_{tot}**	**BA_{rel}**	**N_{tot}**	**DBH**	**H**	**BA_{tot}**
Species	**(%)**	**(ha^{-1})**	**(cm)**	**(m)**	**(m^2 ha^{-1})**	**(%)**	**(ha^{-1})**	**(cm)**	**(m)**	**(m^2 ha^{-1})**	**(%)**	**(ha^{-1})**	**(cm)**	**(m)**	**(m^2 ha^{-1})**
A. campestre	0.2	5.0	13.3	16.2	0.1	0.1	1.5	17.7	19.3	0.0	0.3	4.8	14.8	9.7	0.1
A. platanoides	1.4	11.7	22.7	22.6	0.6	0.4	2.9	25.1	25.2	0.2	0.4	2.2	27.9	19.9	0.2
A. pseudoplatanus	1.3	7.8	27.4	21.0	0.5	0.1	0.7	22.5	20.3	0.0	1.3	7.0	28.3	19.9	0.6
Betula spp.						2.2	18.3	24.3	22.4	0.9					
C. betulus	5.7	111.1	15.0	17.0	2.3	11.0	159.9	17.6	18.4	4.5	3.8	70.0	14.7	12.8	1.6
C. orientalis											1.1	44.6	10.8	9.1	0.5
F. excelsior											0.1	1.3	16.9	13.4	0.0
F. ornus											3.0	86.9	12.6	10.4	1.2
F. sylvatica	27.1	128.0	29.7	29.2	10.7	42.5	244.0	26.1	26.2	17.3	35.2	263.6	22.6	22.9	14.7
Other coniferous	1.9	21.2	20.3	23.3	0.8	0.9	17.6	16.1	17.9	0.4	0.0	2.9	8.6	7.3	0.0
Other deciduous	0.3	1.8	19.8	17.1	0.1	0.3	2.6	21.6	20.9	0.1					
P. avium	1.8	18.4	20.1	20.3	0.7	1.4	10.6	24.3	23.8	0.6					
Populus spp.	0.0	1.1	10.5	6.4	0.0	2.9	11.7	32.2	28.5	1.2	0.2	1.9	23.5	18.8	0.1
Q. cerris	3.6	20.5	28.7	22.6	1.4	3.2	9.5	41.0	31.2	1.3	0.7	4.5	26.8	13.5	0.3
Q. frainetto	1.8	11.7	26.7	21.5	0.7	0.7	1.5	44.5	20.6	0.3	2.4	18.1	24.6	14.8	1.0
Q. petraea	26.9	163.0	26.8	25.2	10.6	9.3	46.1	30.5	25.0	3.8	26.0	172.5	26.6	18.3	10.8
R. pseudoacacia						0.5	6.2	20.0	20.1	0.2	0.5	6.0	19.5	12.2	0.2
S. torminalis	0.3	5.0	15.1	12.9	0.1	0.1	1.8	11.2	9.4	0.0	0.5	9.5	15.2	11.5	0.2
T. tomentosa	27.4	316.2	19.1	21.3	10.8	22.7	117.8	29.2	28.2	9.3	24.2	211.7	21.5	19.2	10.1
Ulmus spp.	0.3	3.9	18.0	25.1	0.1	1.7	6.2	28.1	25.0	0.7	0.3	3.5	19.3	14.1	0.1
Totals		**827.3**			**39.4**		**660.8**			**40.8**		**909.7**			**41.8**

Table A4: Basal area in percent of stand total (BArel), stem density (Ntot), mean DBH, mean tree height (H) and basal area in absolute figures (BAtot) for all tree species pooled over three transects (A–C) for: moist mesic beech forests & low-elevation xeric beech forests (plots with BArel of *F. sylvatica* > 66%), sub-humid / thermophilic oak forests (plots with BArel of Quercus species > 66%), post-disturbance linden forests (plots with BArel of *T. tomentosa:* > 66%), sub-humid mixed beech-oak-hornbeam forests, and all other forests. Given are also the number of inventory plots per forest type (n). Plots with an absolute basal area (∑BAtot;) < 10 m^2 ha^{-1} were classified as non-forests (n=15) and excluded. Coniferous species (*Larix decidua, Pinus spp*. and *Picea abies*) and other rarely encountered broadleaf tree species (*Acer tataricum, Q. robur, Salix spp., T. cordata*) were categorized into the classes Other coniferous or Other deciduous.

	Moist mesic & "rear-edge" xeric beech forests (n=69)					**Sub-humid mixed beech-oak-hornbeam forests (n=106)**					**Sub-humid / thermophilic oak forests (n=52)**					**Post-disturbance linden forests (n=38)**				
Species	**BA$_{rel}$ (%)**	**N$_{tot}$ (ha^{-1})**	**DBH (cm)**	**H (m)**	**BA$_{tot}$ (m^2 ha^{-1})**	**BA$_{rel}$ (%)**	**N$_{tot}$ (ha^{-1})**	**DBH (cm)**	**H (m)**	**BA$_{tot}$ (m^2 ha^{-1})**	**BA$_{rel}$ (%)**	**N$_{tot}$ (ha^{-1})**	**DBH (cm)**	**H (m)**	**BA$_{tot}$ (m^2 ha^{-1})**	**BA$_{rel}$ (%)**	**N$_{tot}$ (ha^{-1})**	**DBH (cm)**	**H (m)**	**BA$_{tot}$ (m^2 ha^{-1})**
A. campestre	0.0	0.5	16.8	15.6	0.0	0.3	5.1	17.3	15.5	0.1	0.2	5.5	11.8	10.5	0.1	0.1	5.0	10.1	14.4	0.0
A. platanoides	0.7	4.6	29.4	26.8	0.3	1.0	6.9	24.6	21.6	0.4	0.4	4.9	18.9	19.7	0.1	0.4	5.9	18.9	20.4	0.2
A. pseudoplatanus	0.4	2.8	26.6	24.3	0.2	2.0	10.8	28.1	19.5	0.8	0.1	0.6	33.2	22.8	0.1	0.1	0.8	20.0	21.1	0.0
Betula spp.	0.5	3.7	28.8	28.2	0.2	1.4	11.1	25.3	23.2	0.6	0.0	0.6	15.0	-	0.0					
C. betulus	1.4	20.3	18.3	18.4	0.6	13.3	202.1	16.8	18.0	5.5	3.2	68.6	14.1	13.4	1.2	3.8	117.3	13.3	14.5	1.9
C. orientalis						0.6	19.5	11.5	10.1	0.2	0.9	36.1	10.4	8.1	0.3	0.2	13.4	9.5	8.7	0.1
F. excelsior						0.1	1.2	16.9	13.4	0.0										
F. ornus	0.1	2.3	13.3	10.0	0.0	1.9	50.4	13.2	11.0	0.8	1.4	49.0	11.3	8.8	0.5	0.5	16.8	12.4	12.2	0.2
F. sylvatica	89.1	559.6	26.8	28.1	41.1	23.6	154.7	23.8	24.9	9.7	2.9	40.4	16.0	16.9	1.1	3.3	46.9	18.0	22.5	1.6
Other coniferous						2.3	32.4	18.4	21.5	1.0										
Other deciduous	0.1	0.9	28.5	32.8	0.1	0.2	4.8	14.8	16.3	0.1	0.4	1.2	24.1	21.4	0.1	0.0	0.8	7.0	7.3	0.0
P. avium	0.5	1.8	40.7	29.6	0.3	1.6	16.2	20.5	21.7	0.6	0.5	4.9	16.7	14.0	0.2	1.2	12.6	22.9	23.2	0.6
Populus spp.	0.3	2.3	26.8	22.4	0.1	2.3	8.1	34.6	29.0	1.0	0.2	3.1	16.7	18.2	0.1	0.0	0.8	19.0	20.7	0.0
Q. cerris	0.2	0.5	44.3	31.8	0.1	1.4	8.4	27.2	22.4	0.6	10.6	42.2	33.4	23.4	4.0					
Q. frainetto						1.0	2.4	43.3	20.8	0.4	7.4	52.6	24.6	16.8	2.8					
Q. petraea	3.1	17.1	31.4	25.9	1.4	19.1	119.5	26.9	21.5	7.9	66.2	360.5	27.9	22.4	25.0	7.7	88.0	21.8	21.2	3.7
R. pseudoacacia						1.0	10.5	20.0	14.7	0.4	0.0	0.6	10.0	9.7	0.0					
S. torminalis	0.0	0.5	19.3	12.1	0.0	0.4	6.6	16.1	12.9	0.2	0.5	12.2	13.0	10.4	0.2	0.1	4.2	12.8	11.2	0.1
T. tomentosa	3.3	17.5	30.0	23.6	1.5	24.8	190.7	22.7	22.4	10.2	5.1	49.0	19.9	17.7	1.9	82.4	917.2	21.3	23.7	39.9
Ulmus spp.	0.2	1.8	26.7	26.6	0.1	1.6	8.7	23.6	20.1	0.7						0.2	5.0	16.2	23.4	0.1
Total		**636.2**			**46.2**		**869.3**			**41.3**		**733.3**			**37.8**		**1234.7**			**48.5**

Table A5: Results (means and SD of the pooled data from the three depths 0–10 cm, 10–20 cm and 20–40 cm) of soil physical and chemical analyses in the different forest types in the transects A, B, and C with the corresponding sample size (n). Soil texture (contents of sand, silt and clay) and water storage capacity at a matric potential > -1.5 (pAWC) were only determined for the 20–40 cm layer. Abbreviations: Soil texture = dominant soil texture class, Sand = Sand content [in %], Silt= Silt content [in %], Clay = Clay content [in %], pAWC = Plant-available water capacity in [%], pH= pH in H_2O, B.D.= Bulk soil density [g cm^{-3}], SOC = soil organic carbon concentration [%], STN = soil total nitrogen concentration [%], P_{av} = resin-exchangeable P [µg g^{-1}], C / N = C / N ratio [g g^{-1}], Ca^{+2}_{ex} = $BaCl_2$-exchangeable Ca^{+2} pool [mol_c m^{-2}], K^{+}_{ex} = $BaCl_2$-exchangeable K^{+} pool [mol_c m^{-2}], Mg^{+2}_{ex} = $BaCl_2$-exchangeable Mg^{+2} pool [mol_c m^{-2}], CEC = cation exchange capacity [µmol_c g^{-1}], BS = base saturation [%]. No soil analyses were conducted in the post-disturbance linden forests.

	Moist mesic beech forests			**Low-elevation xeric beech forests**			**Sub-humid mixed beech-oak-hornbeam forests**			**Sub-humid / thermophilic oak forests**		
Transect	**A (n=3)**	**B (n=3)**	**C (n=4)**	**A (n=3)**	**B (n=3)**	**C (n=3)**	**A (n=5)**	**B (n=7)**	**C (n=8)**	**A (n=5)**	**B (n=3)**	**C (n=3)**
Soil texture	sandy silt	sandy silt	high-silty sand / silty-loamy sand	sandy silt	sandy silt	medium loamy sand	sandy silt / silty loam	sandy silt / silty-loamy sand	high-medium silty sand	sandy silt / poor silty sand	silty-loamy sand	high-medium silty sand
Clay	0.02 (0.03)	0.08 (0.04)	0.09 (0.07)	0.01 (0.01)	0.01 (0.02)	0.10 (0.07)	0.07 (0.09)	0.09 (0.10)	0.05 (0.05)	0.06 (0.08)	0.20 (0.09)	0.01 (0.01)
Silt	0.73 (0.08)	0.56 (0.10)	0.44 (0.03)	0.63 (0.07)	0.66 (0.07)	0.21 (0.14)	0.53 (0.14)	0.72 (0.20)	0.41 (0.14)	0.75 (0.11)	0.49 (0.14)	0.38 (0.04)
Sand	0.25 (0.05)	0.36 (0.08)	0.48 (0.06)	0.36 (0.06)	0.33 (0.06)	0.68 (0.09)	0.4 (0.19)	0.19 (0.13)	0.54 (0.11)	0.19 (0.11)	0.31 (0.23)	0.61 (0.03)
pAWC	0.30 (0.01)	0.30 (0.04)	0.29 (0.11)	0.26 (0.03)	0.35 (0.12)	0.25 (0.03)	0.23 (0.04)	0.34 (0.07)	0.27 (0.04)	0.33 (0.06)	0.33 (0.06)	0.27 (0.02)
B. D.	1.15 (0.17)	1.05 (0.18)	0.85 (0.15)	1.20 (0.20)	0.81 (0.23)	0.91 (0.16)	1.36 (0.13)	1.01 (0.22)	0.96 (0.18)	1.24 (0.17)	1.11 (0.13)	1.05 (0.08)
pH	5.20 (0.26)	5.05 (0.42)	5.03 (0.34)	4.96 (0.25)	4.72 (0.15)	4.60 (0.16)	5.19 (0.46)	5.28 (0.4)	5.27 (0.30)	5.03 (0.29)	4.91 (0.17)	5.03 (0.23)
SOC	1.45 (0.70)	1.68 (1.02)	2.16 (0.95)	1.26 (0.70)	1.26 (0.74)	1.56 (0.80)	1.37 (0.67)	1.26 (0.58)	1.53 (0.96)	1.44 (0.90)	1.12 (0.55)	0.99 (0.44)
STN	0.12 (0.06)	0.14 (0.08)	0.16 (0.07)	0.09 (0.05)	0.10 (0.05)	0.07 (0.03)	0.12 (0.06)	0.12 (0.05)	0.11 (0.07)	0.13 (0.07)	0.12 (0.05)	0.07 (0.02)
P_{av}	3.46 (2.16)	2.25 (1.07)	33.36 (22.07)	1.63 (0.92)	0.67 (0.50)	2.49 (1.36)	7.44 (5.64)	8.13 (11.76)	16.44 (18.2)	6.49 (5.46)	1.26 (0.60)	3.08 (1.92)
C/N	11.87 (1.23)	11.60 (2.98)	14.10 (3.12)	13.46 (1.27)	12.77 (1.80)	21.78 (2.36)	10.96 (1.01)	10.31 (2.29)	13.79 (1.74)	10.94 (1.09)	9.29 (0.97)	14.27 (2.15)
Ca^{2+}_{ex}	4.34 (1.35)	4.19 (3.90)	2.92 (1.73)	1.04 (0.54)	0.33 (0.23)	0.24 (0.15)	3.7 (3.38)	6.54 (4.17)	2.32 (2.05)	2.46 (2.44)	2.78 (2.63)	1.22 (0.47)
K^{+}_{ex}	0.18 (0.09)	0.08 (0.02)	0.12 (0.10)	0.12 (0.03)	0.07 (0.03)	0.09 (0.05)	0.20 (0.13)	0.11 (0.07)	0.19 (0.18)	0.23 (0.19)	0.12 (0.06)	0.11 (0.06)
Mg^{2+}_{ex}	1.02 (0.48)	0.63 (0.32)	0.56 (0.43)	0.43 (0.22)	0.18 (0.15)	0.06 (0.03)	0.70 (0.53)	1.83 (1.09)	0.55 (0.39)	0.95 (0.49)	1.28 (1.07)	0.74 (0.36)
CEC	85.7 (23.3)	96.7 (32.6)	86.0 (27.0)	50.2 (14.6)	60.9 (13.0)	34.7 (13.6)	56.1 (21.1)	123.6 (44.8)	58.6 (33.8)	66.5 (16.5)	91.08 (26.0)	51.5 (5.0)
B.S.	58.2 (17.6)	44.5 (31.9)	48.2 (26.0)	28.5 (14.5)	11.6 (6.8)	13.8 (7.2)	52.2 (30.0)	59.3 (29.8)	52.9 (24.6)	41.1 (24.2)	35.62 (22.8)	39.0 (15.6)

Figures

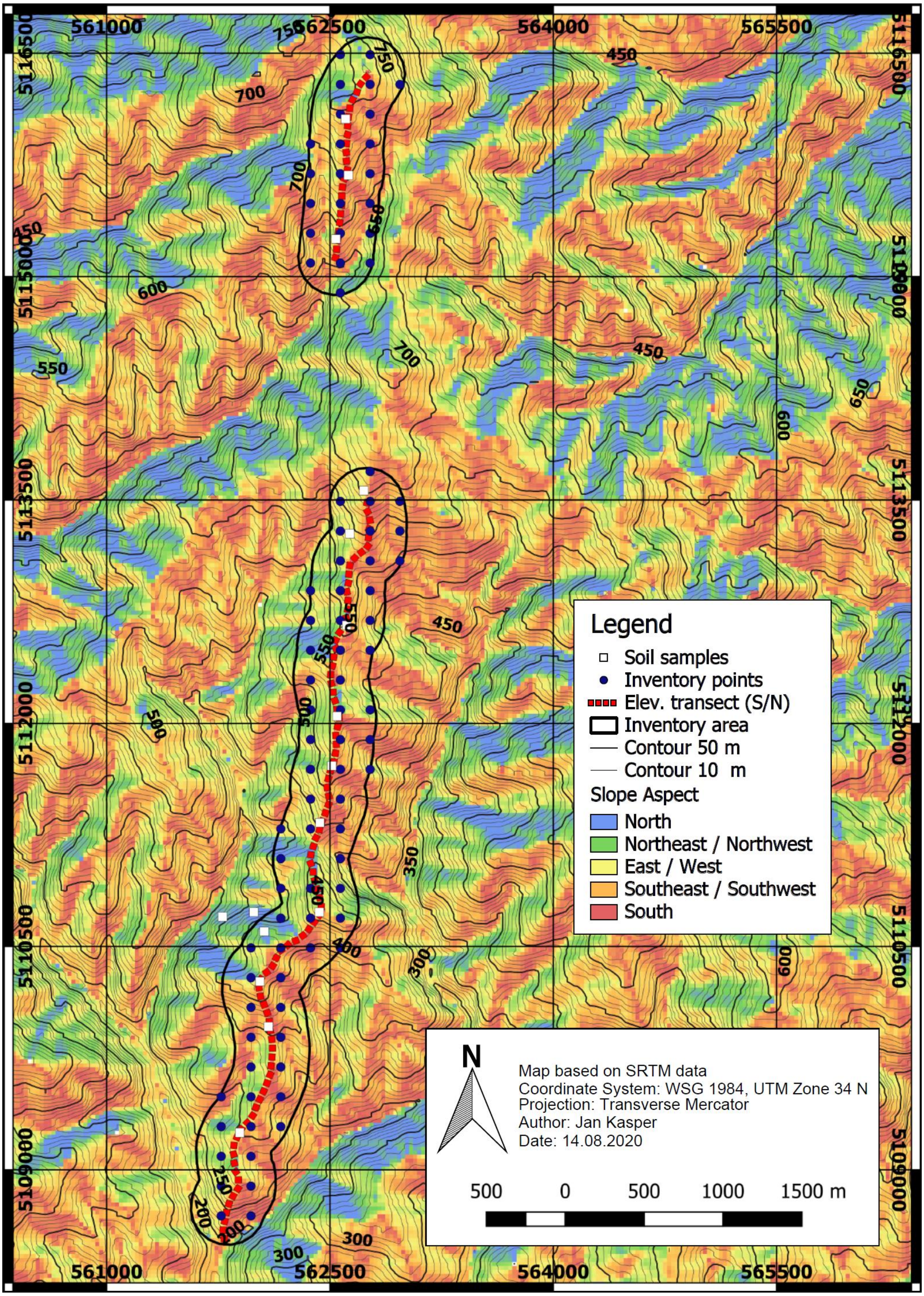

Figure A1: Study transect A (Milova): sampling design showing the elevation transect (North – South orientation) with the contour lines (10 m and 50 m steps), the inventoried area with the inventory points and soil samples as well as slope aspects (N-E-S-W).

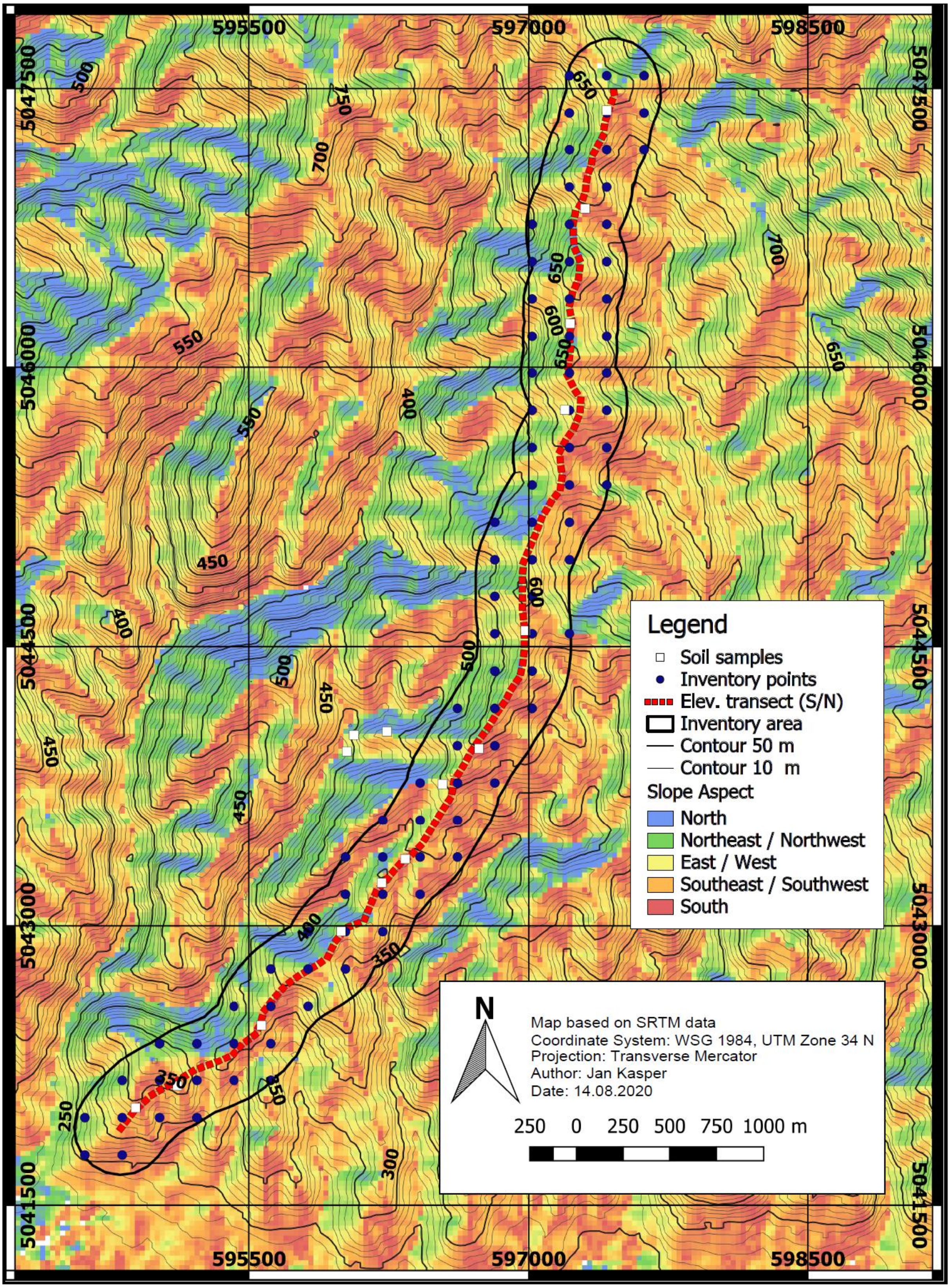

Figure A2: Study transect B (Maciova): sampling design showing the elevation transect (North – South orientation) with the contour lines (10 m and 50 m steps), the inventoried area with the inventory points and soil samples as well as slope aspects (N-E-S-W).

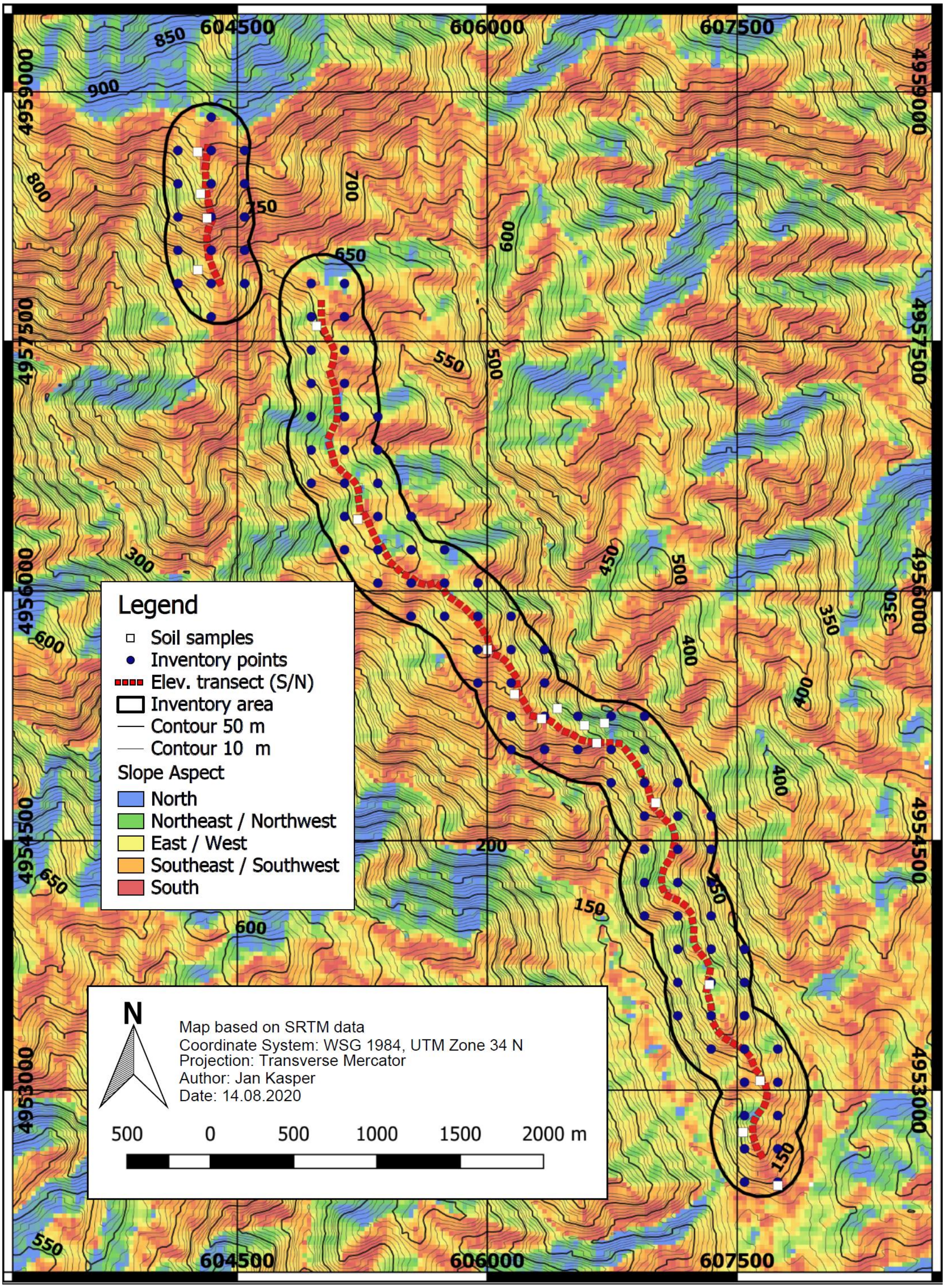

Figure A3: Study transect C (Eşelniţa): sampling design showing the elevation transect (North – South orientation) with the contour lines (10 m and 50 m steps), the inventoried area with the inventory points and soil samples as well as slope aspects (N-E-S-W).

CHAPTER II

CLIMATE WARMING-INDUCED REPLACEMENT OF MESIC BEECH BY THERMOPHILIC OAK FORESTS WILL REDUCE THE CARBON STORAGE POTENTIAL IN ABOVEGROUND BIOMASS AND SOIL

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Published in: Annals of Forest Science (2021) 78:89

Accepted: 23 June 2021 / Published: 15 October 2021

https://doi.org/10.1007/s13595-021-01081-0

2 Climate warming-induced replacement of mesic beech by thermophilic oak forests will reduce the carbon storage potential in aboveground biomass and soil

2.1 Abstract

Climate-warming related replacement of beech by oak forests in the course of natural forest succession or silvicultural decisions may considerably reduce ecosystem carbon storage of central European woodlands. Climate warming may change the carbon (C) storage in forest biomass and soil through future shifts in tree species composition. With a projected warming by 2–3 K over the 21st century, silvicultural adaptation measures and natural succession might lead to the replacement of European beech forests by thermophilic oak forests in drought- and heat-affected regions of central and south-eastern Europe, but the consequences for ecosystem C storage of this species shift are not clear. To quantify the change in C storage in biomass and soil with a shift from beech (*Fagus sylvatica*) to oak forest (*Quercus petraea, Q. frainetto, Q. cerris*), we measured the aboveground biomass (AGC) and soil C pools (SOC). AGC pools and SOC stocks to -100 cm depth were calculated from forest inventory and volume-related SOC content data for beech, mixed beech-oak and oak forests in three transects in the natural beech–oak ecotone of western Romania, where beech occurs at its heat- and drought-induced distribution limit. From the cooler, more humid beech forests to the warmer, more xeric oak forests, which are 1–2 K warmer, AGC and SOC pools decreased by about 22 % (40 Mg C ha^{-1}) and 20 % (17 Mg C ha^{-1}), respectively. The likely main drivers are indirect temperature effects acting through tree species and management in case of AGC, but direct temperature effects for SOC. If drought- and heat-affected beech forests in Central Europe are replaced by thermophilic oak forests in future, this will lead to carbon losses of ~ 50–60 Mg ha^{-1}, thus reducing ecosystem carbon storage substantially.

Key words: beech–oak ecotone, climate turning point, *Fagus sylvatica*, *Quercus petraea*, above ground carbon, soil carbon, soil nutrient pools

2.2 Introduction

Climate warming-related heat-waves and droughts have the potential to destabilize temperate forests, as became visible in the extraordinary heat and drought of the summers 2018 and 2019 in Central Europe. European beech (*Fagus sylvatica* L.), the dominant tree species of Central Europe's natural forest vegetation (Leuschner and Ellenberg, 2017), showed pre-senescent leaf fall and subsequent crown damage in many regions especially on shallow soil, locally causing tree and forest dieback (Schuldt et al., 2020; Walthert et al., 2020). Compared to other native broadleaf tree species of the genera *Quercus, Fraxinus, Carpinus, Tilia* and *Acer, F. sylvatica* is relatively sensitive to drought and heat, and also to elevated atmospheric water vapour pressure deficits (VPD) (Geßler et al., 2007; Hohnwald et al., 2020; Lendzion and Leuschner, 2008; Leuschner, 2020). At its southern and south-eastern distribution limits, European beech most likely is limited by summer droughts and heat (Czúcz et al., 2011; Fang and Lechowicz, 2006), and its occurrence is restricted to the humid montane belt of the mountains (Coldea et al., 2015; Moravec, 1975), avoiding the drier and hotter lowland regions. Here, beech forests are replaced by oak-rich sub-Mediterranean forest communities of the Quercetalia pubescenti-petraeae (thermophilic mixed oak forests) and Carpinetalia betuli (oak-hornbeam forests) orders (Czúcz et al., 2011; Novák et al., 2020). With the recent increase in summer temperatures, VPD and the frequency of heat-waves (Barriopedro et al., 2011; Schär et al., 2004), and regionally decreasing summer precipitation (Caloiero et al., 2018; Schönwiese and Janoschitz, 2005), it is predicted that the climate will become less favourable for beech not only in southern and south-eastern Europe, but also in parts of its Central European distribution range (Dolos et al., 2016; Garamszegi et al., 2020; Mette et al., 2013; Walthert et al., 2020). For western Central Europe, an increase in annual mean temperature (MAT) of 1.6–3.8 °C until 2070 has been projected (Zebisch et al., 2005), which should shift the natural border between beech-dominated mesic forests and oak-dominated thermophilic forests toward higher elevations and to regions with higher precipitation, as VPD rises with the temperature increase. Modelling results based on tree species' climate envelopes and additional information on the species' site requirements indeed predict for the warmer and drier lowlands and lower montane elevations of Central Europe a shift from beech forest to more drought-tolerant, thermophilic forest communities with oak and hornbeam in the course of climate warming in the 21st century (Fischer et al., 2019).

Predictions of a future shift in tree species composition often assume a climate turning point, at which the drought and heat tolerance of a species is exhausted, and more drought-tolerant species gain competitive superiority (Hohnwald et al., 2020). For *F. sylvatica*, which often competes with *Q. petraea* at its dry distribution limit, a turning point close to a MAT of 11–12 °C, a temperature of the warmest months >18 °C, and an annual precipitation of 500–530 mm yr^{-1} has been assumed (Dolos et al., 2016). According to the aridity index EQ, which was introduced by Ellenberg (1963), the turning point is located at an EQ value of 30.

As the majority of European forests are managed and tree species are often selected by foresters, natural climate change-driven shifts in tree species composition will occur in future only in a few protected areas or forests with low management intensity. Such a change has been observed, for example, in England (Cavin et al., 2013) and northern Spain (Penuelas and Boada, 2003). Yet, in various regions of Europe, silviculture has adopted a more natural tree species selection in order to avoid the drawbacks related to conifer plantations, increase forest stability against hazards and to meet the goals of biodiversity conservation (Bolte et al., 2009; Borrass et al., 2017; Spathelf et al., 2018). Oak forests, which most likely would replace beech in many regions in a warmer and drier climate, may thus represent a suitable choice for foresters seeking to adapt production forests to climate warming. Much evidence from ecophysiological and dendroclimatological research shows that *Q. petraea* and other *Quercus* species of thermophilous oak forests, as well as *Carpinus, Fraxinus, Tilia* and *Acer* species, are more drought tolerant than *F. sylvatica* (Brinkmann et al., 2016; Köcher et al., 2009; Kunz et al., 2018; Leuschner et al., 2019; Scharnweber et al., 2011; Scherrer et al., 2011; Thomas, 2000). Thus, it is important to understand the consequences of a future transition from beech to oak-dominated forests, which could take place on quite large areas in central, western, southern and south-eastern Europe, either naturally or aided by foresters. A key ecosystem function, which feeds back on climate warming, is carbon storage and sequestration, which may decrease or increase with a change in tree species composition.

Tree species influence ecosystem carbon storage through species-specific biomass and carbon accumulation trends over the trees' lifetime (Burschel et al., 1993), which lead to different maximum biomass stores (Pretzsch, 2005), and species effects on soil carbon storage (Binkley and Giardina, 1998; Brevik, 2012; Grüneberg et al., 2019; Jandl et al., 2007). As forests are an important element of the global C cycle (Lal, 2005) and storage of C in forest ecosystems is discussed as a means of mitigating anthropogenic climate warming (Ashton et al., 2012), changes in forest C storage with tree species shifts are of considerable scientific and silvicultural interest.

The consequences for C storage of a replacement of mesic beech forests by thermophilic oak forests has not yet received much attention, even though it might influence the climate warming mitigation potential of European forests in the future. One approach to study this question is to study beech and oak forests at their natural ecotone in a climate, which is analogous to that expected in 50 to 80 years in Central Europe. This approach employs a space-for-time substitution to simulate the warming and drying of the climate until the end of the 21st century.

The centre of the distribution range of European beech is located in central and southern Germany, where *F. sylvatica* naturally would cover more than 2/3 of the area, mostly in submontane and montane elevation. The climate in Western Romania is about 2.5 K warmer than in southern Germany, and beech forests occur here at their thermal and drought limits. The colline and submontane belt of the western Romanian Carpathians thus has a climate that may be found in central and southern Germany in 50 to 80 years according to the IPCC global warming projections (IPCC, 2013, Walentowski et al. 2017, Hohnwald et al., 2020). The region may therefore be used as a natural laboratory for studying beech and oak forests in the natural transition zone between the two species under a warmer climate. Mesic beech forests occur in western Romania in a humid climate at elevations above 500/600 m a.s.l., and beech is gradually replaced by mesic mixed beech-hornbeam and hornbeam-oak forests and finally thermophilic oak forests with decreasing elevation towards the colline belt (<300/400 m; Coldea et al., 2015; Doniță et al., 1992; Indreica et al., 2017). While the beech forest climate is similar to that in southern Germany today, the climate of the oak forest zone reflects the projected warmer and drier climate in central and southern Germany in 2070/2100 according to the most probable climate change scenarios. This is clearly beyond the assumed beech/oak climatic turning point (Hampe and Petit, 2005; Mette et al., 2013, Mellert et al., 2016), and beech forests are found at this elevation only extra-zonally on northern slopes or in valleys with higher humidity, representing ‘rear-edge populations, while slopes with southern exposition are covered by oak forests (Doniță, 1992; Lenoir et al., 2013; Maclean et al., 2015).

We used the space-for-time substitution approach (Pickett, 1989) in three elevation transects across the beech–oak ecotone in western Romania to study the carbon storage in aboveground tree biomass and the soil under climatic conditions that likely will be effective in the centre of the beech distribution range at the end of the century. The transects were chosen for sufficient comparability in terms of thermal and hygric conditions, exposition, bedrock type, tree species composition and management history. With a systematic sampling scheme, we measured C stocks in aboveground biomass through forest inventories and soil organic carbon (SOC) stocks in soil pits along plots located continuously along the gradient from pure beech to oak-dominated forests. *F. sylvatica* typically functions as an ecosystem engineer, that modifies stand climate, soil chemistry and hydrology through pronounced effects on radiation transmission to the forest floor and influences on C and nutrient fluxes via a relatively high recalcitrance of its litter (Berg & McClaugherty, 2014; Guckland et al., 2009). This has the consequence that the beech–oak ecotone is not only determined by elevation-dependent temperature and precipitation gradients, but also by strong tree species effects, which have to be taken into account when interpreting the results.

The following hypotheses guided our research:

H1) Tree species diversity increases with the transition from beech to oak dominance, as beech dominance suppresses light- and warmth-loving species.

H2) The aboveground biomass C storage decreases from beech to oak dominance, as drought-affected forests accumulate less biomass.

H3) Soil organic carbon (SOC) storage decreases from beech to oak dominance, as higher temperatures favour mineralization.

H4) The C stock decrease in biomass is primarily a tree species effect, while the decrease in SOC is mainly a climatic (elevation) effect.

2.3 Methods

Study area and transect selection

Three transects were established along elevation gradients in the western Romanian Banat and Crişana regions on the foothills of the south-western Carpathians, extending from the ridge crests in the outermost Carpathian chains at submontane/montane elevation across the natural beech–oak ecotone down to the Western Romanian Plain at colline elevation (Figure 1a). They were located (A) in the Bihar Mountain range (Zarand Mountains) and (B) in the western foothills of the main Carpathian Mountain chain, both in westernmost Romania, and (C) at the foot of the southern Banat Mountains (Almăj Mountains) in south-western Romania (Figure 1b). The transects Milova (A; 46.1°N/21.8°E) and Maciova (B; 45.5° N/22.2° E) are located north-east and south-east of Timisoara, the transect Eșelnița (C; 44.7° N/22.3° E) west of Orşova close to river Danube (Figure 1b). Transects of 500 m width were demarcated covering a spatial sequence from humid beech-dominated forests at submontane/montane elevation over a humid-subhumid ecotone of mixed beech-hornbeam-oak forests (submontane/colline) to the basal subhumid oak-dominated forest at colline elevation (Figure 1c) (Indreica et al., 2019). As the transects were chosen to serve as replicates on the landscape level, they were selected for sufficient comparability in terms of tree species composition, forest management, stand structure, exposition, soil types, and overall climatic conditions.

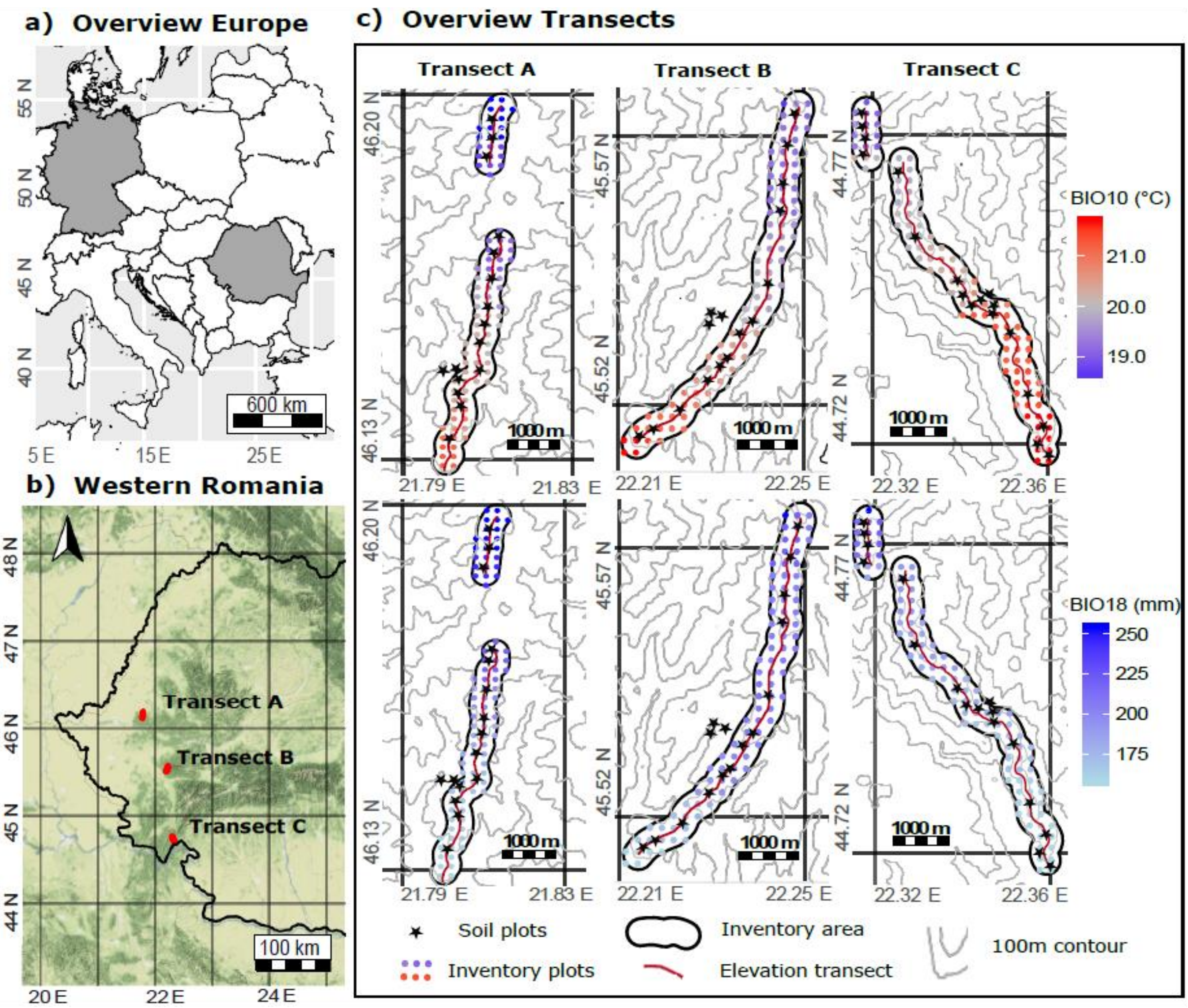

Figure 1: a) Location of Romania in Europe, b) location of the three transects A–C in western Romania from the R- package rworldmap (South, 2011), and c) maps of the three transects with coordinates, contour lines (100 m-elevation distance), the inventoried forest area, and location of inventory and soil sampling plots. The colour of the dots indicates the mean temperature of the warmest quarter (BIO10, upper panels) and the mean precipitation of the warmest quarter (BIO18, lower panels) of the inventory and soil plots according to interpolation from the CHELSA climate data base (Karger et al., 2017).

All forest stands were mature (>60 years old) and of 25–35 m in height with closed canopy. Before the 1960s occasional wood-cutting and coppicing has been conducted at low intensities in all stands. Since then, the forests were transferred to state-ownership and supervised by local forest authorities according to management plans, and previously coppiced stands were allowed to grow into high forests (Öder et al., 2021). The legacy of former coppicing in form of the presence of multi-stemmed trees is still visible in all stands. They were managed according to common Romanian silvicultural schemes, in which stands are lightly to moderately thinned (5–15 % of stand volume) from the pole-wood stage up to an age three quarters of the harvest age (Nicolescu, 2018). Salvage and sanitary loggings were also irregularly conducted at low intensity (<5% of stand volume). Records of the local forest authorities demonstrate that no major harvest operations have occurred in the last 20 years at all sites (Öder et al., 2021).

In the beech and oak forests, beech and three oak species (*Q. petraea, Q. cerris, Q. frainetto*), respectively, each contributed with at least 85 % to total stem number, while remaining stems belonged to accompanying species such as *Carpinus betulus* L., *Acer campestre* L. and *Tilia tomentosa* Moench. In the ecotone, the oak species and beech each contributed with about 30 % to the basal area, while the remainder belonged mostly to *Carpinus* and *Tilia* species. All three transects were placed on predominantly south-west- to south-east-facing slopes.

The climate of the study region is temperate sub-continental with warm summers and relatively cold winters (Table A1 in the Appendix). The lapse rate of annual precipitation was assumed to be +45 mm yr^{-1}/100 m, the temperature lapse rate about −0.5 K/100 m (Maruşca, 2017). For focusing on the most limiting summer period (Bréda et al., 2006; Hohnwald et al., 2020) and comparing our sites with reference sites of beech distribution in Central Europe, we calculated the modified Ellenberg Quotient (EQm) (Mellert et al., 2018) for our study sites, i.e., the ratio of mean temperature during the warmest quarter (BIO10) to precipitation during the warmest quarter (BIO18).

$$\mathrm{EQm} = \left(\frac{\mathrm{BIO10}}{\mathrm{BIO18}}\right) * 1000$$

All forests stock on acidic bedrock, which at many places is covered by a loess layer of up to -100 cm depth. Soil types are predominantly moderately acidic (eutric) Cambisols.

Climate data

High-resolution gridded climate data with a grain of 30 arcsec (~1 km²) was retrieved from the CHELSA (v1.2) climate database (Karger et al., 2017) for monthly temperature and precipitation data sets averaged over the years 1979–2013. For the subsequent statistical analysis, we selected mean temperature of the warmest quarter (BIO10), minimum and maximum temperatures (Tmin and Tmax, average temperatures of the coldest and hottest month, respectively), mean precipitation of the warmest quarter (BIO18), minimum and maximum monthly precipitation (Pmin and Pmax, mean precipitation of the wettest and driest month, respectively), mean monthly temperature (TG) and mean monthly precipitation (PG) data. We extracted the variables BIO10 and BIO18 for the study region to characterize the three gradients with respect to thermal and hygric conditions (Figure 1c). This was done for average elevations of the beech forest, mixed forest (beech–oak ecotone) and the oak forest. The climate data of these 9 locations (3 forest types, 3 transects) were placed in the temperature-precipitation envelope of German climate stations to illustrate the position of the Romanian sites relative to the climate range in the center of the beech distribution range (Figure 2).

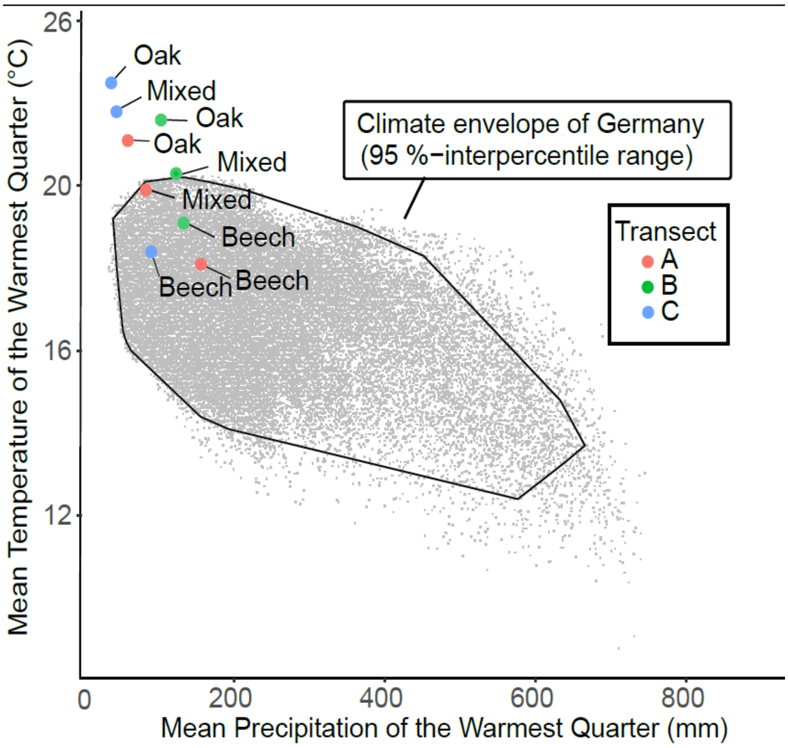

Figure 2: Location of the oak, mixed forest and beech plots of the three transects (red: transect A, green: transect B, blue: transect C) in a biplot of mean temperature of the warmest quarter (BIO10) and mean precipitation of the warmest quarter (BIO18), relative to the climate stations of Germany (grey dots). The black line encloses the 95% inter-percentile range of German climate stations, which is used as a rough approximation of the climate envelope of beech in Central Europe. The climate data were extracted from the CHELSA climate data base (Karger et al., 2017).

Forest inventories and dominant tree species

We obtained forest structure data through systematic sampling in a squared grid of 200 m * 200 m along the studied 500 m-wide north–south oriented transects (Figure 1c). Sample sizes were 90, 90 and 100 plots for transects A, B and C, respectively, with a sample intensity for all sites of approx. 0.8 % of the stand area (Table A2 in the Appendix). For each grid point, the starting point was accessed in the field with a GPS (Garmin GPSmap 64), and a fixed-area plot with 10 m radius was demarcated (314 m^2). Within these plots, all trees with a diameter at breast height (DBH) ≥ 7 cm were determined to species level, and height and diameter measured (DBH with a diameter band covering all individuals; height with a VERTEX IV height meter for max. 3 individuals per species and plot). The mean slope of the plot was determined with the height meter and used to apply a slope correction factor to the measured plot area for plots with slope angle $\alpha > 9\,^{\circ}$ (correction factor $1/\sqrt{\cos(\alpha)}$). Tree height was calculated for all sample trees using DBH-dependent log-height curves fitted for each species and transect, with measured heights being pooled over the transects in case of very infrequent species. We used average allometric equations to estimate biomass adopting the DBH- and height-dependent volume models developed by the Romanian National Forest Inventory described in Vidal et al. (2016) after Giurgiu et al. (2004):

$$\log (v) = a_0 + a_1 * \log (DBH) + a_2 * \log (DBH)^2 + a_3 * \log (h) + a_4 * \log (h)^2$$

with DBH being diameter at breast height (cm), h the modeled tree height (m), and a_0, a_1, a_2, a_3, a_4 species-specific volume coefficients (tree trunk including branches).

Transect-specific wood density data were obtained for the main tree species *F. sylvatica*, *Q. petraea*, *Q. cerris*, *Q. frainetto*, *T. tomentosa* and *C. betulus* by measuring wood cores with a volume of 1 cm^3, which were weighed after drying for 48 h at 105 °C. For all other species, wood densities were taken from values listed in Trendelenburg and Mayer-Wegelin (1955). Wood density was used to convert volume into biomass. With Bosshard (1984) we assumed a mean carbon content of 50 % of the biomass. An overview of the inventory data is given in Table A3 (in the Appendix).

Soil sampling and laboratory methods

Soil samples were taken in soil pits dug to -70 cm depth that were systematically placed along the transects at 50 m elevation steps (13–15 pits per transect; black stars in Figure 1c). Additionally, three pits per site were also dug in “rear edge” beech forests on northern slopes at low elevation; however, they were not included in the analysis. Samples of the organic layer were collected with a metal frame of 30 cm * 30 cm surface area, after larger debris (twigs and branches) had been removed. For the soil physical and chemical analyses, mineral soil samples were extracted in three depths (0–10 cm, 10–20 cm, 20–40 cm) with a metal cylinder of 100 cm^3 volume. To reduce the influence of small-scale soil heterogeneity, three 100 cm^3 samples were extracted per depth and soil pit and mixed. Prior to analysis, the samples were sieved through a 2-mm sieve to manually pick out roots and the coarse-grained soil particle fraction >2 mm from both mineral soil and organic layer. The bulk soil density was determined by drying mineral soil samples of 100 cm3 volume for 48 h at 70 °C and weighing them.

Soil texture was analysed in every pit with a soil particle analyser (Pario, METER Group, Munich) for samples from the depth of 20–40 cm, separating clay, silt and sand fractions. After suspending 40 g of soil in 500 mL H_2O, the organic fraction was dissolved with 30 mL H_2O_2 (30 %) and the soil particles were subsequently dispersed with a solution of 60 g $Na_4P_2O_7$ per 1.0 L H_2O (for details see www.metergroup.com/environment/products/pario/). The potential storage of plant-available water in the soil (pAWC, in %) was calculated with the RETC method after Van Genuchten et al. (1991) from the particle size distribution and bulk soil density, taking into account the coarse-grained particle fraction and subtracting the estimated water capacity at the wilting point (matric potential = -1.5 MPa) from field capacity (matric potential = -60 hPa).

pH (H_2O) was measured in a suspension of 10.0 g fresh sieved soil (2.5 g for the organic layer) in 25 mL deionized water. The total content of K, Mg and Ca in the organic layer was determined after nitric acid-pressure digestion by ICP-OES analysis (Perkin Elmer Optima 5300 DV). In the mineral soil, the concentration of salt-exchangeable cations (K^+, Ca^{2+}, Mg^{2+}, Al^{3+}, Fe^{3+}, Mn^{2+} and Na^+) was determined by percolating 2.5 g of fresh soil with a 0.2 M $BaCl_2$ solution and then determining cation concentrations in the solution by ICP-OES analysis (following Hendershot et al. (2007)). The concentration of exchangeable hydrogen ions (H^+) was calculated during the percolation process from the observed pH change. Since the exchangeable Na^+ concentrations were very low or even below the detection limit at all sites, the Na^+ concentrations were not included in the calculation of the cation exchange capacity (CEC, i.e., the sum of all salt-exchangeable cations plus H^+) and base saturation (BS, % of CEC occupied by Ca^{2+}, Mg^{2+} and K^+). For estimating available base cation pools ($Ca^{+2}{}_{ex}$, $Mg^{+2}{}_{ex}$, $K^+{}_{ex}$) in the mineral soil, the concentration data (in $\mu mol_c\ g^{-1}$) were converted to volumetric data ($mol_c\ m^{-2}$ soil depth) using the bulk soil density data determined separately in all profiles for the studied depths. Total pools of exchangeable cations were then calculated by summing up over all three mineral soil depths investigated. For the organic layer, element concentration values were multiplied with organic layer mass per area to obtain element stocks per ground area ($g\ m^{-2}$).

The organic carbon and total nitrogen contents of ground and dried mineral soil and organic layer samples were analysed by gas chromatography with a vario EL III analyser (Elementar, Hanau, Germany) via detection of CO_2 and N_2 (Skjemstad & Baldock (2007) and McGill et al. (2007)). Soil organic carbon (SOC) and soil total nitrogen (STN) concentrations ($mg\ g^{-1}$) were converted into element densities per area ($Mg\ ha^{-1}$) using the soil bulk density data. Total phosphorus (P) concentration was measured in the organic layer samples with ICP-OES, while in the mineral soil, resin-extractable phosphorus (P_{av}) was determined as an estimate of plant-available P (resin-bag method). To do so, 1.0 g of fresh soil was suspended in 30 mL of water and P_{av} was extracted with the anion exchanger resin Dowex 1 x 8–50. P_{av} was then re-exchanged from the resin with NaCl and NaOH solutions, and the P_{av} concentration determined in a photometer at 712 nm (biochrom Libra S22) against water using the colorimetric molybdate-ascorbic acid method (following Moir & Tiessen (2007)). The soil pools of SOC, STN and P_{av} for profiles to a uniform depth of -100 cm were extrapolated from the values measured in the three depths 0–10 cm, 10–20 cm, and 20–40 cm applying individual depth-dependent decay functions. For comparability of mineral soil element pools among the different forest types and sites, the information on the volume percent of coarse soil particles in the three soil depths (usually < 5 %) was excluded from calculations. To obtain soil data for the stand inventory plots, the soil data from the 13–15 pits per transect were interpolated using weighted means, i.e., the influence of neighboring pits weighted by the inversed squared distance of the soil pits to the inventory plots (for soil chemical raw data see Table A4 in the Appendix).

Data analysis

All data was analyzed with R software version 3.5.1 (R Core Team, 2018) using the R-packages `ggplot2` (Wickham, 2009), `psych` (Revelle, 2015) and `vegan` (Oksanen et al., 2019). We applied ordination techniques to identify the main ecological gradients in the study region and to explore how soil and climate variables are related to the shift in tree species composition along the gradients. In detail, we applied Detrended Correspondence Analysis (DCA, `decorana` in `vegan`), which is well suited for ecological gradient analysis, because it suppresses typical ordination problems inherent to gradient studies including complete species turnover, as in our study, by implementing iterative detrending (Hill and Gauch 1980; Leyer and Wesche 2007).

First, we used the relative basal area of a species per inventory plot as input for the ordination, as it accounts for the number of stems, whilst also representing the species dominance in the forest. To exclude non-forest plots (gaps), all plots with a cumulative basal area < 0.3 m² were excluded from the analysis (n=15). Second, we correlated the standardized values (mean = 0, standard deviation = 1) of individual environmental variables (climate, soil, forest structure, and topography) with the ordination space and tested for significance ($p < 0.05$) of correlations in a 999-fold permutation test (function `envfit`). Here, we accounted for multicollinearity by calculating cross-correlations for all environmental variables in order to eliminate all pairwise correlations by pairwise variable reduction (always retaining the variable of higher correlation to the ordination axes). Further, we accounted for the threefold replication at the transect level by including the transect ID as a spatial term in the tests for significance (permutation testing only within transects, `strata` argument in `envfit` function).

Further, we assessed how the variables aboveground biomass carbon (AGC), soil organic carbon (SOC, only mineral soil), and organic layer carbon (OLC), as well as all soil variables that were significantly correlated to the DCA ordination axes, were related to the complete species turnover from pure oak to pure beech forest along our transects. To do so, we regressed the beech–oak turnover against the variables in the analysis of co-variance (ANCOVA with *F*-

Test, $p < 0.05$) by including the factor "transect" as a spatial term in the models. We calculated the Beech–Oak Index (basal area beech coverage in % - basal area oak coverage in %), ranging from +100 % beech (*F. sylvatica*) to -100 % oak (sum of all *Quercus spp.*). In order to use the exact results from the soil analyses (in comparison to interpolated values for the ordination), we calculated the Beech–Oak index of each soil pit from the four closest forest inventory plots (distance-weighted average). We tested first for a possible interaction between the two explanatory variables (y ~ transect * index). If the interaction was non-significant, the interaction was removed to simplify the model (y ~ transect + species). All model residuals were checked for normal distribution (Q–Q plot, Shapiro Wilk-Test) and, if required, the response variable was log- or square-root transformed to attain a normal distribution of residuals.

2.4 Results

Aboveground carbon-, soil organic carbon-, and nutrient pools in the different forest types

The aboveground carbon pool (AGC) was about 40 Mg C ha^{-1} larger in the beech forests than in the oak forests and the mixed oak-beech forests (difference significant; Figure 3 and Table A5 in the Appendix).

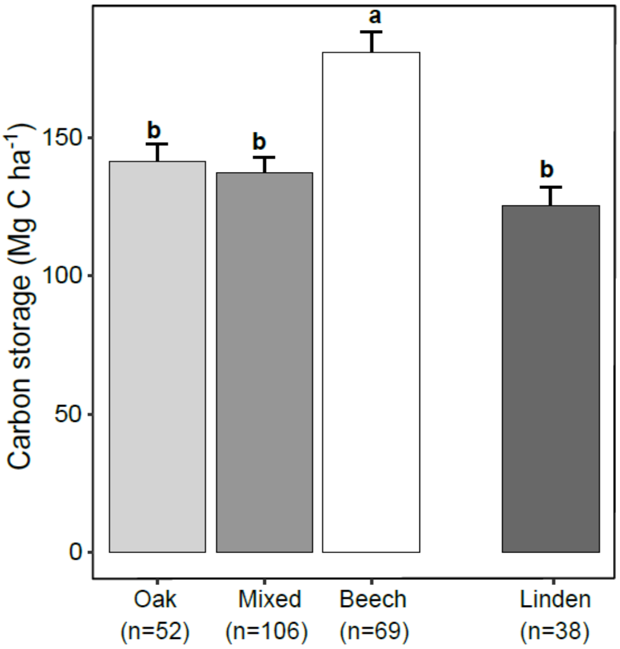

Figure 3: Store of aboveground biomass carbon (in Mg C ha^{-1}) in the oak, mixed and beech forest plots (means and standard error (SE) of the three transects). Plots dominated by linden (basal area of *T. tomentosa* > 66.6 %) are also shown. Beech forests: all plots with basal area of *F. sylvatica* > 66.6 %, oak forests: all plots with basal area of *Quercus* species > 66.6 %, mixed forests: all other forests (except for stands with *T. tomentosa* > 66.6 %). Significant differences between forest types ($p \leq 0.05$) are marked with different small letters (one-way ANOVA with post-hoc Tukey test).

Correspondingly, the mineral soil to -100 cm depth contained about 17 Mg C ha^{-1} more SOC in the beech than the oak and mixed oak-beech stands (significant differences only to mixed forests) (Figure 4 and Table A6 in the Appendix). A similar trend between the forest types existed also for the organic layer C pool, but the differences were smaller and also only significant to the mixed forests (Figure 4 and Table A6 in the Appendix). The difference in AGC between beech forests and oak-, mixed oak-beech- and linden-dominated forests was found in all three transects (Figure A1 in the Appendix), whereas the trend to higher SOC contents in the beech forests was only observed in transects B and C (Figure A2 in the Appendix).

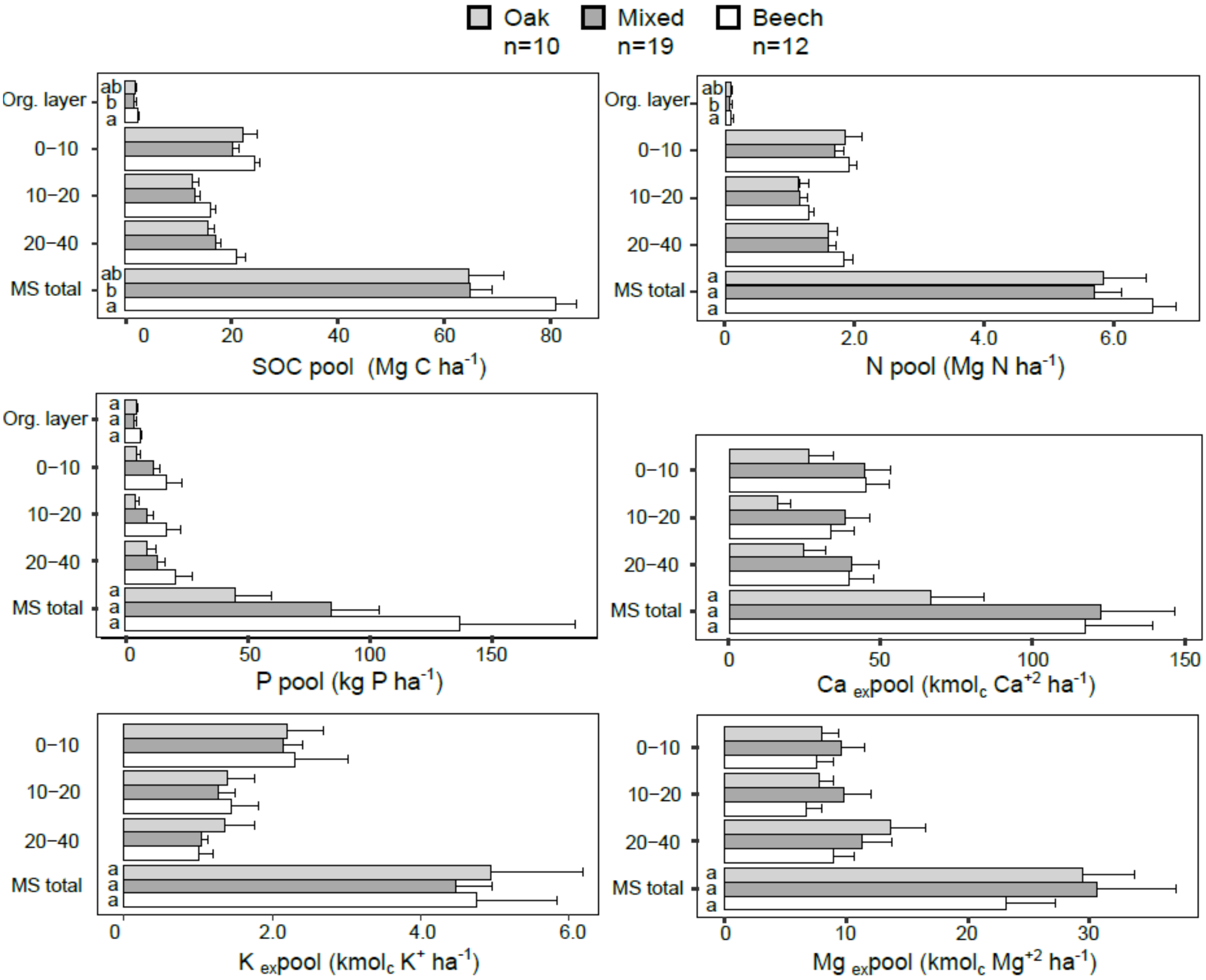

Figure 4: Means (and SE) of C, N, P and cation pools in organic layer and mineral soil of the beech, mixed (beech–oak) and oak stands (n = number of plots). In case of SOC and N, total pools are given for organic layer and mineral soil. P_{av} is resin-extractable P in the mineral soil and total P in the organic layer. For the basic cations (Ca, Mg, K), only $BaCl_2$-exchangeable pools of the mineral soil are given. Profile totals (MS total) of SOC, N and P were calculated for a depth of -100 cm and for Ca^{+2}_{ex}, Mg^{+2}_{ex} and K^{+}_{ex} for a depth of -40 cm. Significant differences for MS total and Org. layer ($p \leq 0.05$) between forest types are indicated by different small letters (Kruskal-Wallis-Test with post-hoc Pairwise Wilcoxon Rank Sum Test). No samples were taken in the linden forests.

The nitrogen pool in the organic layer of the mixed stands and the oak forests was smaller than in the beech forests (Figure 4; difference significant only to beech forests), while the differences in the mineral soil N pools were not significant (Figure 4 and Table A6 in the

Appendix). The significant trends between forest types were more pronounced in the transects B and C than in A (Figure A2 in the Appendix). Soil C/N ratio and base saturation did not differ between the three forest types (Table A6 in the Appendix). We found no significant differences in the mineral soil pool of available P and organic layer total P pool between the beech forests and the other forest types. Yet, transect C exhibited elevated levels of available P in the soil of the beech forests (Figure 4 and Figure A2 in the Appendix). The Ca pool in the organic layer was significantly larger in the beech than the mixed forests (but not the oak forests). In contrast, the mineral soil Ca_{ex} pool was not significantly larger in the beech and mixed forests than in the oak forests (Figure 4 and Table A6, in Appendix). For the Mg and K pools, no clear patterns across the three forest types were found.

Tree species change along the gradients and relationships between forest type and climatic, soil and forest structural factors

Table 1a shows the Eigen- and Decorana values of the DCA ordination axes 1–4 for the inventory plots. The abundance of the four most dominant species in the three transects (*F. sylvatica*, *Q. petraea*, *T. tomentosa* and *C. betulus,* Table 3 in the Appendix) and of the two less abundant thermophilic oak species (*Q. cerris* and *Q. frainetto*, Table 3 in the Appendix) was closely related to the axes 1 and 2 in the ordination. *F. sylvatica* showed the strongest correlation, followed by *Q. petraea* and, at third position, *T. tomentosa* (Table 1b). However, when the three oak species are pooled (*Quercus spp.*) in the ordination, the relationship of the oaks to the axes 1 and 2 became more prominent (Table 1b). Species turnover is in all transects dominated by the shift from *Quercus* species to *F. sylvatica*, despite the frequent occurrence of *T. tomentosa* in the plots (Table 1). The species distribution along the gradients was similar among the three transects, as visible from the equal distribution of the species and transects in the ordination space and the clear separation of the beech- and oak-dominated plots (Figure A4, in the Appendix).

Table 1: Correlation between the tree species' relative basal area (in %) in the plots and the ordination (DCA) axes 1 to 4. (a) Characteristics of the first four axes in the analysis with all tree species. (b) Association of the most dominant tree species (according to their relative basal area in %) to the DCA axes 1 and 2 (expressed as direction cosines) and correlation of the species to the ordination space (given are the R^2 and p-values). While the data set with all tree species was used to establish the ordination in (a), all oak species were pooled to *Quercus spp.* in analysis (b) and this species group was only correlated post hoc to the ordination space.

a) Characteristics of axes 1 to 4					**b) Correlation of main tree species to axis 1 and 2**				
	Axis 1	**Axis 2**	**Axis 3**	**Axis 4**		**Axis 1**	**Axis 2**	**R^2**	**P-value**
Eigenvalue	0.723	0.558	0.489	0.484	*F. sylvatica*	0.294	-0.956	0.879	< 0.001
Decorana value	0.730	0.521	0.376	0.306	*Q. frainetto*	-0.847	-0.532	0.217	< 0.001
Axis length	5.488	3.446	3.763	3.442	*T. tomentosa*	0.305	0.952	0.315	< 0.001
					Q. cerris	-0.816	-0.578	0.146	< 0.001
					Q. petraea	-0.933	-0.360	0.410	< 0.001
					C. betulus	0.366	0.931	0.160	< 0.001
					Quercus spp.	-0.898	-0.440	0.815	< 0.001

The turnover from beech to oak along the first ordination axis as the dominant floristic gradient in the data set correlates with the temperature increase along the gradient, whereas the second axis was related to a shift in precipitation. Tree species turnover was closest associated with temperature variation (elevation), followed by precipitation, and less with the soil and stand structural variables, which showed weaker association with the ordination axes (Table 2). Oak-dominated forests correlated with higher values of the temperature variables and lower values of the precipitation variables and elevation, whereas the opposite was true for the beech-dominated forests (Figure 5a, Table 2a).

Among the soil variables, the association with the ordination axes was strongest for mineral soil SOC and STN with the first ordination axis, revealing increasing C and N pools with decreasing temperature and increasing moisture; the same climatic shifts also explained an increasing proportion of beech in the stands (Figure 5b and Table 2c). While the chemical properties of the organic layer generally were not related to the first two DCA axes, an exception were the stores of OLN and Ca, which tended to be closer associated with lower temperatures and increasing moisture. This was also the case for the Ca^{+2}_{ex} pool and the base saturation in the mineral soil (Figure 5b and Table 2b). None of the soil physical variables like soil texture (sand, silt and clay content) and the calculated pAWC was related to the climatic shift or the tree species turnover along the transects (Table 2c).

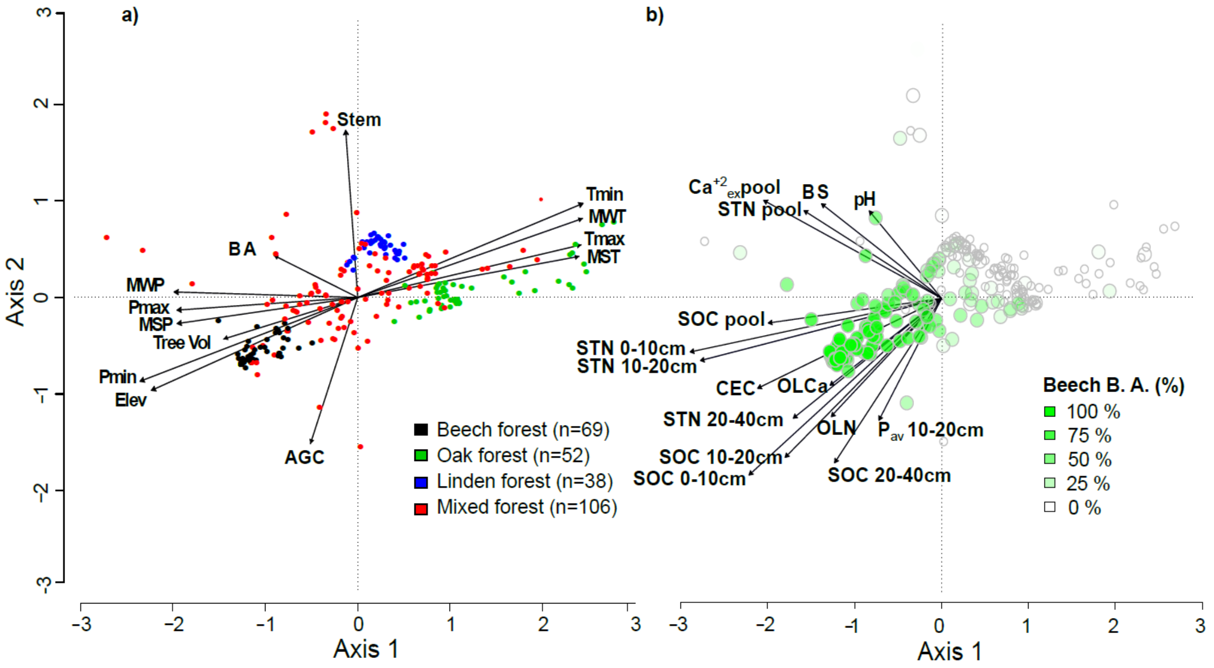

Figure 5: Climatic, edaphic and stand structural variables significantly ($p<0.05$) correlating with the axes 1 and 2 of the DCA ordination space calculated with the tree species` relative basal area (B.A. %) in the plots. The relationships are indicated by the direction of arrows, the strength of correlation (R^2) by the arrow lengths. Symbol position was slightly adjusted to avoid overplotting. For variable units of climate, forest stand, organic layer and soil, see Table 2 and for full names with explanations Table A8 in the Appendix. Plot (a) shows the tested climatic and stand structural variables, plot (b) the organic layer and mineral soil variables. The plots in (a) are coloured according to the dominant tree species (grouped into four forest types according to dominant species (beech forest: *F. sylvatica* B.A. > 66.6 %, oak forest: *Quercus spp.* B.A.> 66.6 %, linden forest: *T. tomentosa* B.A. > 66.6 %; mixed forests: all other species combinations). The plots in (b) are coloured according to the percentage of *F. sylvatica* in the total basal area, indicating the linear shift towards beech dominance along ordination axis 1.

The relationship of stand structural variables with the ordination axes was also weaker than found for the climate variables. Higher values of tree volume and AGC correlated with axis 1 and increased towards the beech-dominated forests, while stem density was more closely related to axis 2 and increased towards the linden-dominated forests. Finally, basal area (BA) increased towards beech- and linden-dominated forests (Figure 5a and Table 2a).

Table 2: Association of the investigated climatic and stand structural (a), organic layer (b) and mineral soil variables (c) with the DCA axes 1 and 2 (given are the direction cosines, and the corresponding R^2 and p-values). The variables are ordered by decreasing R^2; variables with significant association are printed in bold. For the soil chemical variables, either concentrations for mineral soil horizons (0–10 cm, 10–20 cm and 20–40 cm) or total pools (0–100 cm for mineral soil and total for organic layer) are given.

a) Climatic and stand structural variables

Variables	Axis 1	Axis 2	R^2	P-value
Tmin [°C]	**0.93**	**0.37**	**0.38**	**< 0.01**
MWT [°C]	**0.95**	**0.32**	**0.37**	**< 0.01**
Pmin [mm]	**-0.94**	**-0.35**	**0.35**	**< 0.01**
Tmax [°C]	**0.98**	**0.22**	**0.34**	**< 0.01**
MST (BIO10) [°C]	**0.97**	**0.23**	**0.34**	**< 0.01**
Elev. [m a.s.l.]	**-0.92**	**-0.40**	**0.33**	**< 0.01**
MWP [mm]	**-1.00**	**0.03**	**0.22**	**< 0.01**
MSP (BIO18) [mm]	**-0.99**	**-0.14**	**0.22**	**< 0.01**
Pmax [mm]	**-1.00**	**-0.07**	**0.21**	**< 0.01**
Stem [ha^{-1}]	**-0.08**	**1.00**	**0.17**	**< 0.01**
AGC [Mg ha^{-1}]	**-0.32**	**-0.95**	**0.14**	**< 0.01**
Tree vol. [m^3 ha^{-1}]	**-0.94**	**-0.34**	**0.12**	**< 0.01**
Basal area [m^2 ha^{-1}]	**-0.90**	**0.43**	**0.06**	**< 0.01**
Slope [°]	-0.22	0.98	0.01	0.21
Exposition [°]	0.26	0.96	0.01	0.34

b) Organic layer variables

Variables	Axis 1	Axis 2	R^2	P-value
OL N [mg g^{-1}]	**-0.72**	**-0.70**	**0.06**	**< 0.01**
OL Ca pool [kg ha^{-1}]	**-0.81**	**-0.59**	**0.05**	**< 0.05**
OL N/P [g g^{-1}]	-0.98	0.19	0.04	0.14
OL Mg pool [kg ha^{-1}]	-0.74	-0.67	0.03	0.06
OL C [mg g^{-1}]	-0.13	-0.99	0.03	0.09
OL pH [H_2O]	-0.66	0.75	0.03	0.05
OL C/P [g g^{-1}]	-0.92	-0.38	0.02	0.52
OL C/N [g g^{-1}]	0.41	-0.91	0.01	0.88
OL C pool [Mg ha^{-1}]	-0.74	-0.68	0.01	0.77
OL P pool [kg ha^{-1}]	-0.45	-0.89	0.01	0.93
OL N pool [kg ha^{-1}]	-1.00	-0.08	0.00	0.87
Org. matter [kg m^{-2}]	-0.99	-0.13	0.00	0.99
OL K pool [kg ha^{-1}]	0.66	-0.75	0.00	1.00

c) Mineral soil variables

Variables	Axis 1	Axis 2	R^2	P-value
STN 10-20cm [mg g^{-1}]	**-0.98**	**-0.20**	**0.16**	**< 0.01**
SOC 10-20cm [mg g^{-1}]	**-0.76**	**-0.65**	**0.16**	**< 0.01**
STN 0-10cm [mg g^{-1}]	**-0.98**	**-0.20**	**0.15**	**< 0.01**
SOC 0-10cm [mg g^{-1}]	**-0.72**	**-0.69**	**0.11**	**< 0.01**
CEC [mol$_c$ kg^{-1}]	**-0.91**	**-0.42**	**0.10**	**< 0.01**
Ca$^{+2}_{ex}$ pool [kmol$_c$ ha^{-1}]	**-0.89**	**0.46**	**0.10**	**< 0.01**
SOC 20-40cm [mg g^{-1}]	**-0.57**	**-0.82**	**0.09**	**< 0.01**
STN 20-40cm [mg g^{-1}]	**-0.80**	**-0.61**	**0.08**	**< 0.01**
SOC pool [Mg ha^{-1}]	**-0.99**	**-0.13**	**0.07**	**< 0.01**
STN pool [Mg ha^{-1}]	**-0.88**	**0.47**	**0.07**	**< 0.01**
Base saturation [%]	**-0.80**	**0.60**	**0.05**	**< 0.01**
P$_{av}$10-20cm [mg kg^{-1}]	**-0.48**	**-0.88**	**0.04**	**< 0.05**
C/P 0-10cm [g g^{-1}]	-0.85	-0.53	0.04	0.09
N/P 0-10cm [g g^{-1}]	-0.82	-0.57	0.03	0.17
P$_{av}$ 0-10cm [mg kg^{-1}]	-0.26	-0.97	0.03	0.05
pH [H_2O]	**-0.66**	**0.75**	**0.03**	**< 0.05**
C/N 0-10cm [g g^{-1}]	0.73	-0.68	0.03	0.19
P$_{av}$ pool [kg ha^{-1}]	-0.44	-0.90	0.03	0.06
P$_{av}$ 20-40cm [mg kg^{-1}]	-0.33	-0.94	0.03	0.05
Silt [%]	-0.98	-0.18	0.02	0.18
Sand [%]	1.00	0.08	0.02	0.53
C/P 10-20cm [g g^{-1}]	-0.17	0.98	0.02	0.67
N/P 10-20cm [g g^{-1}]	-0.18	0.98	0.01	0.73
C/N 10-20cm [g g^{-1}]	0.53	-0.85	0.01	0.83
K$^{+}_{ex}$ pool [kmol$_c$ ha^{-1}]	-0.30	0.95	0.01	0.54
Mg$^{+2}_{ex}$ pool [kmol$_c$ ha^{-1}]	-0.42	0.91	0.01	0.83
C/N 20-40cm [g g^{-1}]	0.12	-0.99	0.01	0.99
Clay [%]	0.69	0.72	0.00	0.89
pAWC [%]	-0.63	-0.78	0.00	0.95
N/P 20-40cm [g g^{-1}]	0.38	-0.93	0.00	1.00
C/P 20-40cm [g g^{-1}]	0.72	0.69	0.00	1.00

Relatedness of the Beech–Oak Index to aboveground biomass carbon, soil carbon and nutrient stocks

The relationships of the significantly correlating mineral soil variables (SOC and STN pools, P$_{av}$ pool, Ca$^{+2}_{ex}$ pool, CEC, BS and pH), organic layer variables (OLC, OLN, P, and Ca pools) as well as of AGC with the abundance of beech and oak, expressed through the Beech–Oak Index, were tested with an ANCOVA model of the form y ~ transect * index. None of the variables were related to the interaction between transect and Beech–Oak index. Yet, when a simplified ANCOVA model of the form y ~ transect + index was run, numerous soil and climate variables showed a significant transect effect, revealing regional differences between the three study sites (Table A7 in the Appendix). A significant relationship to the Beech–Oak Index was found only for a minority of variables, notably AGC, the SOC pool in the mineral soil (Figure 6 and Table 3), and the organic layer Ca pool (results of the ANCOVA modeling in Table A7 in the Appendix).

Table 3: ANCOVA table for models testing the influence of transect A–C and Beech–Oak Index (index) on (a) aboveground biomass carbon (AGC in Mg C ha^{-1}) and (b) soil organic carbon (SOC in Mg C ha^{-1}) in the mineral soil (0–100 cm) in the plots of the three transects. The model was of the form: *AGC* or *SOC ~ transect + index*.

	a) **Aboveground biomass carbon** (Square-root transformed)					b) **Soil organic carbon** (Log 10-transformed)				
	Df	Sum Sq.	Mean Sq.	F-value	p-value	Df	Sum Sq.	Mean Sq.	F-value	p-value
Transect	**2**	**195.39**	**97.70**	**19.96**	**< 0.001**	**2**	**0.11**	**0.05**	**4.72**	**< 0.05**
Index	**1**	**110.32**	**110.32**	**22.54**	**< 0.001**	**1**	**0.07**	**0.07**	**6.48**	**< 0.05**
Residuals	261	1277.31	4.89			37	0.43	0.01		
	Adjusted R^2: 0.1838					Adjusted R^2: 0.2443				

The linear models show consistently for all three transects that AGC and SOC decrease from the beech-dominated to the oak-dominated forests, despite differences in the climatic, edaphic and stand structural characteristics between the transects (Figure 6). Despite this uniform trend, the absolute size of carbon pools was significantly different between transects, with transect B having the largest AGC pool and transect A the highest SOC pool (Figure 6).

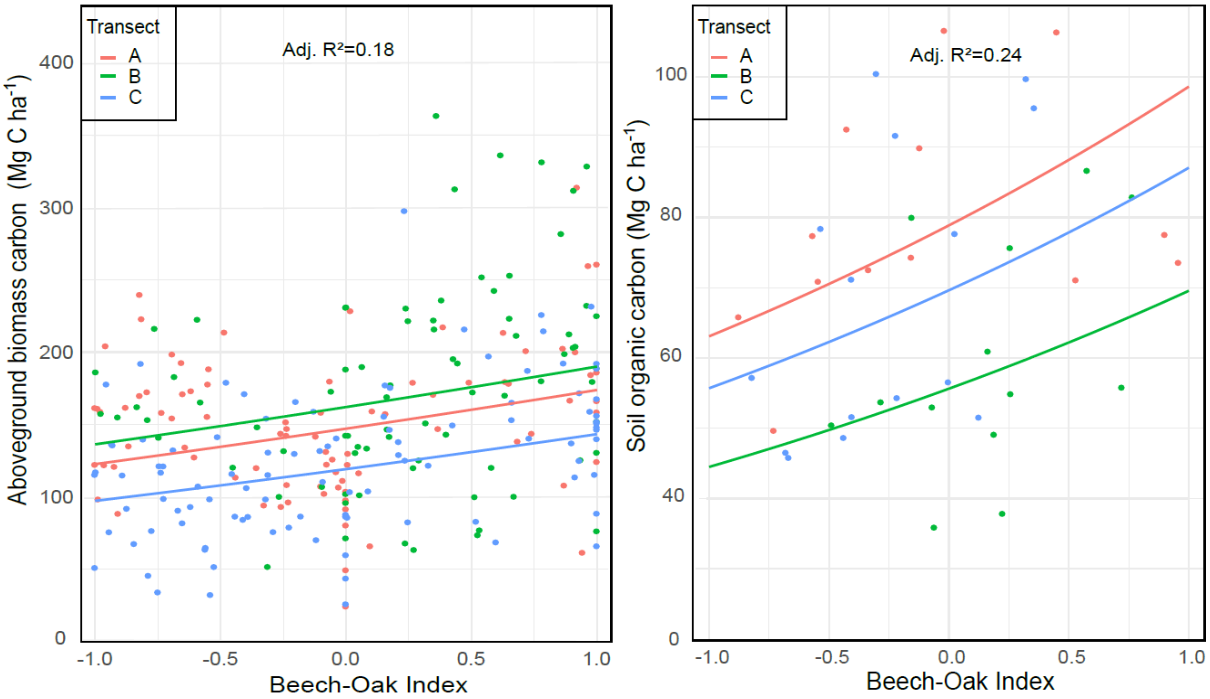

Figure 6: Left panel: Aboveground carbon (Mg C ha^{-1}) and right panel: soil organic carbon (Mg C ha^{-1}) in dependence of the Beech–Oak Index (-1 for 100 % Oak to 1 for 100 % Beech relative basal area) for the three transects according to the model predictions. The adjusted R^{2} of the model fit is also given. The abundance of plots near an index value of 0 is caused by plots in which *T. tomentosa* forms pure stands.

2.5 Discussion

Climatic conditions across the beech–oak ecotone

Our study of oak and beech forests in the relatively undisturbed contact zone between the two species allows defining the thermal and hygric limits of beech in central-eastern Europe to 18.4–21.8 °C mean temperature of the warmest quarter (BIO10) and 140–200 mm precipitation in the warmest quarter (BIO18). Since the shift from beech to oak occurs roughly in the middle of the three transects, the thermal beech/oak turning point must be in the range of 19.5–20.5 °C of the BIO10 quarter. Using the modified formula of the Ellenberg Aridity Index after Mellert et al. (2018), the turning point appears at EQm = 97.5. This agrees quite well with the hot and dry limit of the 95 %-inter-percentile range of temperature and precipitation data from German climate stations that enclose most of the beech distribution range in Central Europe. In fact, the three oak forests of the Romanian study region lie well beyond the climate envelope of beech forests in Germany, and two of the three mixed oak-beech forests are located exactly on the 95 %-demarcation line, confirming that most of Germany currently has a climate still supporting beech growth. However, an increase of the BIO10 by at least 2.3 °K, as projected for 2061–2080 in southern Germany for the intermediate climate warming scenarios (RCP 4.5, RCP 6.0), will shift part of the current beech forest area into the oak forest domain.

Earlier studies of forest structure and community composition in the western Romanian study region have shown that the beech forests are in many structural aspects very similar to Central European beech forests of the Galio-Fagion, and the oak-rich forests resemble Central European communities of the Quercetalia pubescenti-petraeae (thermophilic mixed oak forests) and Carpinetalia betuli (oak-hornbeam forests), despite the admixture of additional tree species with sub-Mediterranean and southeast European origin (Heinrichs et al., 2016; Indreica et al., 2017, 2019; Walentowski et al., 2015). The forest inventory and soil chemical data show that the three transects are located on mesic to eutric soils, and they are more or less comparable among the transects. Similar soil conditions are quite widespread in the beech forest region of central and southern Germany (Bohn et al., 2000; Fleck et al., 2019; Wellbrock et al., 2019).

The beech–oak forest ecotone is associated with a shift from mesic to thermophilic tree species

While *F. sylvatica*, *Q. petraea* and *T. tomentosa* were the most abundant tree species in the studied beech–oak forest ecotone of western Romania, *C. betulus* occurred as another relatively abundant co-dominant species in the mixed forests. The next most frequent species were *Q. cerris* and *Q. frainetto,* which are characteristic for thermophilic forests of the Balkans. *T. tomentosa, Q. cerris* and *Q. frainetto* do not occur in the thermophilic forests of Central Europe, which are rich in oak, hornbeam and linden and replace beech forests in the hottest and driest regions (Bohn et al., 2000). The three species are elements of the (eastern) sub-Mediterranean thermophilous oak forests (Coldea et al., 2015; Horvat et al., 1974) and presumably are more drought- and heat-tolerant not only than *F. sylvatica* but also than *Q. petraea* (Petritan et al., 2021).

As predicted, the average tree species richness increased from the species-poor beech forests to the mixed oak-beech and also to the oak forests, where usually several oak species coexisted with other light-demanding species. The ordination grouped *Q. cerris* and *Q. frainetto* together with the rarer accompanying species *Fraxinus ornus, Carpinus orientalis, Sorbus torminalis* and *Acer tataricum,* while *F. sylvatica* associated with the mesophilous species *Betula pendula, Populus* ssp., and to a lesser degree, *A. pseudoplatanus* and *Alnus glutinosa*. Species turnover in the ordination was in the DCA best represented by the first two ordination axes, which also display the variable presence of *F. sylvatica* and the *Quercus* species in the stands and therefore represent the elevation gradient in the three transects. *C. betulus* and *T. tomentosa* group somewhat in between beech and oak in the DCA; they characterize stands where neither beech nor oak species achieved dominance. Our vegetation gradient reflects the typical altitudinal zonation of forest communities in Romanian mountains, in which the thermophilic oak forest zone is replaced upslope by the mixed oak-hornbeam and beech-hornbeam zone, which finally gives way to the mesic beech forest zone (Coldea et al., 2015; Doniță, 1992; Indreica et al., 2017). *T. tomentosa* as a species of the south-east European flora plays an important role in the forests of the study region. It often forms stands with high linden dominance, which is thought to be a result of timber extraction in the distant past. *T. tomentosa* is able to rapidly colonize forest gaps and form nearly pure stands (Dinic et al., 1999; Radoglou et al., 2009).

The shift from oak to beech forest is associated with pronounced change in climatic, but not edaphic, conditions

The elevation distance between the level of typical oak and typical beech forests varies between 205 and 315 m in the three transects, which is equivalent to a temperature difference of 1.0–1.6 °K. We assumed a precipitation increase of 45 mm yr^{-1}/100 m in the study region, which results in an estimated precipitation increase of 90–140 mm yr^{-1} from the oak to the beech forest level. Microclimatic measurements inside the stands showed that the temperature difference in mid-summer is even greater (2 °K; Hohnwald et al., 2020). The somewhat cooler and moister climate in the beech forests may well be the main cause of the higher SOC pool in this forest type as compared to the oak and mixed forests further downslope.

Our ordination which analysed the association of climatic and edaphic factors with the beech–oak abundance gradient, showed a dominant influence of climatic factors, while edaphic variables associated only weakly with the species turnover from beech to oak. Climate factors explained a maximum of 38 % (in case of Tmax) and a minimum of 21 % (Pmin) of the species variation in the ordination, demonstrating the expected association of beech and oak forests with variation in temperature and moisture. This fits with range-wide dendroecological analyses, which typically show that beech is very sensitive to high summer temperatures and low precipitation (Di Filippo et al., 2007; Jump et al., 2006; Muffler et al., 2020). In contrast, dendrochronological data show for Central European oak species a much smaller influence of drought and heat on radial growth (Härdtle et al., 2013; Harvey et al., 2020; Scharnweber et al., 2011), which largely explains the dominance of oak forests in the hotter and drier foot zone of the Romanian mountains.

Unlike the climatic factors, the association between soil chemical properties and the beech–oak abundance gradient was weaker and for many variables not significant. This is explained by the only minor change in soil properties across the beech–oak ecotone and the fact that both beech and the oak species show a broad tolerance for variation in soil acidity and base saturation (Leuschner and Ellenberg, 2017). The observed soil chemical differences between beech and oak forests may in part be explained by elevation effects on pedogenesis, while tree species effects on soil chemistry likely are of minor importance. Variation in soil physical properties, notably clay content and storage capacity for plant-available water, were not related to the tree species turnover from beech to oak forest. This confirms that oak replaces beech because the climate becomes unfavourable at lower elevations, and not due to changes in soil texture that increases edaphic aridity in the foot zone of the mountains.

Aboveground biomass and soil carbon stocks are higher in beech than in oak forests

The studied beech forests stored on average about 28 % more C (≈ 40 Mg ha^{-1}) in aboveground biomass and 25 % more C (≈ 17 Mg ha^{-1}) in the soil than the oak forests, in total (AGC and SOC) about 55 Mg C ha^{-1} in excess. While the difference in AGC between beech and oak forests was large in all three transects (A,B,C), the SOC pool differed between beech and oak forest only in Maciova (transect B) and Eșelnița (transect C), whereas no SOC difference was found in Milova (transect A). With about 180 Mg C ha^{-1} in aboveground biomass, our beech forests stored somewhat more biomass C than 100-yr-old beech forests in Romania are containing on average according to the national forest inventory (150 Mg C ha^{-1}, Bouriaud et al. (2019)). Our AGC figures are closer to mature managed age-class beech forests in central Germany (mean of 14 stands: 180 Mg C ha^{-1}, Meier and Leuschner, 2008). Burschel et al. (1993) give an average C storage over all stages of a beech management cycle in Germany of 142 Mg C ha^{-1}, which is lower due to the inclusion of younger trees. Oak forests store in the temperate region of Europe in general less biomass than beech forests, which is often a consequence of lower stem densities. For example, Burschel et al. (1993) give average biomass C stores of <120 Mg C ha^{-1} for German oak forests up to 160 years in age. Our figures of about 140 Mg C ha^{-1} are relatively high due to the high stem densities (on average 733 ha^{-1}), likely as a consequence of low management intensity in these Romanian oak forests. This is in stark contrast to most Central European oak forests, which are intensively thinned at higher age to produce large-diameter stems of high value.

The higher carbon storage in aboveground biomass and deadwood in the beech as compared to the oak forests coincides with a larger SOC pool: The by about 40 Mg C ha^{-1} greater biomass C store in the beech stands was associated with a by 20 m^3 ha^{-1} larger deadwood volume (Öder et al., 2021), and the SOC pool was ca. 15 Mg ha^{-1} larger in the beech than the oak forests. It is unlikely that this represents a causality, as the higher SOC stock under beech is easily explained by the elevational distance between oak and beech forests. The greater elevation of the beech stands corresponds to a by 1.0–1.6 °K lower annual mean temperature, which reduces decomposition rate. Correspondingly, SOC stores under forest have been found to increase by about 12.4 Mg C ha^{-1} per 100 m increase in elevation according to a global meta-analysis (Tashi et al., 2016), which can fully explain the difference. Thus, possible effects of tree species and the larger biomass in the beech forests likely are playing only minor roles.

Soils under Central European oak and beech forests generally accumulate similar amounts of C and N, when bedrock and climate are comparable. This is evident from the national forest soil inventory of Germany, where more than hundred profiles each under beech and oak forest did not differ significantly with respect to SOC stores in the mineral soil and the organic layer (Grüneberg et al., 2019). Similarly, beech and oak stands planted on similar soil contained after 40 years similar amounts of SOC in the mineral soil (Gurmesa et al., 2013). In our transects, organic layers under beech and oak had very similar C/N ratios, which points at only minor species differences in litter decomposability. The finding that N pools both in the mineral soil and organic layer tend to be higher in beech-dominated forests is not surprising, as C and N accumulation in the soil are usually closely coupled and the differences thus likely relate to the species effect (Zaehle, 2013).

Less expected is the result that the pools of calcium in the organic layer (total pool) and in the mineral soil (exchangeable pool) increased toward higher beech dominance and base saturation. Although the association of Ca content and base saturation with the turnover from beech to oak forests along the gradient was less close than for the soil C and N contents, there were significantly larger Ca pools in the organic layer of the beech forests, and a tendency for higher exchangeable stocks in the mineral soil. This cannot be explained by variation in bedrock types and rather suggests a physiological effect, with beech apparently being more efficient than oak in mobilizing cations, in particular Ca^{2+}, in the subsoil. The ions are transferred with plant uptake and litter fall to the organic layer, where this 'base pump' leads to a long-term enrichment of basic cations in the topsoil (Binkley and Valentine, 1991; Guckland et al., 2009). The significance of such an effect has to be verified by analyses of element fluxes with leaf litter in the beech and oak forests.

Implications for beech forests in the core of the species' distribution range

Given that the current climate in the studied oak forest zone in western Romania is about 2.5 °K warmer than in the beech-dominated submontane belt in southern Germany (Walentowski et al., 2017), we use our findings in a space-for-time substitution approach to predict that natural succession driven by a temperature increase by 2–3 °K would transform large parts of the southern German beech forests in oak-dominated communities with higher drought and heat tolerance. This is in line with projections from climate-driven forest vegetation models for this region (e.g. Fischer et al., 2019). This would cause a significant reduction in ecosystem carbon storage of roughly 20 % or in the magnitude of 50–60 Mg C ha^{-1}. Widespread crown damage and dieback of beech, especially on shallow soils after the exceptional 2018/2019 drought episode, has demonstrated the vulnerability of beech forests in many regions of Central Europe (Schuldt et al., 2020), suggesting that the scenarios of community shifts are not unrealistic. Clearly, it must be kept in mind that a space-for-time substitution approach is a simplification of a predicted reality, and factors such as different latitudes, the continentality of the climate (Bohn et al., 2000; Leuschner & Ellenberg, 2017), and proximity to tree species pools (Reznicek et al., 1993; Jäger and Welk 2003; Willner et al., 2009; Walentowski et al., 2010; Walentowski et al., 2014) are all influencing forest community composition and may distinguish the two regions.

Additional important factors influencing forest structure are human influence and the browsing pressure of game, which might differ between Germany and western Romania (Müller et al., 2005; Schulze et al., 2014; Winter et al., 2015). In all three transects, timber extraction has occurred in the past, but no major activities have occurred during the last 20 years (Öder et al., 2021). This is similar to production forests in Central Europe that have been set aside more recently for conservation purposes. With respect to browsing pressure, game densities appear to be lower in western Romania than in Central Europe, where the regeneration of broadleaf trees, in particular of oaks, is strongly suppressed in many forest regions (König & Baumann, 1990). Roe dear densities for the regions around Milova (Transect A), Maciova (Transect B) and Eșelnița (Transect C) have been estimated from the regional forest authorities at 1.30, 0.41 and 0.80 animals 100 ha^{-1}, respectively, and red deer densities at 1.0, 0.13 and 0.30 animals 100 ha^{-1}, respectively (A. Petritan, pers. comm.). With this low browsing pressure in western Romania, oak forests might show more vital regeneration and be species-richer than under the higher game densities in many Central European forest regions.

2.6 Conclusions

Our study of stand structure and ecosystem carbon pools in three near-natural beech-oak forest ecotones demonstrates some possible consequences of climate change-driven forest transformation. The size of biomass and soil carbon pools was in our models clearly related to the beech–oak abundance gradient, confirming that, despite a marked effect of region or transect location, the decrease in ecosystem C storage from beech to oak forests is significant, underpinning the more general validity of our findings. While the biomass C difference is mainly caused by tree species and related management effects, it is likely that the SOC difference is largely a consequence of the elevation difference and thus temperature change. A warming by 2–3 K in the near future will generally increase both forest productivity and decomposition rate, as long as other factors such as drought or nutrient shortage are not limiting, but empirical evidence suggests that forest soils in the temperate zone are responding with a SOC pool decrease (Hopkins et al., 2012; Melillo et al., 2017). Our results demonstrate that carbon inventories across forest ecotones along temperature and/or precipitation gradients are one option for scientists and foresters to explore putative changes in biomass and soil C stores that result from man-made or natural tree species shifts.

2.7 Acknowledgements

We would like to thank the forestry departments of Radna, Caransebeș, Oțelu Roșu and Orșova for their collaboration. Furthermore, our gratitude goes out to all the students and field assistants incorporated into the realization of the field work, as well as all the NEMKLIM project partners.

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2.9 Appendix

Tables

Table A1 Location of the three transects with longitude (Long.) and latitude (Lat.), elevation (Elev.) and climatic characteristics of the highest (top end) and lowest (bottom end) plots. The highest-elevation plots are located in typical beech forests, the lowest plots in typical oak forests. Given are annual mean temperature (Tm), temperature of the warmest month (Tmax), temperature of the coldest month (Tmin), mean temperature of warmest quarter (BIO10), mean annual precipitation (Pm), precipitation of the wettest month (Pmax), precipitation of the driest month (Pmin), and precipitation of the warmest quarter (BIO18) according to data extracted from the CHELSA climate data base (Karger et al., 2017).

Locality	**County**	**Transect position**	**Long.**	**Lat.**	**Elev. [m]**	**Tm [C°]**	**Tmax [C°]**	**Tmin [C°]**	**BIO10 [C°]**	**Pm [mm yr^{-1}]**	**Pmax [mm]**	**Pmin [mm]**	**BIO18 [mm]**
Milova (Transect A)	Arad	Top end	21.8135	46.1973	759	7.9	23.4	-6.5	18.2	892	125	48	254
		Bottom end	21.8022	46.1290	216	10.8	26.5	-6.5	21.2	690	132	52	248
Maciova (Transect B)	Caraș-Severin	Top end	22.2460	45.5749	719	8.2	23.8	-7.1	18.6	951	100	54	216
		Bottom end	22.2116	45.5248	256	11.1	26.9	-4.0	21.7	791	81	41	157
Eselnita (Transect C)	Orsova	Top end	22.3188	44.7754	907	7.8	23.6	-3.8	18.3	844	106	45	201
		Bottom end	22.3578	44.7173	147	11.9	28.0	-3.5	22.6	598	69	40	137

Table A2: Transect length, inventoried forest area, number of inventory plots, sampling intensity (plot area per forest area in %), and total sampled areas in the three transects. All plots had a size of 314.2 m^2.

Transects	**Length** [m]	**Area** (ha)	**No. of plots** (n)	**Sampling intensity** (%)	**Sampled area** (m^2)
Transect A	6694	357.7	90	0.79	28278 m^2
Transect B	6696	352.5	90	0.80	28278 m^2
Transect C	7465	405.0	100	0.76	31416 m^2

Table A3: Results (means and SD in brackets) of the forest inventories (trees with DBH ≥ 7cm) along the three transects (A, B, C) with the corresponding sample size (n inventory plots). Given are for the different species the relative basal area in % (BA), the estimated stems per ha (Stem), the diameter in cm (DBH), the height in m (h), the basal area per ha in m² (BA), the tree volume per ha in m³ (Vol) and the tree biomass per ha Mg in DM. (Bio). Coniferous species (*Larix decidua*, *Pinus* spp. and *Picea abies*) occurring on single plots as well as additional deciduous broadleaf species (*A. tataricum*, *Q. robur*, *Salix* spp., *T. cordata*) were grouped to the classes *Other coniferous* and *Other deciduous*.

	Transect A (n=90)							**Transect B (n=90)**							**Transect C (n=100)**						
Species	**BA**	**Stem**	**DBH**	**h**	**BA**	**Vol**	**Bio**	**BA**	**Stem**	**DBH**	**h**	**BA**	**Vol**	**Bio**	**BA**	**Stem**	**DBH**	**h**	**BA**	**Vol**	**Bio**
A. campestre	0.2	5.0	13.3 (4.4)	16.2 (3.4)	0.1	0.7	0.3	0.1	1.5	17.7 (10.1)	19.3 (10.3)	0.0	0.4	0.2	0.3	4.8	14.8 (8.4)	9.7 (3.9)	0.1	1.0	0.5
A. platanoides	1.4	11.7	22.7 (9.6)	22.6 (5.9)	0.6	6.3	3.3	0.4	2.9	25.1 (10.3)	25.2 (2.1)	0.2	1.8	1.0	0.4	2.2	27.9 (13.7)	19.9 (1.7)	0.2	2.1	1.1
A. pseudoplatanus	1.3	7.8	27.4 (9.6)	21 (9.4)	0.5	5.2	2.7	0.1	0.7	22.5 (7.1)	20.3 (n.a.)	0.0	0.3	0.1	1.3	7.0	28.3 (14.7)	19.9 (4.8)	0.6	6.1	3.2
***Betula* spp.**								2.2	18.3	24.3 (7.4)	22.4 (6.3)	0.9	9.0	4.7							
C. betulus	5.7	111.1	15.0 (5.9)	17 (4.4)	2.3	22.2	13.5	11.0	159.9	17.6 (7.8)	18.4 (5.2)	4.5	47.6	28.9	3.8	70.0	14.7 (8.7)	12.8 (4.5)	1.6	13.8	8.3
C. orientalis															1.1	44.6	10.8 (4.1)	9.1 (2.4)	0.5	2.5	1.5
F. ornus															3.0	86.9	12.6 (4.9)	10.4 (3.4)	1.2	7.9	5.1
F. sylvatica	27.1	128.0	29.7 (13.5)	29.2 (6.1)	10.7	160.7	94.2	42.5	244.0	26.1 (16.0)	26.2 (7.8)	17.3	254.1	148.9	35.2	263.6	22.6 (14.1)	22.9 (5.0)	14.7	171.3	100.4
P. avium	1.8	18.4	20.1 (9.4)	20.3 (7)	0.7	8.0	3.9	1.4	10.6	24.3 (12.0)	23.8 (6.5)	0.6	7.5	3.7							
***Populus* spp.**	0.0	1.1	10.5 (0.5)	6.4 (0.9)	0.0	0.0	0.0	2.9	11.7	32.2 (17.6)	28.5 (5.7)	1.2	20.2	7.5	0.2	1.9	23.5 (9.5)	18.8 (7.3)	0.1	1.2	0.4
Q. cerris	3.6	20.5	28.7 (8.0)	22.6 (3.3)	1.4	15.5	10.1	3.2	9.5	41.0 (12.1)	31.2 (2.8)	1.3	19.6	12.7	0.7	4.5	26.8 (10.2)	13.5 (4.9)	0.3	2.0	1.3
Q. frainetto	1.8	11.7	26.7 (6.3)	21.5 (8.0)	0.7	8.2	5.5	0.7	1.5	44.5 (27.7)	20.6 (6.5)	0.3	4.3	2.8	2.4	18.1	24.6 (10.3)	14.8 (5.2)	1.0	9.2	6.1
Q. petraea	26.9	163.0	26.8 (10.4)	25.2 (4.6)	10.6	147.9	95.7	9.3	46.1	30.5 (12.5)	25 (5.0)	3.8	52.8	34.1	26.0	172.5	26.6 (9.6)	18.3 (4.3)	10.8	113.1	73.2
R. pseudoacacia								0.5	6.2	20.0 (8.1)	20.1 (7.9)	0.2	2.0	1.3	0.5	6.0	19.5 (9.7)	12.2 (5.0)	0.2	1.4	0.9
S. torminalis	0.3	5.0	15.1 (6.2)	12.9 (4.2)	0.1	0.7	0.4	0.1	1.8	11.2 (5.2)	9.4 (2.7)	0.0	0.1	0.1	0.5	9.5	15.2 (5.7)	11.5 (3.9)	0.2	1.3	0.7
T. tomentosa	27.4	316.2	19.1 (8.2)	21.3 (5.6)	10.8	119.7	51.5	22.7	117.8	29.2 (13.6)	28.2 (6.7)	9.3	127.2	54.7	24.2	211.7	21.5 (12)	19.2 (4.7)	10.1	102.3	44.0
Ulmus spp.	0.3	3.9	18 .0 (4.3)	25.1 (2.9)	0.1	1.1	0.6	1.7	6.2	28.1 (26.5)	25 (7.0)	0.7	9.7	5.4	0.3	3.5	19.3 (6.6)	14.1 (6.6)	0.1	1.3	0.7
Other coniferous	1.9	21.2			0.7	9.0	3.8	0.9	17.6			0.3	4.4	2.0							
Other deciduous	0.3	2.8			0.1	1.4	0.8	0.3	2.6			0.1	1.3	0.6	0.1	2.9			0.0	0.4	0.2
Total	**100.0**	**827.3**			**39.4**	**506.6**	**286.3**	**100.0**	**658.9**			**40.7**	**562.3**	**308.7**	**100.0**	**909.7**			**41.7**	**436.9**	**247.6**

Table A4: Mean soil physical and chemical properties (SD in brackets) in the organic layer and three depths in the mineral soil (0–10 cm, 10–20 cm, 20–40 cm) of the three transects (A, B, C) with the corresponding sample size (n). In case of SOC and N, concentrations (mass %) are given for organic layer (OLC and OLN) and mineral soil (SOC and STN). For P, total contents in the organic layer and resin-exchangeable contents (P_{av}) in the mineral soil are given. For the basic cations (Ca, Mg, K), totals contents in the organic layer and $BaCl_2$-exchangeable contents in the mineral soil are given. Also given are CEC (cation exchange capacity), BS (base saturation), soil texture (percent sand, silt, clay) and storage capacity of available soil water (pAWC). Soil texture analyses were only conducted for the depth of 20–40 cm.

	Organic layer				**Mineral Soil**								
	Transect A (n=16)	**Transect B (n=16)**	**Transect C (n=18)**		**Transect A (n=16)**			**Transect B (n=16)**			**Transect C (n=18)**		
Depth [cm]	2.7 (0.9)	1.6 (0.9)	4.1 (1.0)	**Depth class**	**0-10 cm**	**10-20 cm**	**20-40 cm**	**0-10 cm**	**10-20 cm**	**20-40 cm**	**0-10 cm**	**10-20 cm**	**20-40 cm**
Mass [Mg DM ha^{-1}]	10.3 (4.7)	3.5 (2.1)	3.8 (1.4)	**Bulk density [g cm^{-3}]**	1.11 (0.15)	1.28 (0.12)	1.37 (0.15)	0.94 (0.20)	1.00 (0.23)	1.06 (0.21)	0.85 (0.17)	0.97 (0.17)	1.01 (0.12)
pH (H_2O)	5.8 (0.4)	5.5 (0.3)	5.4 (0.4)	**pH (H_2O)**	5.0 (0.4)	5.1 (0.3)	5.2 (0.3)	5.0 (0.3)	5.0 (0.4)	5.2 (0.4)	5.1 (0.4)	5.0 (0.3)	5.2 (0.3)
OLC [mg C g^{-1}]	292.4 (68.0)	404.0 (52.0)	407.6 (24.7)	**SOC [%]**	2.23 (0.54)	1.26 (0.29)	0.68 (0.12)	2.01 (0.67)	1.18 (0.39)	0.74 (0.23)	2.46 (0.89)	1.37 (0.60)	0.92 (0.45)
OLN [mg N g^{-1}]	11.5 (2.0)	11.8 (1.3)	12.2 (2.4)	**STN [%]**	0.19 (0.05)	0.11 (0.03)	0.06 (0.01)	0.18 (0.06)	0.11 (0.03)	0.08 (0.02)	0.16 (0.09)	0.09 (0.05)	0.07 (0.03)
C/N [g g^{-1}]	25.3 (2.7)	34.7 (5.8)	34.1 (4.6)	**C/N [g g^{-1}]**	12.06 (1.36)	11.67 (1.24)	11.04 (1.65)	11.52 (2.44)	11.09 (2.62)	9.86 (2.00)	16.17 (3.54)	15.70 (3.75)	13.93 (3.56)
P pool [mg P kg^{-1}]	0.78 (0.38)	0.23 (0.16)	0.37 (0.21)	**P_{av} pool [mg P_{av} kg^{-1}]**	6.13 (5.69)	5.27 (4.58)	4.52 (4.68)	4.63 (8.71)	4.63 (9.83)	3.76 (7.00)	22.19 (24.41)	15.65 (18.48)	9.11 (11.63)
Ca pool [kg Ca ha^{-1}]	136.2 (83.6)	47.3 (29.7)	57.6 (22.2)	**Ca $_{ex}$pool [kmol$_c$ Ca^{+2} ha^{-1}]**	35.89 (34.40)	25.37 (22.12)	26.70 (20.11)	37.67 (39.71)	40.08 (40.68)	49.18 (44.36)	26.94 (23.84)	13.84 (13.32)	16.92 (14.00)
K pool [kg K ha^{-1}]	31.8 (15.6)	10.3 (8.3)	12.8 (3.8)	**K $_{ex}$pool [kmol$_c$ K^{+} ha^{-1}]**	2.20 (1.62)	1.94 (1.34)	1.56 (1.06)	1.43 (0.76)	0.79 (0.34)	0.76 (0.28)	2.39 (1.86)	1.12 (0.72)	0.87 (0.45)
Mg pool [kg Mg ha^{-1}]	30.0 (26.3)	7.3 (5.9)	6.9 (2.7)	**Mg $_{ex}$pool [kmol$_c$ Mg^{+2} ha^{-1}]**	7.43 (4.95)	6.75 (4.21)	9.44 (5.57)	9.61 (9.16)	11.28 (10.21)	14.91 (12.66)	5.34 (4.32)	4.04 (3.55)	5.60 (4.45)
				CEC [mol$_c$ kg^{-1}]	78.5 (24.9)	60.8 (18.0)	52.1 (14.3)	105.4 (42.5)	98.9 (38.5)	97.9 (46.1)	75.6 (37.2)	55.5 (25.9)	47.4 (21.7)
				BS [%]	46.2 (28.9)	40.9 (25.0)	49.2 (22.4)	40.7 (30.7)	39.4 (31.5)	49.3 (32.0)	51.1 (29.5)	33.2 (21.9)	44.8 (22.0)
				Clay [%]			0.04 (0.07)			0.09 (0.09)			0.06 (0.06)
				Silt [%]			0.66 (0.14)			0.63 (0.17)			0.38 (0.13)
				Sand [%]			0.3 (0.15)			0.27 (0.15)			0.56 (0.11)
				pAWC [%]			0.28 (0.06)			0.33 (0.07)			0.27 (0.06)

Table A5: Stand structural characteristics of beech, mixed (beech–oak), oak and linden forests (means (SD), averaged over the three transects, n = number of plots). Plots dominated by beech: all plots with basal area of *F. sylvatica* > 66.6 %, oak: all plots with basal area of *Quercus* species > 66.6 %, linden: all plots with basal area of *T. tomentosa*: > 66.6 %, mixed: all other forests (except for stands with *T. tomentosa* > 66.6 %) for the three transects (A, B, C). Stem ha^{-1}, DBH, height (h), basal area (BA), stem volume (Vol) and carbon in stem biomass (AGC). Significant differences ($p \leq 0.05$) between forest types are indicated by different small letters (one-way ANOVA with post-hoc Tukey test).

	Beech (n=69)	**Mixed** (n=106)	**Oak** (n=52)	**Linden** (n=38)
Stem [ha^{-1}]	636.3 (311.3) a	869.3 (469.8) b	733.4 (267.4) a b	1234.7 (486.4) a b
DBH [cm]	26.8 (14.4) a	21.3 (12.3) b	23.0 (11.4) b	20.1 (9.7) b
h [m]	26.5 (6.2) a	20.5 (7.2) c	17.7 (7.5) b	20.5 (6.7) c
BA [m^2 ha^{-1}]	46.2 (3.2) a	41.3 (14.2) b	37.8 (9.5) b	48.5 (13.3) a
Vol [m^3 ha^{-1}]	621.9 (211.5) a	499.2 (229.8) b c	446.1 (149.1) c	544.6 (191.8) a b
AGC [Mg C ha^{-1}]	180.9 (61.6) a	137.2 (60.3) b	141.3 (46.7) b	125.3 (41.6) b

Table A6: Pools of SOC, N, P and basic cations in soil profiles under beech, mixed and oak forests (means and SD of n plots in the three transects). In case of SOC and N, total pools are given for organic layer (OLC and OLN) and mineral soil (SOC and STN). For P, total pools in the organic layer and resin-exchangeable pools (P_{av}) in the mineral soil are given. For the basic cations (Ca, Mg, K), totals pools of the organic layer and $BaCl_2$-exchangeable pools of the mineral soil are given. Pools of SOC, STN and P_{av} were calculated to a depth -100 cm, the pools for Ca^{+2}_{ex}, Mg^{+2}_{ex} and K^{+}_{ex} to a depth of -40 cm. Base saturation (BS) and C/N ratios for the mineral soil were averaged over the three depths 0–10 cm, 10–20 cm and 20–40 cm. No soil samples were taken in the linden forests. Significant differences ($p \leq 0.05$) between forest types are indicated by different small letters (Kruskal-Wallis-Test with post-hoc Pairwise Wilcoxon Rank Sum Test). Variables with significant differences are in bold.

	Organic layer				**Mineral soil**		
	Beech	**Mixed**	**Oak**		**Beech**	**Mixed**	**Oak**
	(n=11)	(n=19)	(n=11)		(n=11)	(n=19)	(n=11)
OLC pool [Mg C ha^{-1}]	**2.28 (0.89) a**	**1.69 (1.78) b**	**1.84 (0.76) a b**	SOC pool [Mg C ha^{-1}]	**81.05 (12.47) a**	**64.78 (18.47) b**	**64.58 (22.01) a b**
OLN pool [kg N ha^{-1}]	**84.5 (46.3) a**	**59.9 (75.0) b**	**68.9 (36.3) a b**	STN pool [Mg N ha^{-1}]	6.58 (1.24) a	5.68 (1.85) a	5.83 (2.19) a
C/N ratio [g g^{-1}]	29.54 (6.46) a	33.19 (6.73) a	28.84 (5.16) a	C/N ratio [g g^{-1}]	11.91 (2.61) a	10.97 (1.92) a	10.06 (1.68) a
P pool [kg P ha^{-1}]	6.22 (3.43) a	3.99 (4.32) a	4.77 (2.54) a	P_{av} pool [kg P_{av} ha^{-1}]	137.60 (156.55) a	84.60 (86.75) a	45.09 (51.04) a
Ca pool [kg Ca ha^{-1}]	**117.98 (99.80) a**	**62.83 (54.30) b**	**77.45 (48.05) a b**	Ca_{ex}pool [$kmol_c$ Ca^{+2} ha^{-1}]	116.98 (73.63) a	121.89 (106.22) a	66.29 (57.21) a
Mg pool [kg Mg ha^{-1}]	25.30 (33.19) a	8.97 (7.72) a	17.29 (15.16) a	Mg_{ex}pool [$kmol_c$ Mg^{+2} ha^{-1}]	23.15 (13.23) a	30.65 (27.99) a	29.42 (14.17) a
K pool [kg K ha^{-1}]	22.03 (14.82) a	14.59 (10.30) a	23.90 (20.34) a	K_{ex}pool [$kmol_c$ K^{+} ha^{-1}]	4.76 (3.62) a	4.48 (2.17) a	4.95 (4.15) a
				BS [%]	57.05 (26.98) a	54.46 (25.01) a	46.27 (19.31) a

Table A7: Results of ANCOVA models on the effect of transect and Beech–Oak Index on 13 variables related to soil chemical properties, and biomass and soil carbon pools in the three transects. The models had the form: *Response variable ~ transect + Beech–Oak Index*. Significant effects are printed in bold.

	Transect		**Beech–Oak Index**	
Dependent variable	F value	p value	F value	p value
Above ground biomass carbon (AGC) pool [Mg C ha^{-1}]	**19.96**	**<0.001**	**22.54**	**<0.001**
Soil organic carbon (SOC) pool [Mg C ha^{-1}]	**4.72**	**0.015**	**6.48**	**0.015**
Organic layer carbon (OLC) pool [Mg C ha^{-1}]	**12.37**	**<0.001**	2.15	0.151
Soil total nitrogen (STN) pool [Mg N ha^{-1}]	**5.74**	**0.007**	2.08	0.158
Organic layer nitrogen (OLN) pool [kg N ha^{-1}]	**17.92**	**<0.001**	2.59	0.116
Mineral soil P_{av} pool [kg P_{av} ha^{-1}]	**4.66**	**0.016**	0.29	0.595
Organic layer P pool [kg P ha^{-1}]	**21.02**	**<0.001**	1.74	0.196
Mineral soil Ca^{+2}_{ex} pool [$kmol_c$ Ca^{+2} ha^{-1}]	2.35	0.109	3.06	0.088
Organic layer Ca pool [kg Ca ha^{-1}]	**21.44**	**<0.001**	**9.91**	**0.003**
Base saturation (BS) [%]	0.01	0.986	1.86	0.181
Cation exchange capacity (CEC) [mol_c kg^{-1}]	**10.39**	**<0.001**	2.49	0.123
pH (H_2O)	0.03	0.986	1.16	0.289

Table A8: List of the abbreviations with explanations and units for a) climate and stand structural variables, b) organic layer variables and c) mineral soil variables used in the detrended correspondence analysis (DCA).

a) Climate and stand structural variables

Abbreviation	Explanation	Unit
Tmin	Average temp. of coldest month	°C
Tmax	Average temp. of hottest month	°C
Pmin	Average prec. of driest month	mm
Pmax	Average prec. of wettest month	mm
MST (BIO10)	Mean summer (Jun, Jul, Aug) temp.	°C
MWT	Mean winter (Dec, Jan, Feb) temp.	°C
MSP (BIO18)	Mean summer (Jun, Jul, Aug) prec.	mm
MWP	Mean winter (Dec, Jan, Feb) prec.	mm
Elev.	Elevation above sea level	m
Slope	Plot slope angle	°
Exposition	Plot exposition	°
Stem	Mean number of stems	ha^{-1}
BA	Mean basal area of stems	m^2 ha^{-1}
Tree vol.	Mean tree volume	m^3 ha^{-1}
AGC	Mean above ground carbon pool	Mg ha^{-1}

b) Organic layer variables

Abbreviation	Explanation	Unit
Org. matter	Weight of org. matter	Mg ha^{-1}
OL pH	pH (in H_2O) of org. layer	
OL C	C concentration in org. layer	mg g^{-1}
OL C pool	C pool in org. layer	Mg ha^{-1}
OL N	N concentration in org. layer	mg g^{-1}
OL N pool	N pool in org. layer	kg ha^{-1}
OL P pool	P pool in org. layer	kg ha^{-1}
OL Ca pool	Ca pool in org. layer	kg ha^{-1}
OL Mg pool	Mg pool in org. layer	kg ha^{-1}
OL K pool	K pool in org. layer	kg ha^{-1}
OL C/N	C / N ratio in org. layer	g g^{-1}
OL C/P	C / P ratio in org. layer	g g^{-1}
OL N/P	N / P ratio in org. layer	g g^{-1}

c) Mineral soil variables

Abbreviation	Explanation	Unit
Sand [%]	Sand content in 20-40 cm	%
Silt [%]	Silt content in 20-40 cm	%
Clay [%]	Clay content in 20-40 cm	%
pAWC [%]	Plant available water capacity in 20-40 cm	%
pH	Mean soil pH (in H_2O) from all 3 depths	
Ca^{+2}_{ex} pool	$BaCl_2$-exchangeable Ca^{+2} pool in 0-40 cm	kmol$_c$ ha^{-1}
Mg^{+2}_{ex} pool	Total $BaCl_2$-exchangeable Mg^{+2} in 0-40 cm	kmol$_c$ ha^{-1}
K^{+}_{ex} pool	Total $BaCl_2$-exchangeable K^+ in 0-40 cm	kmol$_c$ ha^{-1}
CEC	Cation exchange capacity	mol$_c$ kg^{-1}
BS	Base saturation	%
SOC 0-10cm	SOC concentration in 0-10 cm	mg g^{-1}
SOC 10-20cm	SOC concentration in 10-20 cm	mg g^{-1}
SOC 20-40cm	SOC concentration in 20-40 cm	mg g^{-1}
SOC pool	Total SOC pool in 0-100 cm	Mg ha^{-1}
STN 0-10cm	STN concentration in 0-10 cm	mg g^{-1}
STN 10-20cm	STN concentration in 10-20 cm	mg g^{-1}
STN 20-40cm	STN concentration in 20-40 cm	mg g^{-1}
STN pool	Total STN pool in 0-100 cm	Mg ha^{-1}
P_{av} 0-10cm	Resin exchangeable P concentration in 0-10cm	mg kg^{-1}
P_{av}10-20cm	Resin exchangeable P concentration in 10-20cm	mg kg^{-1}
P_{av} 20-40cm	Resin exchangeable P concentration in 20-40cm	mg kg^{-1}
P_{av} pool	Resin exchangeable P pool in 0-100 cm	kg ha^{-1}
C/N 0-10cm	C / N ratio in 0-10cm	g g^{-1}
C/N 10-20cm	C / N ratio in 10-20cm	g g^{-1}
C/N 20-40cm	C / N ratio in 20-40cm	g g^{-1}
C/P 10-20cm	C / P ratio in 10-20cm	g g^{-1}
C/P 0-10cm	C / P ratio in 0-10cm	g g^{-1}
C/P 20-40cm	C / P ratio in 20-40cm	g g^{-1}
N/P 0-10cm	N / P ratio in in 0-10cm	g g^{-1}
N/P 10-20cm	N / P ratio in 10-20cm	g g^{-1}
N/P 20-40cm	N / P ratio in 20-40cm	g g^{-1}

Figures

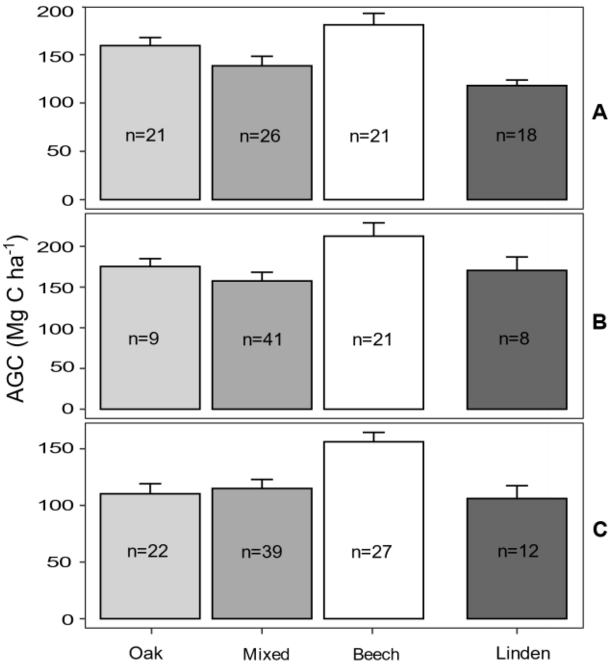

Figure A1: Store of aboveground carbon (AGC; in Mg C ha^{-1}) in the oak, mixed and beech forest plots (means and SE) of each transect A–C. Plots dominated by linden (basal area of *T. tomentosa* > 66.6 %) are also shown. Beech forests: all plots with basal area of *F. sylvatica* > 66.6 %, oak forests: all plots with basal area of *Quercus* species > 66.6 %, mixed forests: all other forests (except for stands with *T. tomentosa* > 66.6 %).

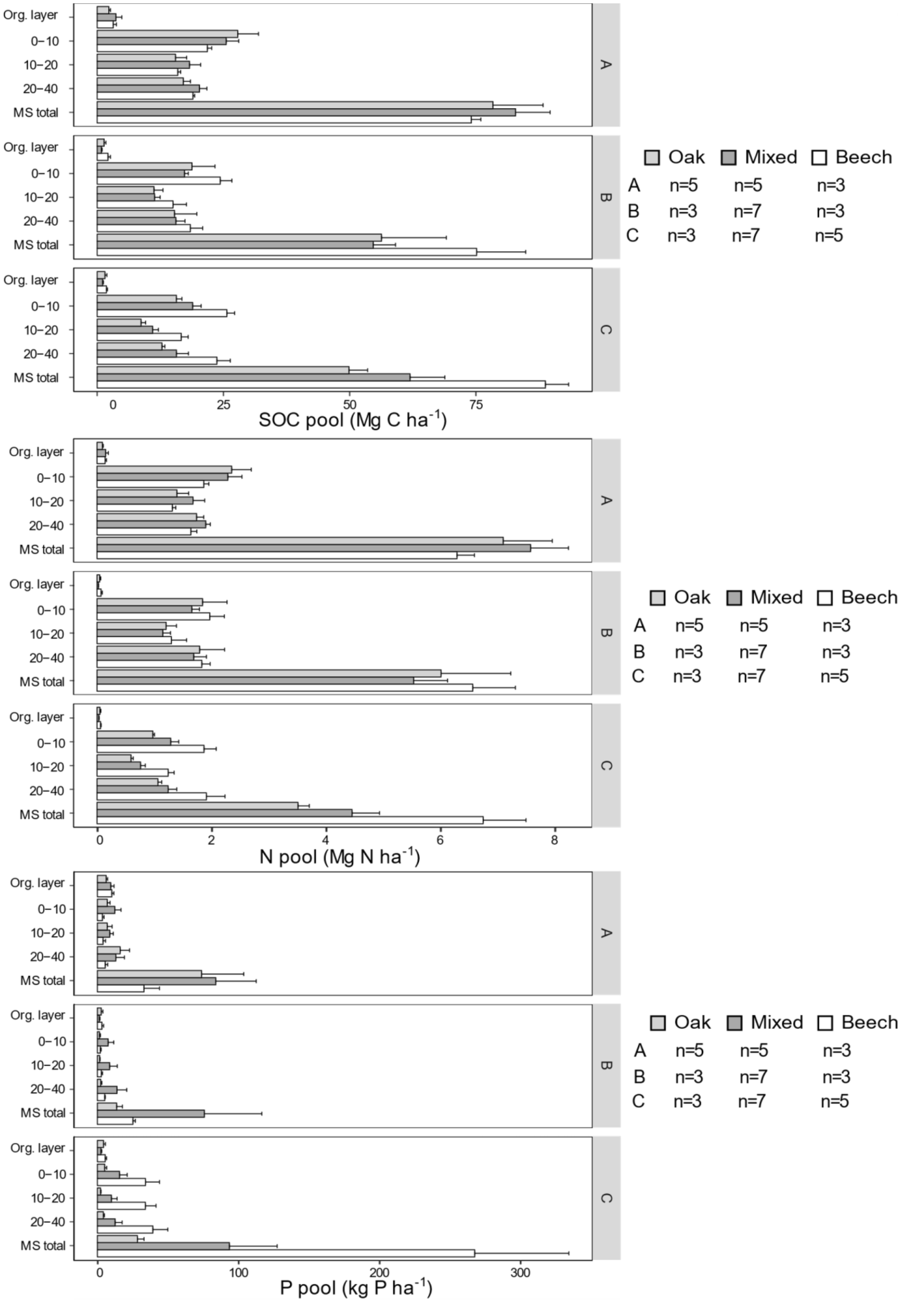

Figure A2: Means (and SE) of SOC, N and P in organic layer and mineral soil of the beech, mixed (beech–oak) and oak stands in the three transects A–C (n = number of plots). In case of SOC and N, total pools are given for organic layer and mineral soil. P is resin-extractable P in the mineral soil and total P in the organic layer. Profile totals (MS total) of SOC, N and P were calculated for a depth of -100 cm by extrapolation. No samples were taken in the linden forests.

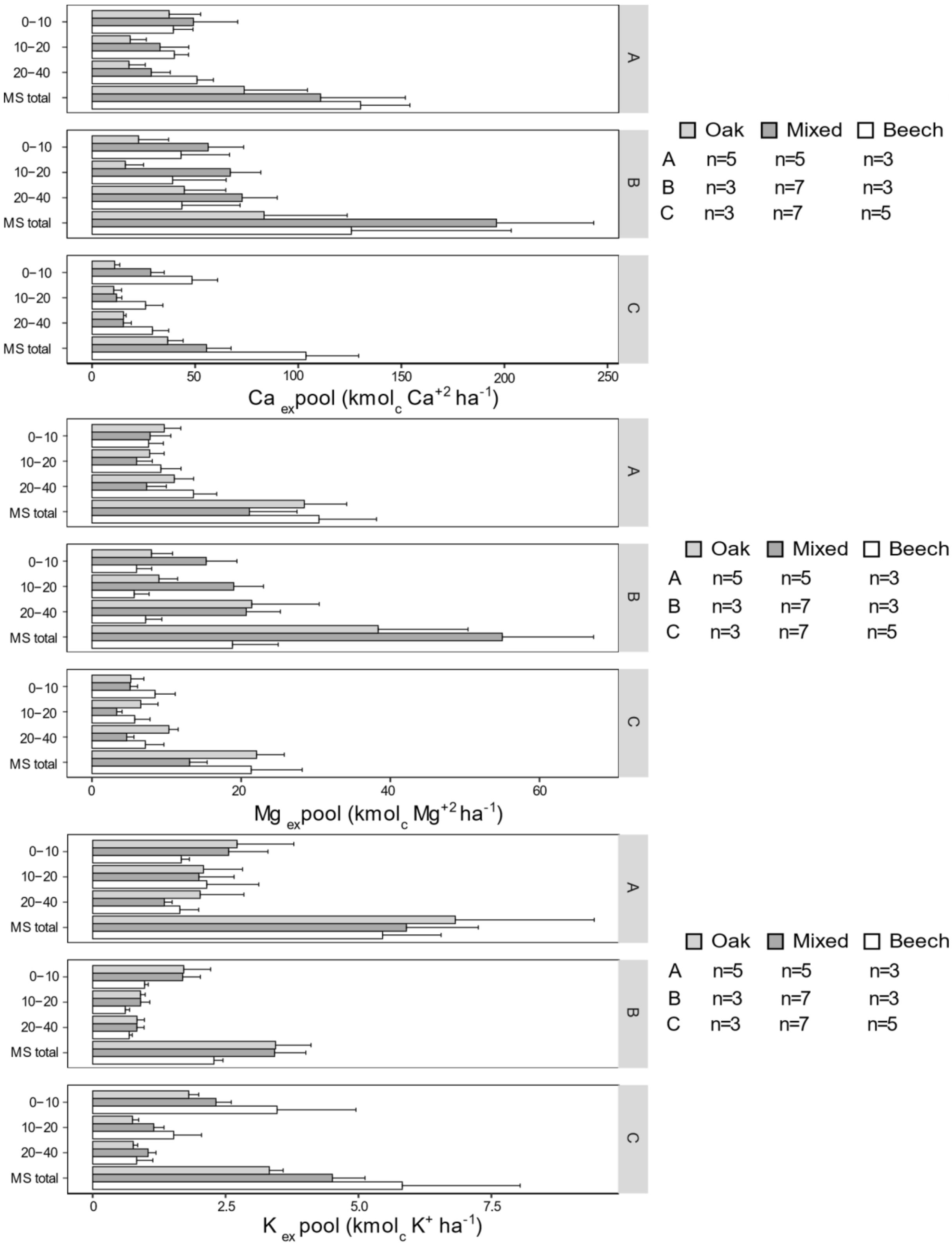

Figure A3: Means (and SE) of the pool of BaCl2-exchangeable basic cations in the mineral soil of the beech, mixed (beech–oak) and oak stands of the three transects A–C (n = number of plots). Profile totals (MS total) for Ca+2ex, Mg+2ex and K+ex are given for a depth of -40 cm. No samples were taken in the linden forests.

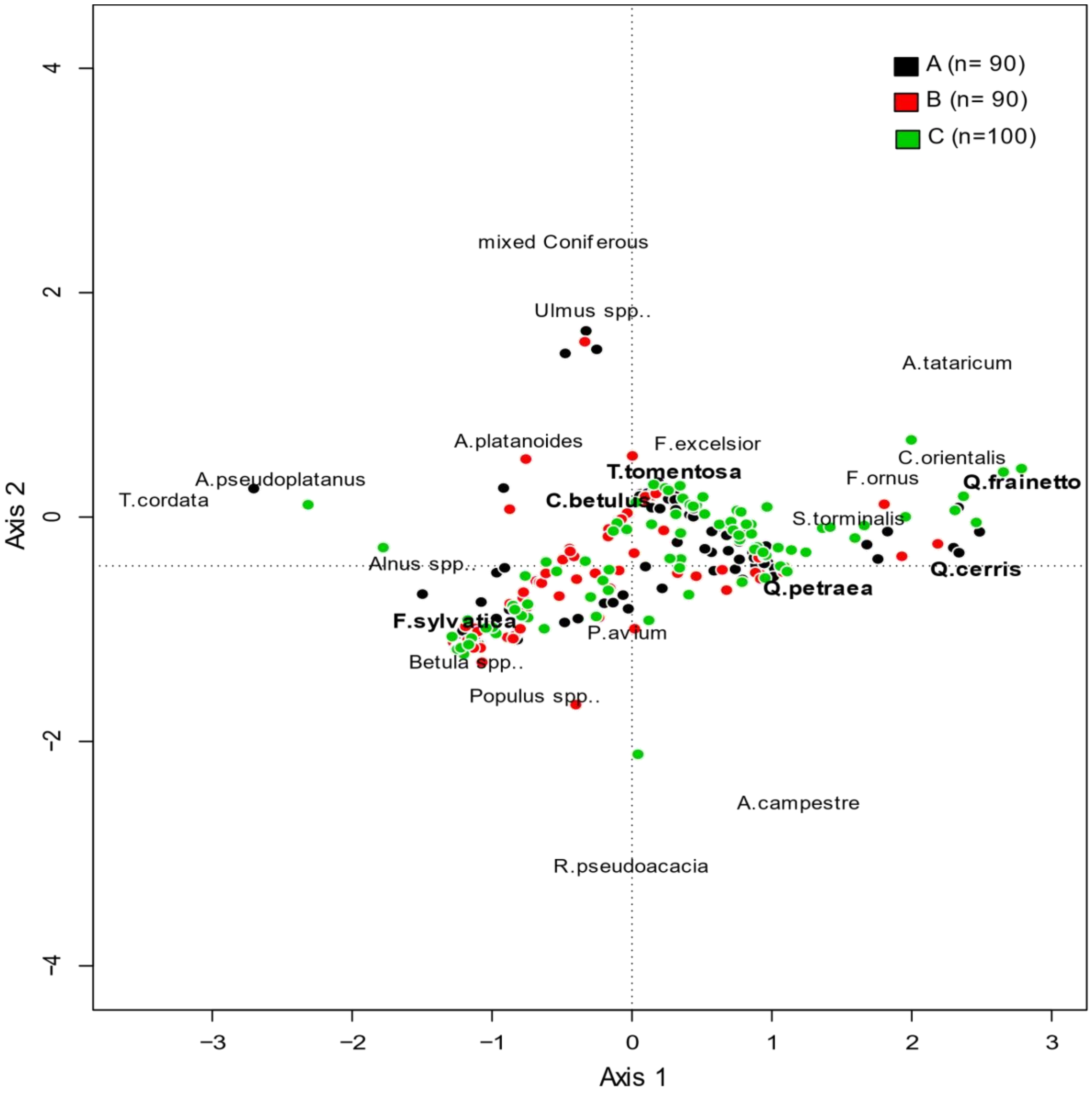

Figure A4: Detrended correspondence analysis ordination (DCA) calculated with the species' relative basal area, conducted for all species and for the three transects A–C. The plots are marked with different colours for the three transects (n = number of plots). The main tree species are in bold, minor tree species in normal font.

CHAPTER III

WINNERS AND LOSERS OF CLIMATE WARMING: DECLINING GROWTH IN FAGUS AND TILIA VS. STABLE GROWTH IN THREE QUERCUS SPECIES IN THE NATURAL BEECH–OAK FOREST ECOTONE (WESTERN ROMANIA)

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Published in: Forest Ecology and Management (2022) 506

Accepted: 20 November 2021 / Published: 15/02/2022

https://doi.org/10.1016/j.foreco.2021.119892

3 Winners and losers of climate warming: Declining growth in Fagus and Tilia vs. stable growth in three Quercus species in the natural beech–oak forest ecotone (western Romania)

3.1 Abstract

Global warming and increasing drought severity are exposing temperate forests to increasing stress, challenging silvicultural decision making. Growth analyses in marginal tree populations at drought-induced range limits may provide valuable information on tree species' adaptive potentials and species-specific climate turning points. We studied the climate sensitivity and resilience to drought of radial growth, and long-term growth trends of mesic and rear-edge populations of *Fagus sylvatica* in comparison to three oak species (*Quercus petraea, Q. frainetto, Q. cerris*) and *Tilia tomentosa* in natural ecotones from mesic beech to xeric oak forests along three elevation transects in western Romania. Radial growth of all species was positively influenced by summer precipitation and low drought intensity, and negatively by high summer temperatures. The basal area increment (BAI) of *F. sylvatica* and *T. tomentosa* has declined in the last 10–20 years with warming and a deterioration of the summer water balance, while the three *Quercus* species maintained stable growth rates, though at lower BAI levels, suggesting a negative relationship between mean BAI and drought resistance among the five species. Growth reductions during three severe drought events (2000, 2003, 2012) were stronger, and growth resilience lower, in *F. sylvatica* and *T. tomentosa* than in the *Quercus* species, pointing at a thermal limit of beech at June–August temperatures of 20–21 °C. As the climate of the studied ecotones is similar to the predicted climate at colline/submontane elevation in Central Europe in about 50 years, a decline in beech growth and vitality is likely also in drought-affected regions in the distribution centre with future warming. Our results demonstrate that choosing stress-tolerant *Q. petraea* (as well as *Q. frainetto* and *Q. cerris*) instead of more productive timber species is a relatively safe option for Central European forestry in a warmer climate.

Key words: basal area increment, dendrochronology, climate sensitivity, drought resilience, European beech, growth decline, silver lime

3.2 Introduction

Growing season temperature has increased by more than 1 °C in many temperate regions of Europe during the last four decades, resulting in a higher atmospheric evaporative demand (IPCC, 2013; Kaspar et al., 2017). In correspondence, the length of summer heat waves has doubled in western Europe between 1880 and 2006 (Barriopedro et al., 2011; Della-Marta et al., 2007). Locally, reductions in summer precipitation have been recorded as well, as in eastern Germany, in the UK and in central Italy (Pal et al., 2004; Schönwiese and Janoschitz, 2008). Widespread reduction in tree vitality and increases in mortality in temperate forests and elsewhere have been linked to an increasing aridification of the climate in recent time (Allen et al., 2015, 2010; Schuldt et al., 2020; Van Mantgem et al., 2009). In particular at the low-elevation and low-latitude range margins of temperate tree species, growth is increasingly limited by summer drought and / or heat (Dittmar et al., 2003; Grace et al., 2002; Mäkinen et al., 2002; Takahashi et al., 2001).

In the mesic woodlands of Central Europe, European beech (*Fagus sylvatica* L.) is the predominant tree species due to its high competitiveness and tolerance of a broad range of edaphic conditions (Leuschner & Ellenberg, 2017; Schmidt, 2009). Towards southern and south-eastern Europe, summer heat and low summer precipitation are the main climatic factors limiting the distribution range of beech (Czúcz et al., 2011; Fang and Lechowicz, 2006). Accordingly, dendroclimatological analyses show that the radial growth of beech responds negatively to low precipitation and high temperatures in previous year's mid-summer, and often also to low precipitation and high temperatures in current-year May, June and July (Harvey et al., 2020; Knutzen et al., 2017; Scharnweber et al., 2011). Recent reports about long-term growth decline, mortality and displacement by more drought-tolerant tree species in beech forests at the southern distribution edge in Hungary, Italy and Spain are all related to increased drought exposition in the course of climate warming (Jump et al., 2006; Lakatos and Molnár, 2009; Piovesan et al., 2008). However, the severe drought episode of 2018–2020 has also led to canopy dieback and tree death in various regions of Central Europe (Schuldt et al., 2020; Walthert et al., 2020), in the centre of the distribution range of *F. sylvatica*. In the face of proceeding climate warming, the future of beech in lowland and lower montane regions of Central Europe may become increasingly unsecure, especially where the climatic water balance in summer turns negative (Leuschner, 2020).

European beech has been found to be more drought-sensitive than many other temperate broadleaf tree species, for example, sessile oak (*Quercus petraea* (Matt.) Liebl.) and English oak (*Q. robur* L.), common hornbeam (*Carpinus betulus* L.), common ash (*Fraxinus excelsior* L.) and small-leaved linden (*Tilia cordata* L.) (Brinkmann et al., 2016; Köcher et al., 2009; Leuschner, 2020; Zang et al., 2014; Zimmermann et al., 2015). Thus, if climate warming is driving beech to its climatic limits, a shift to more drought-tolerant species may take place, among them oak, linden and hornbeam species. Foresters seeking for more drought-tolerant timber species may consider oak and linden species, as they are thought to be more drought-tolerant than other major timbers such as beech, spruce and even Scots pine (Walentowski et al., 2007; Zang, 2012). Comparing tree species in respect to their drought tolerance is best done in mixed stands or along ecotones between different forest types, where the climatic conditions can be precisely characterized (Fuchs et al., 2021; Kunz et al., 2018; Walentowski et al., 2017; Zimmermann et al., 2015). Such a comparison provides valuable information, on which decisions to select suitable tree species for silviculture in a warmer world can be based on.

Regional climate models predict that temperatures will increase by up to (2.0) 2.3 –2.7 (3.1) °C until 2070 in Central Europe, while summer precipitation is expected to decrease moderately in parts (Jacob et al., 2012; Schwarz et al., 2007). One approach to study the performance of tree species in a warmer and drier climate is to search for regions that currently experience a climate that may establish in the target region. The climate in western Romania is about 2.5 °C warmer than in central and southern Germany today and thus may represent an analogue climate for a climate warming scenario (Figure 1a and A1 in the Appendix) (Falk and Hempelmann, 2013; Heinrichs et al., 2016; Kasper et al., 2021; Kölling and Zimmermann, 2014; Mellert et al., 2016, 2015). On the foothills of the southern Carpathians in western Romania, the zonal deciduous forest vegetation changes from humid mesic beech forests at elevations above 600 m a.s.l., with similar temperature and precipitation patterns as found today in the submontane beech forest zone in large parts of Central Europe, to subhumid mesic mixed beech-hornbeam and hornbeam-oak forests, and finally to subhumid-thermophilic oak forests at colline elevation on the mountain foot. This beech–oak ecotone mirrors the predicted transition to a warmer and drier climate in Central Europe in about 50 years. At the mountain foot, beech forests retreat to small pockets in north-exposed valleys, where the climate is more humid (Doniță et al., 1992, Coldea et al. 2015, Indreica et al., 2017). Both the mesic beech forests at higher elevation and the low-elevation rear-edge beech forests may serve as study objects for assessing the species' adaptive capacity to a warmer and drier climate (Mellert et al., 2016), as they are located precisely at or even beyond the climatic turning point of *F.*

sylvatica in the natural ecotone to oak-dominated forests (Jump et al., 2006; Penuelas & Boada, 2003). The dendrochronological study of recent and past growth patterns may allow assessing tree vitality, as climate change impacts can manifest in declining radial growth rates long before increases in mortality and changes in species composition become visible (Cailleret et al., 2017; Gillner et al., 2013).

We chose the natural beech–oak ecotone in western Romania with climates close to those expected for Central Europe in 50 years (Indreica et al., 2017; Kasper et al., 2021; Walentowski et al., 2017) as field laboratories for studying the vitality and growth of *F. sylvatica* at rear-edge sites close to the species' drought and heat limit. We selected natural mixed forests for comparing the growth of beech with that of three co-occurring oak species (sessile oak – *Quercus petraea*, Turkey oak – *Q. cerris* L., Hungarian oak – *Q. frainetto* Ten.) and silver linden (*Tilia tomentosa* Moench). We did this in three south-exposed transects across the beech–oak ecotone that were sufficiently comparable in terms of climatic and edaphic conditions (Hohnwald et al., 2020; Kasper et al., 2021). We explored past growth trends and the climate sensitivity of growth by employing tree-ring analysis to all five species, covering beech-dominated stands, mixed oak-hornbeam-linden stands, and oak-dominated stands. In addition, we investigated *F. sylvatica* trees in north-exposed, rear-edge beech stands at lower elevation.

The following questions guided our research:

Q1) Which climatic factors (precipitation, temperature, or climatic aridity) are the dominant limiting factors of radial growth in beech, linden and oak in the natural beech–oak ecotone?

Q2) Do long-term trends in radial growth differ between mesic and xeric (rear-edge) beech stands as well as between beech, linden and oak species?

Q3) What relationship exists between long-term radial growth trends and trends in summer temperature, summer precipitation and climatic water balance in the five species, and what are climatic thresholds for growth decline?

Q4) Do the five species differ in their growth response to severe 21st century summer droughts?

3.3 Material and methods

Study area, climatic conditions and transect selection

The study region is located in western Romania in the Banat and Crişana regions, extending from the crests of the outermost chains of the south-western Carpathians down to the Western Romanian Plain. The region mirrors climatic conditions projected by RCP scenarios 2.6, 4.5 and 8.5 for large parts of Central Germany (Figure A1 in the Appendix). Three transects were established along elevation gradients extending from ca. 600–800 m a.s.l. at submontane / montane elevation across the natural beech–oak ecotone down to colline elevation at ca. 200–300 m. Transect A was located in the Bihor Mountain range (Zarand Mountains) north-east of Timisoara (Milova; 46.1°N / 21.8°E), transect B on the western foothills of the main Carpathian Mountain chain south-east of Timisoara (Maciova; 45.5° N / 22.2° E), both in westernmost Romania, and transect C at the foot of the southern Banat Mountains (Iron Gate) in south-western Romania (Eşelniţa, 44.7° N / 22.3° E), west of Orşova close to river Danube (Figure 1b). The transects covered a spatial sequence from humid beech-dominated forests at submontane / montane elevation over a humid-subhumid ecotone of mixed beech-hornbeam-oak forests with *T. tomentosa* (submontane / colline) to the basal subhumid-thermophile oak-dominated forest at colline elevation (Figure 1c) (Indreica et al., 2019, Kasper et al., 2021). The transects had a width of 500 m and were chosen to serve as replicates on the landscape level. Thus, selection criteria were sufficient comparability in terms of exposition, tree species composition, stand structure, forest management, soil types, and overall climatic conditions (Tables A1–A2 and A4–A7 in the Appendix).

All forest stands were mature (> 60 years old) with closed canopy and a height of 21–33 m (Table 1). While being subjected to occasional wood-cutting and low-intensity coppicing in the years before 1960, the forests have been transferred to state-ownership since then and were managed by local forest authorities according to management plans, and previously coppiced stands were allowed to grow into high forests (Öder et al., 2021). Management followed common Romanian silvicultural schemes, in which stands are lightly thinned (5–15 % of stand volume) from the pole-wood stage onwards until three quarters of the harvest age are reached (Nicolescu, 2018). Salvage and sanitary loggings were also irregularly conducted at low intensity (< 5% of stand volume). According to records of the local forest administrations, no major harvest operations have occurred in the last 20 years at all sites (Öder et al., 2021).

All three transects were demarcated on predominantly south-west- to south-east-facing slopes. In the beech forests, *F. sylvatica* contributed with at least 85 % to total stem basal area, while the thermophilic oak forests were dominated by three oak species (*Q. petraea, Q. cerris, Q. frainetto;* > 83 % of stem basal area). The remaining stems belonged to accompanying species such as *Carpinus betulus* L., *Acer campestre* L. and *Tilia tomentosa*. In the ecotone (subhumid mixed beech–oak and hornbeam forests), the oak species and beech each contributed with about 20–30 % to the total basal area (except for Transect B), while the remainder belonged mostly to *Carpinus* and *Tilia* species (Table A6 in the Appendix).

The study region has a temperate sub-continental climate with warm summers and relatively cold winters (Tables A1–A2 in the Appendix). In the mountains, mean annual precipitation increases by about 45 mm yr^{-1} / 100 m, while the temperature lapse rate is about -0.5 °C / 100 m (Maruşca, 2017). Following a cooling trend from 1960–1979, temperature increased at all sites from 1980 onwards. Mean summer precipitation (MSP) varied without a clear trend and mean climatic water balance in summer (i.e. the mean summer water balance) decreased at all sites after about 2005 (Figures 3 and A5 in the Appendix). We focused on the warmest months for characterizing the local climate, as growth rate peaks in mid-summer in beech and critical drought stress occurs most likely in this period (Leuschner, 2020). All studied forests stock on acid bedrock, which is covered by an up to 100 cm thick loess layer at many places (Table A7 in the Appendix). Soil types are moderately acidic (eutric) Cambisols (Kasper et al., 2021).

Site comparability, species selection and wood core sampling

The three transects were selected under criteria that ensured sufficient comparability in terms of forest structure, tree species composition and soil conditions (for details see Appendix, Chapter: Information on forest inventories and soil sampling, and Kasper et al. 2021). Five characteristic tree species of the four identified forest types in the beech–oak ecotone (Table A6 in the Appendix) were selected for dendrochronological study, i.e. *F. sylvatica* as the dominant species of the moist mesic beech forests (mesic beech), *Q. petraea, Q. frainetto* and *Q. cerris* as the dominant species of the subhumid-thermophilic oak forests (oak), and *F. sylvatica, Q. petraea* and *T. tomentosa* as a typical element of the subhumid mixed beech-oak-hornbeam forests (mixed) in the transition zone. These species were sampled in a 500 m-wide zone placed on the south-east to south-west facing transects (Figure 1c). In addition, north-facing *F. sylvatica* stands were sampled at colline elevation as “rear-edge” xeric beech forests (xeric beech), which exist within the thermophilic oak forest zone in pockets of moister microclimates. In total, we thus sampled five species and, in case of *F. sylvatica*, two site types.

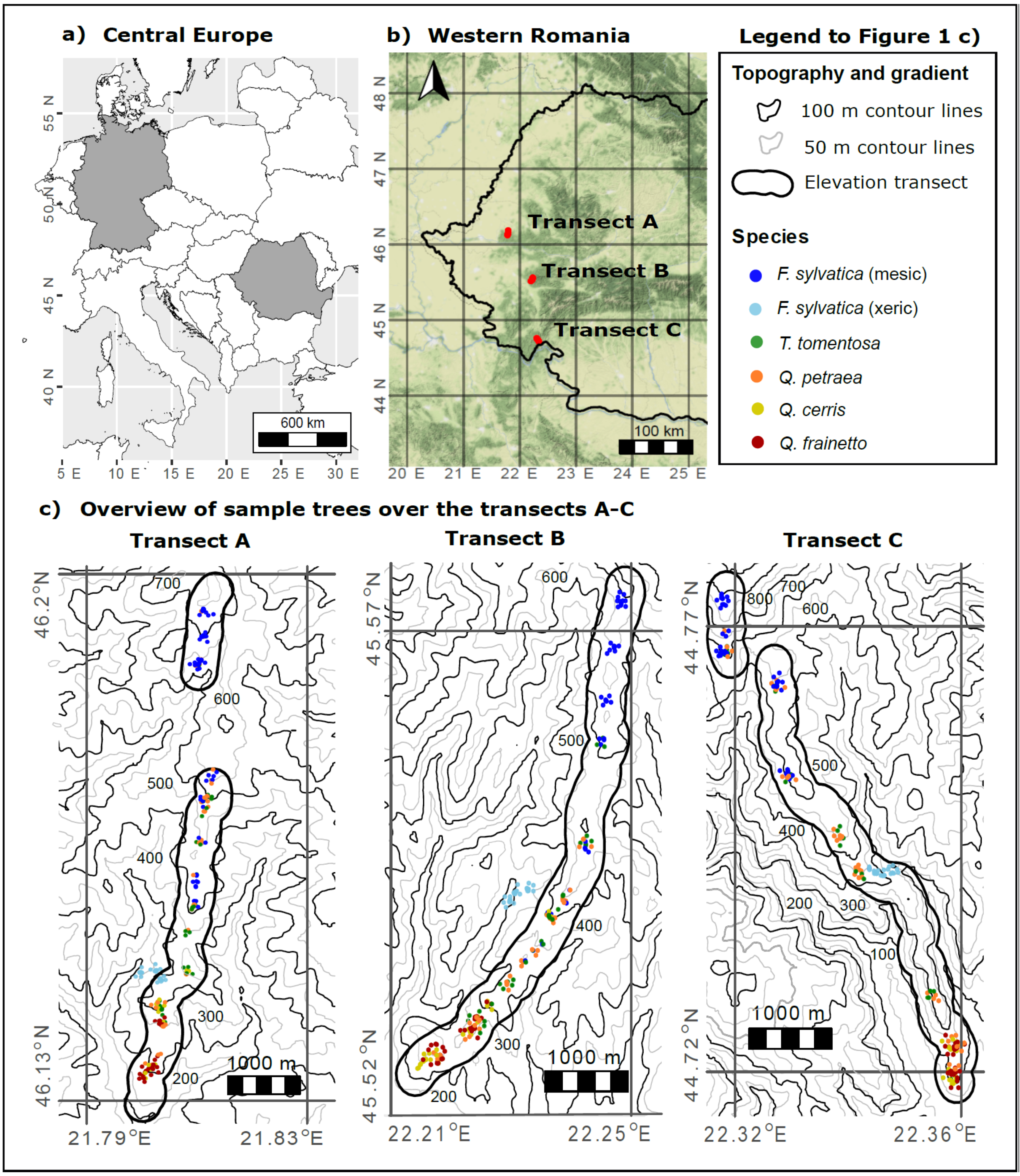

Figure 1: a) Location of Romania and Germany in Europe and b) location of the three transects A, B and C in western Romania. c) Location of cored trees of the five species in the three transects with the transect coordinates and elevation (100 m and 50 m contour lines). *F. sylvatica* (mesic), *F. sylvatica* (xeric), *T. tomentosa*, *Q. petraea*, *Q. cerris* and *Q. frainetto*. The positions of the sample tree symbols were slightly adjusted to avoid overplotting.

Climate data characterizing the transects and the individual sample trees

High-resolution gridded climate data (30 arcsec, ~1 km²) were obtained from the CHELSA (CHELSAcruts) climate database (Karger et al., 2017) to assemble monthly and seasonal (winter: previous December–current February; spring: March–May; summer: June–August; autumn: September–November) temperature and precipitation time series of the period

1940–2016 for the studied forest stands. For every tree, we extracted all climate data from the 1 km² grid cell in which the tree was located. To compare the climatic conditions during the growing season among the five species (and two site types for beech), the mean values of all sampled tree populations per transect and species were computed; this was also done for the intra-specific comparisons across the three transects. To compare the species, stands and transects in terms of the climatic water balance (CWB), the mean summer water balance (SWB, i.e. the mean of June, July and August) was calculated by subtracting mean monthly potential evapotranspiration (PET) from mean monthly precipitation. PET was calculated with R-package `SPEI` (Santiago and Vicente-Serrano, 2017) based on the Hargreaves equation (Hargreaves, 1994) which uses mean monthly minimum and maximum temperatures, mean monthly precipitation and a correction factor derived from latitude.

We also calculated the locally standardized derivate of CWB, the Standardized Precipitation-Evapotranspiration Index (SPEI) (Vicente-Serrano et al. 2010). SPEI was calculated for 3- and 6-month time intervals for different summer months that stand for different phases of physiological- and growth activity. Further, we used the 3-month and 6-month August-SPEI to identify the three most severe summer drought events in the region since the year 2000 that were common across all sites in order to compare the drought impacts across sites under similar reference conditions (Martínez-Vilalta et al., 2012; Zang et al., 2014). Thus, we considered the climatic aridity during mid-summer (3-month SPEI) and the whole growing season (6-month SPEI). Drought severity was categorized according to the classification proposed by Nam et al. (2015) with a severe summer drought being defined as a period with a 3-month SPEI < -1.5 and a 6-month SPEI < -1.

Preparation of tree-ring data

Tree-ring series of ring width length (RWL) were cross-dated based on the coefficient of agreement ("Gleichläufigkeit" GLK; Eckstein & Bauch, 1969), the cross-dating index (CDI; Dobbertin & Grissino-Mayer, 2004), and Student's t-value (TVBP; Baillie & Pilcher, 1973). A chronology consisted of all trees of a species in a transect (except for *F. sylvatica,* where mesic and xeric populations were separately analysed). All tree-ring series used for the chronologies had a GLK > 65%, a CDI > 2.0, and a TVBP > 3.0. Mean GLK was calculated for tree ring series as well as the first-order autocorrelation (AC1). Subsequently, ring width series were detrended applying a 30-year moving average standardization with frequency cut-off at 50 %, and master chronologies were built for every study site and population by calculating Tukey's bi-weight robust mean of the standardized ring width index (RWI) series. The within-chronology growth coherence was subsequently quantified through the mean inter-series correlation (Rbar), and the expressed population signal (EPS). Chronologies were considered reliable, if EPS exceeded a threshold of 0.85 (Wigley et al., 1984). The age of the tree individuals was approximated by counting the number of rings from tree pith to bark.

Climate sensitivity and long-term growth trends

To explore the importance of selected climate variables of the summer period on radial growth, we first analyzed climate-growth relationships by correlating RWI chronologies with mean monthly precipitation (P), mean monthly temperature (T) and climatic aridity (3-month SPEI value) for the months in the interval from previous year's June to current year's September in the common observation period 1940–2016 using a 1000-fold bootstrapping procedure, R-package `treeclim` (Zang and Biondi, 2013). Since radial increment in mature trees decreases with age, long-term growth trends are better investigated on the basis of basal area increment (BAI) instead of RWL (Jump et al., 2006; Speer, 2010). This standardization method (conversion of RWL to BAI) retains low- and mid-frequency growth variance caused by climate fluctuation, which would be removed when using conservative detrending techniques. In managed temperate forests, age-related BAI trends are generally positive, culminating in a stationary phase of high BAI that can be sustained at maturity for many decades under favourable conditions. A negative BAI trend is a strong indication of stress-induced growth decline (Jump et al., 2006; Leblanc, 1990; Pedersen, 1998; Piovesan et al., 2008). RWL was converted to BAI according to the equation:

$$BAI_t = \pi\,(r_t^2 - r_{t-1}^2)$$

where r is the in the field measured stem radius, t the given year and BAI_t the corresponding BAI. Master chronologies of BAI series were built by calculating Tukey's bi-weight robust means for every species in a given stand. BAI chronologies were plotted from 1940 (1950 for *T. tomentosa* in transect B) onwards for inspecting and analysing climate-related growth trends. For visually inspecting long-term growth trends, the BAI chronologies were smoothed through 20-yr moving-average standardization with frequency cut-off at 50 %. A similar smoothing procedure was applied to the MSP, MST and SWB time series in order to recognize long-term climate trends and compare climate and BAI data.

Growth changes and drought reaction

Growth changes (GC) during the recent climate warming were calculated for each tree by comparing mean radial growth in the periods 1960–1979 (before the temperature increase) with 1980–1999 (at the onset of warming) as well as 1980–1999 and 2000–2017 (when SWB decreased) as:

$$GC_1 = mean\ BAI\ 1980 - 1999\ /\ mean\ BAI\ 1960 - 1979$$

$$GC_2 = mean\ BAI\ 2000 - 2017\ /\ mean\ BAI\ 1980 - 1999$$

In addition, we quantified the growth response to single drought events by calculating growth ratios of BAI during drought compared to reference periods (Fekedulegn et al., 2003). Following Lloret et al. (2011), we adopted the drought tolerance indices drought resistance (Rt), which is the ratio between growth during (Dr) and prior to drought ($PreDr$), drought recovery (Rc), i.e. the ability to recover after a growth reduction ($PostDr$) during the drought event, and drought resilience (Rs), which measures the ability to regain the growth level observed prior to the drought. With the BAI during drought (Dr) used as a reference, the three tolerance indices were calculated for every species as:

$$Rt\ =\ Dr\ /\ PreDr,$$

$$Rc\ =\ PostDr\ /\ Dr, \text{ and}$$

$$Rs\ =\ PostDr\ /\ PreDr.$$

To reduce the risk of including drought years into reference periods (*PreDr* and *PostDr*), various authors proposed to select only single drought events (Hartl-Meier et al., 2014a; Zang et al., 2014), to choose very short reference periods (Vitali et al., 2017), or to select reference periods lacking droughts (Cavin and Jump, 2017; Hereş et al., 2021). This procedure often leads to the omission of distinct drought years from the analysis and in our case would have narrowed our drought query down to one year (2012) (Table A8 in the Appendix). To mitigate such problems, some authors selected longer reference periods (Camarero et al., 2018; Kunz et al., 2018; Schwarz et al., 2020). Following Schwarz et al. (2020), we repeatedly computed growth responses in terms of *PreDr* and *PostDr* for reference periods of 2–5 years, which encompasses the range of most growth reaction studies reported, in order to analyze and minimize the effect of reference period length on our results. In addition, we computed and compared the tolerance indices for each drought year separately (2000, 2003 and 2012, Figure A9 in the Appendix). For the sake of clarity, only the results of the 2- and 5-year reference periods and the pooled drought impact are given in the Results section.

Statistical analyses

To test for the effect of SWB on BAI while accounting for possible age effects on individual tree growth, we fitted linear mixed models with the R packages `lme4` and `lmerTest` (Kuznetsova et al., 2017; Pinheiro et al., 2021) for each site and transect to explain annual BAI in the years 1940–2016 as a function of SWB and tree-ring age (which is the number of years passed when a tree grows from 1 to n years of age). The models also included the calendar year as grouping factor (random effect as intercept). Subsequently, we used the models to predict tree growth (BAI) free of age trends by modelling tree growth for theoretically never-aging trees of standard age 60 years as a function of SWB from 1940–2016. We averaged the tree-individual predictions to site averages (Tukey's bi-weight robust mean) and then compared these chronology predictions to the truly measured BAI chronologies in order to assess and exclude any potential impact of age trends in our analysis. To explain differences in GC, a multifactorial ANOVA, followed by a Tukey's HSD test, with BAI as response and species plus transect as factorial variables was performed to test for growth differences within species comparing the epochs 1960–1979, 1980–1999 and 2000–2017, as well as for comparing pre-drought, drought and post-drought periods. The factor "transect" was included to account for site-specific differences in the data. Between-species differences were tested for the response variables GC, Rt, Rc, and Rs in the same way. If required, response variables were either log- or square-root transformed and all model residuals were visually checked for normal distribution (qq-plot) as well as with the Kolmogorov-Smirnov test. In the analysis of GC of a given species, deviations from GC = 0 (i.e. no difference between observed and reference period) were considered significant, if the 1000-fold bootstrapped empirical 95 %-confidence interval was either fully above or fully below GC = 0. All tests were performed at a significance level of $p \leq 0.05$. All statistical procedures were performed in R 4.0.3 (R Core Team, 2020) using the package `dplR` (Bunn et al., 2020). Arithmetic means (± SD) are presented in all graphs and tables.

3.4 Results

Stand characteristics and quality of tree ring series

Mean RWL and mean BAI were generally highest in *T. tomentosa* followed by *F. sylvatica* (mesic) in the transects A and B (Table 1). *Q. frainetto* showed the lowest RWL and BAI values of all species in the transects A and B, while it was the xeric *F. sylvatica* stand in the driest transect C (Figure A4 in the Appendix). Except for one *T. tomentosa* stand in transect B (56 years), mean age ranged from 72 to 113 years (Table 1) with notable differences among species and across transects (Figure A4 in the Appendix). The mean GLK for all species was well above the 0.65 threshold (Table 1) and mean first-order autocorrelation (AC1) varied uniformly between 0.49 and 0.65. The mean inter-series correlation of the RWI series (Rbar) ranged from 0.41–0.60 and the estimated population signals (EPS) indicated a very high internal signal strength (EPS > 0.93) for all sites (Table 1). All stands had similar mean competition indices (CI) in the range 0.40–0.58 (Table 1). Only mesic beech in transect C had a significantly higher mean CI than the conspecifics in the other transects (Figure A4 in the Appendix).

Table 1. Descriptive statistics (mean with SD in brackets) for the five tree species in the three transects. Transect (T), species (Sp), sampled trees (N), tree age (Age), elevation (Elev), diameter at breast height (DBH) tree height (H), Hegyi competition index (CI), ring width length (RWL) for the 1940–2017 period (except T. tomentosa, transect B: 1950–2017), "Gleichläufigkeitswert" (GLK) and first-order auto-correlation (AC1). Given are also the inter-series correlation (Rbar) and estimated population signal (EPS) as calculated from the detrended (30-year moving average standardization with frequency cut-off at 50 %) ring width series. Species are abbreviated as: FM = *F. sylvatica* (mesic), FX = *F. sylvatica* (xeric), QP = *Q. petraea*, TT = *T. tomentosa*, QC = *Q. cerris* and QF = *Q. frainetto.*

			Stand structural data					**Chronology data for 1940–2017**				
T	**Sp**	**N**	**Age**	**Elev**	**DBH**	**H**	**CI**	**RWL**	**GLK**	**AC1**	**Rbar**	**EPS**
		trees	years	m a.s.l.	cm	m		mm				
A	FM	54	82 (14)	648 (72)	44.4 (5.7)	31.0 (3.1)	0.43 (0.20)	2.38 (0.52)	0.69 (0.06)	0.55 (0.12)	0.49	0.98
B	FM	55	75 (17)	574 (105)	47.6 (9.1)	31.6 (3.7)	0.42 (0.24)	2.88 (0.76)	0.67 (0.08)	0.56 (0.17)	0.42	0.97
C	FM	44	105 (32)	721 (113)	45.3 (5.8)	27.0 (3.1)	0.72 (0.24)	1.63 (0.43)	0.67 (0.07)	0.53 (0.11)	0.51	0.98
A	FX	29	93 (11)	368 (40)	46.0 (5.1)	32.4 (3.4)	0.43 (0.20)	1.78 (0.33)	0.69 (0.06)	0.55 (0.10)	0.52	0.97
B	FX	26	102 (20)	412 (26)	48.1 (8.0)	33.5 (3.5)	0.49 (0.26)	1.85 (0.44)	0.66 (0.06)	0.58 (0.13)	0.46	0.96
C	FX	27	94 (28)	397 (40)	37.6 (6.1)	21.7 (4.9)	0.58 (0.25)	1.30 (0.33)	0.69 (0.07)	0.53 (0.10)	0.47	0.96
A	QC	32	102 (10)	382 (69)	42.9 (5.9)	28.6 (4.2)	0.45 (0.30)	1.56 (0.34)	0.70 (0.06)	0.63 (0.10)	0.57	0.98
B	QC	32	76 (15)	377 (44)	44.0 (6.1)	31.5 (3.8)	0.44 (0.30)	2.14 (0.49)	0.70 (0.07)	0.61 (0.20)	0.53	0.97
C	QC	30	82 (12)	225 (16)	41.2 (5.2)	22.0 (3.9)	0.53 (0.29)	1.78 (0.49)	0.71 (0.06)	0.61 (0.09)	0.60	0.98
A	QF	32	99 (10)	321 (30)	39.7 (4.0)	27.0 (3.6)	0.47 (0.22)	1.44 (0.30)	0.70 (0.06)	0.49 (0.12)	0.57	0.98
B	QF	30	83 (15)	365 (19)	42.4 (7.7)	28.3 (3.7)	0.40 (0.27)	1.75 (0.63)	0.68 (0.06)	0.65 (0.13)	0.46	0.96
C	QF	30	84 (13)	233 (15)	39.2 (5.9)	19.6 (7.4)	0.56 (0.28)	1.76 (0.59)	0.69 (0.06)	0.64 (0.12)	0.56	0.97
A	QP	49	95 (11)	521 (118)	45.0 (6.2)	28.5 (3.3)	0.40 (0.24)	1.79 (0.47)	0.71 (0.06)	0.51 (0.16)	0.49	0.98
B	QP	42	82 (18)	455 (82)	44.3 (5.6)	29.2 (4.1)	0.50 (0.40)	2.33 (0.61)	0.68 (0.06)	0.61 (0.18)	0.41	0.96
C	QP	59	113 (29)	520 (201)	44.3 (7.1)	22.7 (4.0)	0.53 (0.25)	1.44 (0.40)	0.68 (0.06)	0.56 (0.13)	0.49	0.98
A	TT	36	72 (26)	492 (90)	45.3 (9.2)	27.7 (4.4)	0.34 (0.22)	2.64 (0.94)	0.70 (0.08)	0.56 (0.15)	0.53	0.97
B	TT	28	56 (10)	485 (88)	46.9 (9.5)	30.6 (4.2)	0.38 (0.24)	3.17 (0.55)	0.65 (0.08)	0.54 (0.25)	0.41	0.93
C	TT	30	89 (26)	561 (164)	45.3 (6.2)	22.4 (2.8)	0.56 (0.20)	1.76 (0.59)	0.67 (0.07)	0.56 (0.13)	0.44	0.96

Climate trends and severe summer droughts

The modeled climate data show for the oak stands higher summer temperatures, especially in transect C, than in the mixed and pure beech stands (Figure A2 in the Appendix). On average, *Q. petraea* grew in cooler conditions than *Q. cerris* and *Q. frainetto* (Figure A5 in the Appendix), although the occurrence of the three species partly overlapped (Figure 1c). The low-elevation, xeric *F. sylvatica* trees on northern exposition grew under warmer conditions than the higher-elevation mesic *F. sylvatica* (Figure A2 in the Appendix). Summer temperatures were particularly high in the *Q. frainetto* and *Q. cerris* and xeric *F. sylvatica* stands of transect C, which was also the driest, whereas transect B was the wettest in summer (Figure A5 in the Appendix). SWB exhibited an increase in the 1960s / 70s, followed by a decrease in the 1980s / 90s, and a subsequent strong decrease since 2005 / 2010 at all sites, resulting in an overall SWB decrease by about 25 mm since the 1960s (Figure 4 and Table A2 in the Appendix). The most severe 20th century summer droughts occurred in 2000, 2003 and 2012 and were similar in terms of SPEI (3-months SPEI < -1.5; 6-months SPEI < -1.0) and temperature (1.5–2 °C above the average), all having very low MSP and thus reduced SWB (Table A8 in the Appendix).

Climate sensitivity of growth and long-term growth trends

Summer temperature had in most cases a significant negative effect on RWI in the five species in the three transects, while the spring temperature signal was less influential and winter and autumn temperatures had no influence (Figure 2). Summer precipitation consistently influenced RWI positively except for *Q. petraea* in transect A and *Q. frainetto* in transect C. Spring precipitation was less important and autumn and winter precipitation had no influence in any of the species (Figure 2). Similarly, summer SPEI was significantly positively related to growth in all species except for one *Q. petraea* stand in transect A. In spring, a significant influence of SPEI was only recorded for *Q. cerris* (transect A) and *Q. frainetto* (transect A and B). Climatic aridity in autumn only had an influence on *F. sylvatica* (xeric) in transect B, *Q. cerris* (transect C) and *Q. frainetto* (transect B) whereas winter had no influence. The climate sensitivity analysis conducted for individual months shows similar overall patterns for the five species in the three transects, but also demonstrates some species differences, notably a somewhat larger summer heat sensitivity of beech in comparison to the other species (Figure A6 in the Appendix). Correlation analyses between RWI and MST, MSP and SWB for data pooled over the three transects showed similar results (Table A9 in the Appendix) where, as in the individual transects, *Q. petraea* and *Q. frainetto* generally achieved lower correlation coefficients for climate dependence of growth.

With respect to long-term growth trends (Figure A7 in the Appendix), all five species had in common that their BAI increased from the 1950s to the late 1970s, a trend most conspicuous in the driest transect C (Figure 3). Subsequently, the growth rate of all species remained stable in the moister transects A and B until the beginning of the 21st century, while it tended to decrease in transect C. Averaged over the period 1940–2017, mean BAI (and mean RWL) was highest in the *T. tomentosa* and mesic *F. sylvatica* populations (except transect C), intermediate in *Q. petraea, Q. cerris,* and lowest in the *Q. frainetto* and xeric *F. sylvatica* populations (Table

1 and Figure A4 in the Appendix). Xeric beeches had a 20–30 % lower mean BAI than mesic beech and all species (except *Q. frainetto*) had the highest increments in the moistest transect B and the lowest (except *Q. cerris* and *Q. frainetto*) in the hottest and driest transect C (Table 1 and Figure A4 in the Appendix). *T. tomentosa* and the xeric *F. sylvatica* populations, mean BAI declined since about 2000 especially in the warmer and drier transects C and A (Figure 3). *T. tomentosa* showed the strongest growth decline in the last 20 years of all species, followed by the xeric *F. sylvatica* stands, while the mesic beech stands suffered only in the drier transects A and C, which is also where we observed the lowest share of vital trees in a systematic forest inventory of the study transects (Figure A10 and Table A5 in the Appendix). In contrast, all three oak species showed more stable growth trends and no distinct decline in recent years (Figure 3), which is mirrored by more vital oak than beech trees in the transects (Figure A10 in the Appendix). During the increasingly hot summers of the most recent years, the relatively high growth rates of *F. sylvatica* (mesic and xeric stands) and *T. tomentosa* even dropped in the warmest transect (C) below the BAI of the oak species. Similar growth trends seem currently to develop in transect A, where *T. tomentosa* growth already has dropped to the level of *Q. petraea*, and in transect B, where the growth rate of *Q. petraea* is approaching that of the mesic *F. sylvatica* stands and *T. tomentosa*, pointing at a dominance shift to happen in future.

Relating the growth trends to the trends in climate variables, the linear mixed models, which accounted for age trends, indicate for the *F. sylvatica* and *T. tomentosa* stands a strong dependence (high F-values) on the SWB, which is weaker in the oak species (non-significant in *Q. petraea* and *Q. cerris* on transect A) (Table 2). This difference in the relationships is also visible when relating current and previous year SWB to RWI data (Table A9 in the Appendix). Further, the visual comparison of observed BAI and age-independent model predictions (Figure A8 in Appendix) showed that the recognized climate change-related BAI trends remain valid, when controlling for age in the models.

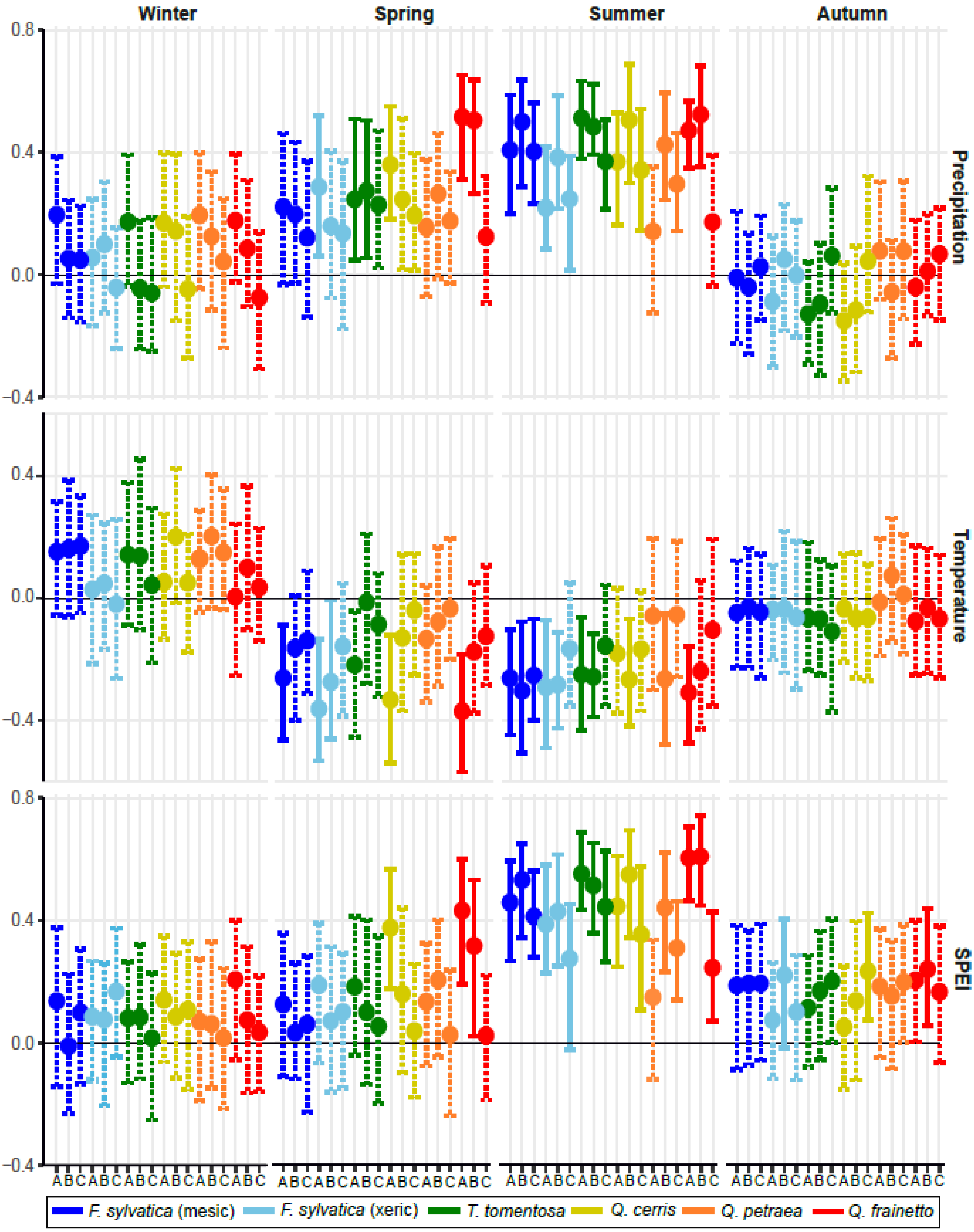

Figure 2: Correlation of ring width indices (spline-detrending with 30-year moving window and 50 % frequency cut-off) with: winter (wt), spring (sp), summer (sm), and autumn (at) mean monthly precipitation (P), mean monthly temperature (T), and mean monthly Standard Precipitation Evaporation Index (SPEI, 3-month interval). The y-axis depicts the correlation coefficients, whereas the x-axis shows the three transects A, B and C grouped by species and populations (*F. sylvatica*: mesic and xeric). Species and populations are depicted in different colours. Significant correlations are shown through solid whiskers for the 2.5% and 97.5% empirical 1000-fold bootstrapped confidence interval.

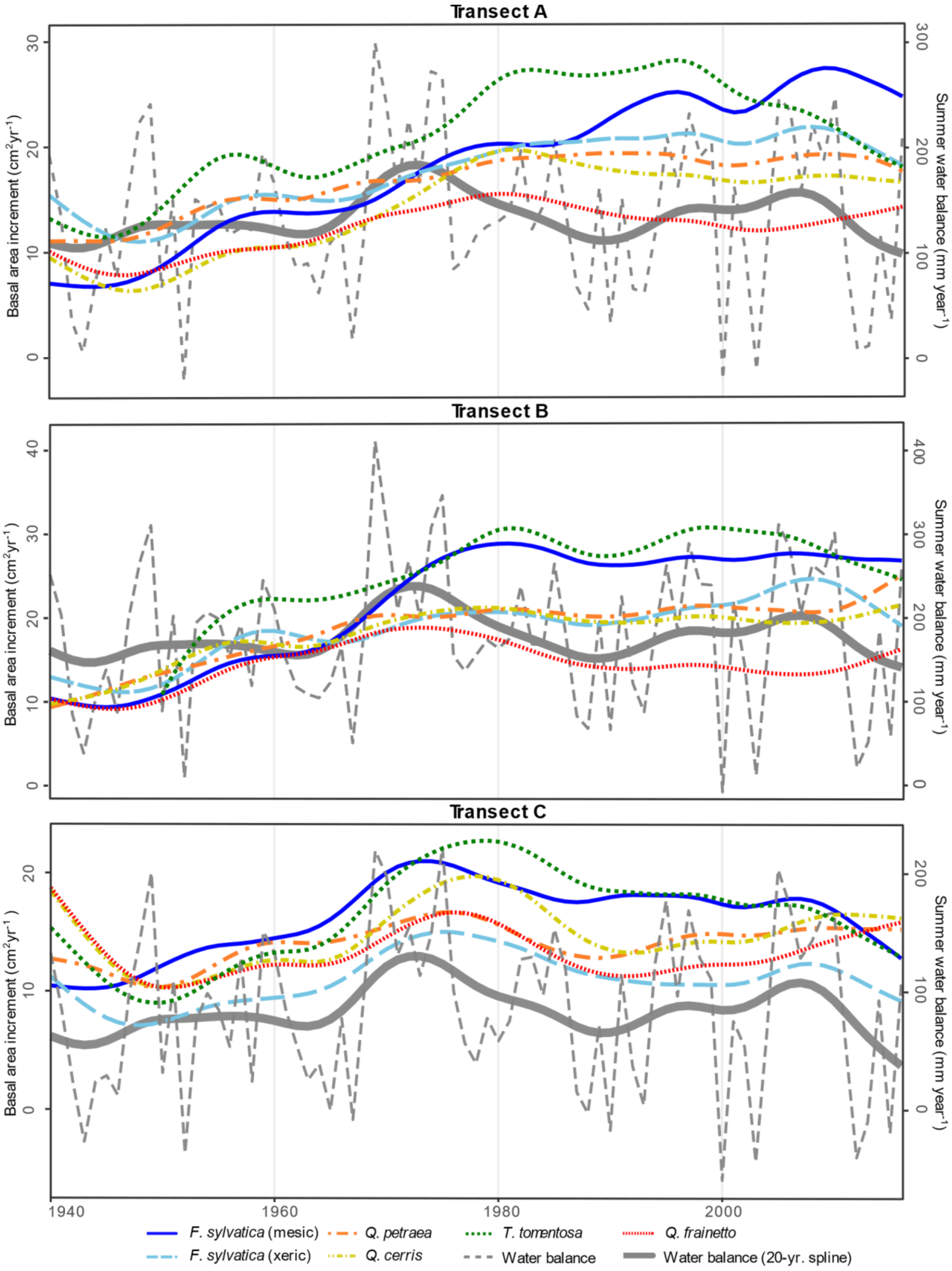

Figure 3: 20-yr smoothing spline of mean basal area increment of the five species (and two site types for beech) in the transects A–C in relation to summer water balance (annual values: grey dashed line; 20-yr smoothing spline: continuous grey line) for the period 1940–2016. *F. sylvatica* mesic: upper elevation beech forest on south-exposed slope; *F. sylvatica* xeric: lower elevation beech forest on northern slope.

Table 2: Summary statistics for the linear mixed models describing tree-individual basal area increment (BAI in mm^2 $year^{-1}$) as a function of summer water balance (SWB in mm $year^{-1}$) plus tree age (year of age) as fixed effects and calendar year as random intercept grouping factor. Significant effects are highlighted in bold.

				SWB			Age	
Transect	**Species**	**N (Trees)**	**F value**	**P value**	**Slope (BAI / SWB)**	**F value**	**P value**	**Slope (BAI / tree age)**
A	FM	54	**11.7**	**<0.01**	**3.7**	3.3	0.071	2.2
B	FM	55	**16.3**	**<0.001**	**4.4**	3.8	0.051	3.0
C	FM	44	**25.1**	**<0.001**	**3.9**	**34.4**	**<0.001**	**-2.8**
A	FX	29	**11.3**	**<0.01**	**3.2**	3.8	0.051	-3.0
B	FX	26	**20.0**	**<0.001**	**3.4**	3.5	0.062	-2.2
C	FX	27	**10.3**	**<0.01**	**2.0**	**48.9**	**<0.001**	**-3.5**
A	TT	36	**16.7**	**<0.001**	**4.7**	0.01	0.842	0.2
B	TT	28	**25.3**	**<0.001**	**4.0**	**46.7**	**<0.001**	**22.1**
C	TT	30	**14.9**	**<0.001**	**3.9**	**34.8**	**<0.001**	**-5.0**
A	QC	32	2.9	0.09	2.3	**179.2**	**<0.001**	**-16.4**
B	QC	32	**16.7**	**<0.001**	**2.3**	0.5	0.492	-0.8
C	QC	30	**10.8**	**<0.01**	**2.8**	**32.4**	**<0.001**	**-6.2**
A	QP	32	0.3	0.60	0.6	**270.0**	**<0.001**	**-18.0**
B	QP	30	**9.9**	**<0.01**	**2.3**	**40.9**	**<0.001**	**-5.7**
C	QP	30	**10.3**	**<0.01**	**1.6**	0.3	0.600	0.2
A	QF	49	**6.9**	**<0.05**	**1.7**	**35.4**	**<0.001**	**-4.9**
B	QF	42	**19.0**	**<0.001**	**2.2**	0.8	0.366	1.1
C	QF	59	**4.4**	**<0.05**	**1.9**	**189.9**	**<0.001**	**-15.2**

Growth change and response to severe 20th century summer droughts

We observed a trend towards increasing mean BAI rates in all species except *Q. frainetto* in the period 1980–1999 as compared to the previous interval (1960–1979); yet the difference was significant only for the mesic *F. sylvatica,* the *Q. cerris* and *T. tomentosa* stands (Table 3). The increase was most pronounced in *T. tomentosa* and the mesic *F. sylvatica* stands, and smallest in the xeric *F. sylvatica* stands (Table 3). BAI was lower in all species (except *Q. petraea)* in the period 2000–2017 than in 1980–1999; yet the difference was significant only in *T. tomentosa*, which showed the steepest growth decline followed by both *F. sylvatica* site types and *Q. cerris* (Table 3). Growth changes for GC_1 (1980–99 vs. 1960–79) increased for *F. sylvatica* (mesic and xeric), *T. tomentosa* and *Q. cerris* and were highest for *F. sylvatica* (mesic) and *T. tomentosa* (Table 3). Contrarily for GC_2 (2000–2017 vs. 1980–99) growth changes decreased for *F. sylvatica* (mesic and xeric), *T. tomentosa* and *Q. cerris* and were lowest *for T. tomentosa* and *F. sylvatica* (xeric) (Table 3).

Table 3: a) Mean (SD) basal area increment (BAI in cm2 yr-1) of the five species (and two site types of beech) in the time intervals 1960–1979, 1980–1999 and 2000–2017 averaged over all three transects. Significant differences of BAI between the three time periods are marked with different small letters. (b) Mean (SD) growth change ratio (GC, BAI value of later period divided by earlier period) and derived mean percentage change in growth in the periods 1980–99 vs. 1960–79, and 2000–2017 vs. 1980–99. Significantly different GC from 0 % are highlighted in bold and significant differences of GC between species are indicated by different small letters. Species (SP) are abbreviated as: FM = *F. sylvatica* (mesic), FX = *F. sylvatica* (xeric), QP = *Q. petraea*, TT = *T. tomentosa*, QC = *Q. cerris* and QF = *Q. frainetto*. Trees = number of trees sampled.

		a) BAI in cm^2 year^{-1}						**b) Growth change**					
SP	**Trees**	**1960–1979**		**1980–1999**		**2000–2017**		**GC$_1$ (SD)**	**Mean %**		**GC$_2$ (SD)**	**Mean %**	
FM	153	19.7 (10.4)	a	25.0 (11.2)	b	23.7 (11.5)	b	**1.43 (0.77)**	**43.0%**	**a**	**0.99 (0.41)**	**-1.0%**	**a**
FX	82	16.8 (6.7)	a	18.9 (8.1)	a	17.8 (8.9)	a	**1.14 (0.30)**	**14.0%**	**b**	**0.95 (0.33)**	**-5.0%**	**ab**
TT	94	20.7 (10.1)	a	27.6 (11.3)	b	22.6 (11.0)	a	**1.54 (0.82)**	**54.0%**	**a**	**0.85 (0.34)**	**-15.0%**	**b**
QC	94	17.0 (6.5)	a	19.0 (6.5)	b	17.9 (6.6)	ab	**1.18 (0.34)**	**18.0%**	**ab**	**0.96 (0.24)**	**-4.0%**	**a**
QP	150	17.4 (6.3)	a	18.4 (6.8)	a	18.8 (7.6)	a	1.10 (0.35)	10.0%	bc	1.03 (0.23)	3.0%	a
QF	92	15.8 (6.8)	a	15.0 (6.2)	a	14.5 (6.3)	a	0.99 (0.33)	-1.0%	c	0.99 (0.23)	-1.0%	a

Growth responses in the three severe drought years (2000, 2003 and 2012) showed that the mesic *F. sylvatica* stands suffered the largest growth reductions during the droughts (i.e. the lowest drought resistance Rt), followed by *T. tomentosa* and the xeric beech stands, while the three oak species showed higher resistance (Table 4, Figure 4). On the other hand, drought recovery (Rc) was most pronounced in the mesic *F. sylvatica* and the *T. tomentosa* stands, whereas the xeric beech stands and the oak species reached lower Rc scores, not differing from each other (Table 4, Figure 4). In correspondence to the stronger drought-induced growth decline, the *F. sylvatica, T. tomentosa* and (to some extent) the *Q. cerris* stands showed low drought resilience (Rs), whereas *Q. petraea* and *Q. frainetto* revealed full recovery and thus high resilience (equal post-drought and pre-drought growth rates). The lowest Rs score was recorded for the xeric beech stands and *T. tomentosa*, followed by the mesic beech stands (Table 4, Figure 4). The species' drought response differed somewhat between the three drought years. In 2000, only the mesic *F. sylvatica* and the *T. tomentosa* stands showed a response to drought (Table A10 in the Appendix). In 2003, post-drought BAI of beech (mesic and xeric stands) was even higher than the pre-drought growth rate, and the other species all showed full recovery from the drought in that year. For the xeric beech stands and the *T. tomentosa* stands, BAI decreased significantly in 2012 and did not recover until 2017 from that drought-year level anymore (Table A10 in the Appendix).

Table 4: Basal area increment (BAI, in cm^2 yr^{-1}) prior to, during, and after the three droughts 2000, 2003 and 2012 in the five species (and two site types of beech), averaged over the three droughts. Species (SP) and sampled trees (Trees). Significant differences for a species between pre-drought, drought and post-drought periods are indicated with different small letters. Species are abbreviated as: FM = *F. sylvatica* (mesic), FX = *F. sylvatica* (xeric), QP = *Q. petraea*, TT = *T. tomentosa*, QC = *Q. cerris* and QF = *Q. frainetto*. The left part of the table shows the results from an analysis using a 5-year reference period and the right side shows the same for a 2-year reference period.

		BAI (SD), 5-years reference period						**BAI (SD), 2-years reference period**					
SP	**Trees**	**Pre-drought**		**Drought**		**Post-drought**		**Pre-drought**		**Drought**		**Post-drought**	
FM	153	26.5 (12.2)	a	17.4 (8.5)	b	24.7 (12.3)	a	25.4 (12.6)	a	17.4 (8.5)	b	23.1 (12.2)	c
FX	80	20.8 (10.2)	a	14.5 (6.5)	b	17.6 (8.7)	c	19.7 (10.4)	a	14.5 (6.5)	b	15.2 (8.1)	c
TT	94	27.0 (12.0)	a	18.0 (7.1)	b	23.4 (11.8)	c	26.5 (13.3)	a	18.0 (7.1)	b	22.4 (13.1)	c
QC	94	18.9 (6.9)	a	15.3 (4.7)	b	17.7 (6.8)	a	19.1 (7.9)	a	15.3 (4.7)	b	17.0 (7.9)	a
QP	150	18.9 (7.6)	a	17.1 (7.2)	b	19.4 (8.1)	a	17.6 (7.8)	a	17.1 (7.2)	b	19.2 (8.9)	a
QF	92	15.0 (6.7)	a	12.6 (5.4)	b	14.5 (6.6)	a	15.2 (7.5)	a	12.6 (5.4)	b	14.1 (7.8)	a

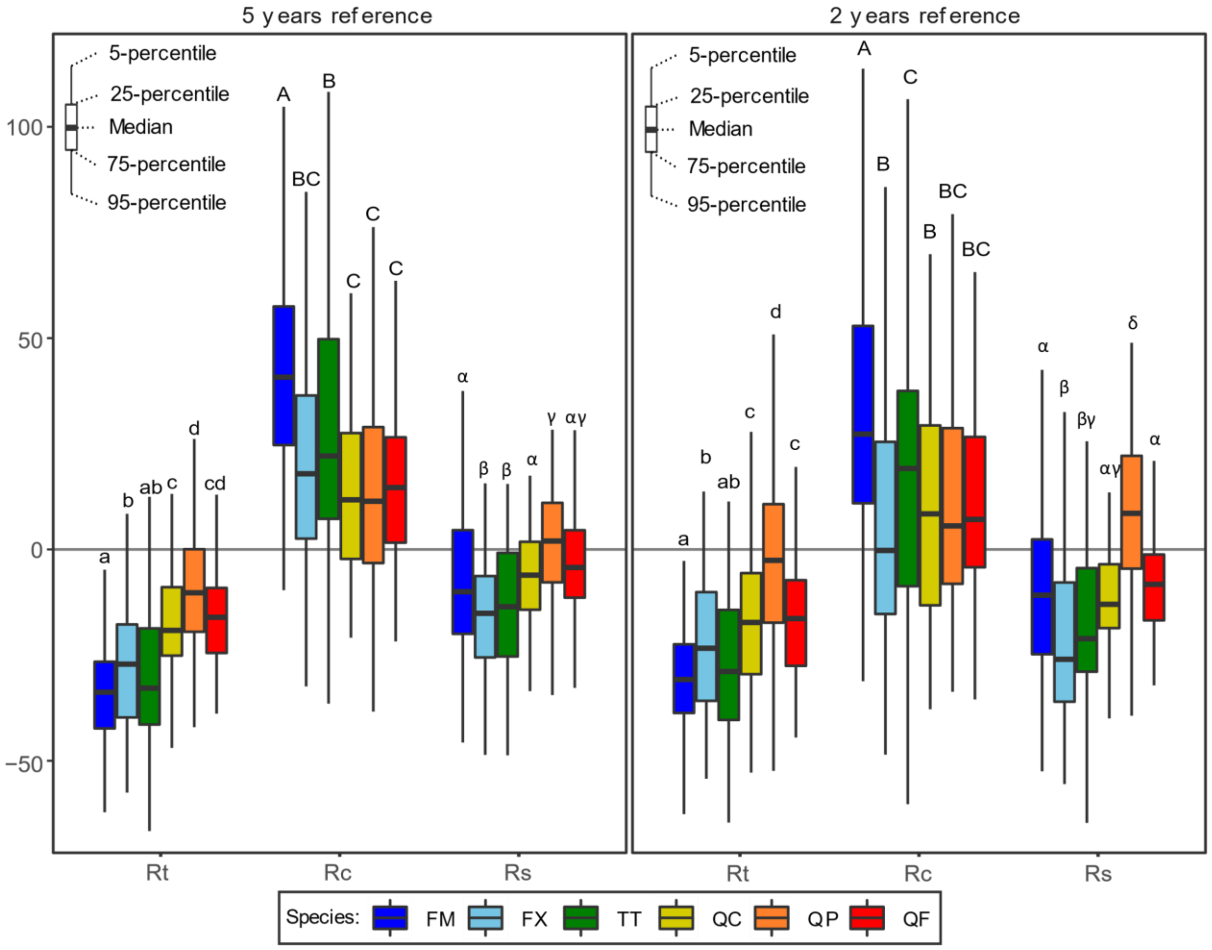

Figure 4: Drought responses: drought resistance (Rt: mean BAI drought / mean BAI pre-drought), drought recovery (Rc, mean BAI post-drought / mean BAI drought) and drought resilience (Rs, mean BAI post-drought / mean BAI pre-drought) for the pooled summer-drought events 2000, 2003 and 2012 for the five species (and two site types of beech). The left panel shows the results from an analysis using a 5-year reference period and the right panel shows the same for a 2-year reference period. Significant differences between species are marked with different small letters. Species are abbreviated as: FM (dark blue) = *F. sylvatica* (mesic), FX (light blue) = *F. sylvatica* (xeric), TT (green) = *T. tomentosa*, QC (yellow) = *Q. cerris*, QP (orange) = *Q. petraea*, and QF (red)= *Q. frainetto*.

3.5 Discussion

Limiting climate factors and long-term growth trends

The climate sensitivity analysis demonstrates that all five species studied in the south-east European beech–oak ecotone are primarily limited by climatic aridity and high temperatures in the summer months, while water availability and temperature in spring are of lower importance (question 1). These results comply with findings for temperate beech and oak forests of Central, Southern- and Eastern Europe (Berki et al., 2009; Bose et al., 2021; Bosela et al., 2018; Dittmar et al., 2003; Grace et al., 2002; Jump et al., 2006; Mäkinen et al., 2002; Petritan et al., 2021; Scharnweber et al., 2011; Takahashi et al., 2001)

All species showed a long-term BAI increase from the 1950s to the late 1970s, which presumably reflects a release phase in the stand development cycle, when the young trees left the pole-wood phase with intense competition prior to 1960 and approached maturity. According to a tree growth model that assumes a sigmoid growth curve during lifetime (Weiner and Thomas, 2001), this phase of rapid growth passes finally over to a phase of reduced growth at maturity, which the trees of our study may have reached around the 1980s. In fact, all five species exhibited roughly thirty years of more or less constant basal area increment between 1980 and 2010, albeit at different species-specific BAI levels. Similar long-term growth patterns with stable or slightly decreasing growth rates during the mature phase have been reported from studies on *F. sylvatica* (Jump et al., 2006), *Q. petraea* (Härdtle et al., 2013; Petritan et al., 2017) and other deciduous tree species of the temperate zone (Duchesne et al., 2003; Fekedulegn et al., 2003; Leblanc, 1990). Even at high age, BAI can remain on quite high levels in many temperate broadleaved and conifer tree species (Härdtle et al., 2013; Leblanc et al., 1992; Phipps and Whiton, 1988), if the trees are not hit by environmental hazards or pest attack. Long-term BAI declines in visually healthy mature stands are thus unexpected and usually must be seen as indication of impending premature senescence (Duchesne et al., 2003; Jump et al., 2006; Leblanc, 1990), as caused by asymmetric competition (Duchesne et al., 2002; Schweingruber, 1996), climatic stress (Allen et al., 2010; Leuschner, 2020; Schuldt et al., 2020), infestations with insects, fungi or other pathogens (Galiano et al., 2011; Hogg et al., 2002), or the impact of atmospheric pollution (Muzika et al., 2004).

In our stands, a lasting BAI decline during the last 10–20 years was most prominent in the xeric *F. sylvatica* stands and in *T. tomentosa*, but it also occurred in the mesic beech stands, where growth rate declined from a relatively high level compared to the stands of the other species (questions 2 and 3). The growth decline in beech and linden seems to follow a decrease in SWB by roughly 25 mm in the period 1960–2017. June is usually the most important month for ring formation in beech in Central Europe (Čufar et al., 2008), with water deficits in this early-summer period being crucial for ring width. Yet, a clear SWB threshold that might have triggered the growth decline since about 2010 was not visible in the three transects. While MSP itself showed no trend and thus is an unlikely driver, the continuous MST increase since 1980 may well be physiologically important. Linking the temperature to the growth curves suggests that the beech growth curve turned negative, when mean summer temperature (June–August) surpassed 20–21 °C. The foliage of beech has been found to be relatively sensitive to heat, especially when it occurs together with drought (Leuschner, 2020; Peltzer, 2001). Rising summer temperatures may negatively influence the cambial water status through a higher evaporative demand that increases water loss via transpiration. Specifically, MST increased from 1960–1979 to 2000–2016 by 1.9 °C, while MSP remained constant in the western Romanian study region, deteriorating the climatic water balance in summer (June–August) by -24 mm through an increase in atmospheric evaporative demand (Table A2 in the Appendix). Indeed, inter-annual MSP fluctuation, together with SWB variation, was in all species the most influential climatic factor driving the BAI variation, even in the absence of precipitation trends and also when controlling for age in the models. In agreement with our findings, various dendrochronological studies in southern and south-eastern Europe, but also in Central Europe, have demonstrated long-term growth declines in beech in recent time, which coincide with the warming trend and often an increased drought frequency in summer (Jump et al., 2006, Scharnweber et al. 2011, Knutzen et al. 2017, Bosela et al., 2018).

In southern and south-eastern Europe, where beech occurs close to its drought and heat limit, negative growth trends prevailed in beech stands at lower elevation at the mountain foot (Bosela et al., 2018; Jump et al., 2006; Peñuelas et al., 2008; Piovesan et al., 2008; Serra-Maluquer et al., 2019), while stable or positive growth trends have been found at higher elevation (Hacket-Pain and Friend, 2017; Tegel et al., 2014). Our coring across the beech–oak ecotone and in isolated rear-edge beech populations at the mountain foot in western Romania close to the species' distribution limit demonstrates that mean BAI is lower and negative growth trends are more pronounced in the by ~1.5 °C warmer low-elevation xeric *F. sylvatica* stands as compared to the higher and somewhat cooler mesic beech stands (question 2). However, evidence has been found that marginal (southern) *F. sylvatica* populations may be less drought-sensitive in their growth than more central populations, suggesting successful acclimation or adaptation to drought (Cavin and Jump, 2017; Hacket-Pain et al., 2016). Yet, the mesic and xeric beech stands in our study indicate that beech adaptation to the warmer and drier climate in the rear-edge populations was not sufficient to avoid lasting growth reduction.

Comparison of the growth trends of the five tree species in the beech–oak ecotone may point at future change in the species composition of these forests. During the last decade, the growth rates of the mesic *F. sylvatica* stand in the driest transect C and of the xeric beech stands in two of the three transects dropped to the BAI level of the slower-growing oak species, suggesting a loss of competitive superiority of beech in the course of climate warming (Leuschner, 2020; Schuldt et al., 2020). Surprisingly, the south-east European species *T. tomentosa* was even more susceptible to warming than *F. sylvatica*, exhibiting a BAI decline already since 2000 or earlier to reach the low growth rate of *Q. petraea*. While all three oak species exhibited markedly lower average BAI rates than beech and linden, their growth trends remained stable or even increased in the face of the warming trend. This does not match the observation that inter-annual growth variation in the three oak species was driven by current-year MSP and SWB variation in a similar manner as it was found for *F. sylvatica* and *T. tomentosa* (question 3). Only previous-year SWB and MSP variation had a smaller growth impact in *Q. frainetto* and *Q. petraea* (but not *Q. cerris*) than in beech and linden. However, the oak species responded to the three severe drought events with higher growth resistance (smaller growth depression) and also higher resilience than beech and linden, matching earlier dendrochronological and physiological observations on Central European oak species (Friedrichs et al., 2009a; Fuchs et al., 2021; Härdtle et al., 2013; Leuzinger et al., 2005).

Given the similarity in climatic conditions, tree age, forest structure, levels of competition and soil properties among the studied forests (Tables A1–A2 and A4–A7 in the Appendix), the coincidence in the recent BAI decline in beech and linden is not explicable by tree age effects or stand dynamic processes. We can also rule out biotic effects such as insect or fungal attack on radial growth patterns, as we inspected the cored trees for signs of infestation prior to selection. This indicates that climate is a main driver of growth change.

Immediate responses to single drought events

Growth resistance (Rt) to severe drought was weaker in *F. sylvatica* and *T. tomentosa* than in the three *Quercus* species (question 4). Part of the difference in sensitivity is explained by the generally lower mean BAI rates of the oaks, as faster growing species are usually more sensitive. However, differences in the phenology of radial growth may also be influential. Early-wood formation in the ring-porous oaks usually occurs before and during bud burst, making these species less sensitive to summer drought than the diffuse-porous species, which have a later onset of growth (Barbaroux & Bréda, 2002; Elliott et al., 2015; García González & Eckstein, 2003; Kitin & Funada, 2016). In correspondence, spring droughts have been found to harm oaks (Bose et al., 2021). It is also possible that the species are differing in their plasticity of carbon allocation to support compensatory root growth during drought years, which appears to occur to a lesser extent in *Q. petraea* (Fuchs et al., 2020; Hertel and Leuschner, 2002) which should reduce the potential for inter-annual stem growth variation as caused by allocation shifts. Investigations in mixed forests have shown that *F. sylvatica* is more drought-sensitive than, for example, *Q. petraea*, *Q. robur*, *Fraxinus excelsior, Acer platanoides*, *A. campestre* and *Sorbus torminalis* (Dittmar et al., 2003; Friedrichs et al., 2009b; Gutierrez, 1988; Kunz et al., 2018; Lebourgeois et al., 2005; Leuschner 2020; Scharnweber et al., 2011; Zimmermann et al., 2015). A dendrochronological study in mixed *T. cordata* and *Q. petraea* stands in central Europe showed that small-leaved linden is less drought-resistant than *Q. petraea* (Fuchs et al., 2021). The relatively high drought sensitivity of *T. tomentosa* is surprising, given the species' mainly Pannonian distribution range with a gravity center in more continental climates (Dinic et al., 1999; Indreica et al., 2017; Radoglou et al., 2009). *T. cordata*, and probably also *T. tomentosa*, pursue different drought response strategies to the Central European *Fagus* and *Quercus* species, with high leaf tissue elasticity, the ability to tolerate temporal leaf wilting, and a relatively high stem-wood capacitance (Aasamaa et al., 2004; Köcher et al., 2009; Leuschner et al., 2019). From our study, it appears that *T. tomentosa* is a fast-growing, but drought-avoiding, pioneer and mid-successional tree, which is very disturbance-tolerant through its high capacity for recovery after damage.

Drought recovery (Rc) and resilience (Rs) are often used synonymously; yet, their calculation and ecological meaning are clearly different (Lloret et al., 2011; Van Ruijven and Berendse, 2010). When comparing different species, the Rc index may be a poor indicator of drought resistance, as small growth rates during a drought due to low resistance (as in *F. sylvatica* and *T. tomentosa*) typically lead to higher Rc scores than in more resistant species, which have to compensate a smaller growth depression, as seen in the oaks. For assessing the longer-term drought impact on growth, resilience (Rs) may be a more informative measure, especially when several severe droughts in sequence are analyzed as we did. During the most severe drought (2000), all five species seem to have met their drought limits, as none achieved full growth resilience within five years. This was different in the less severe 2003 and 2012 droughts, when the oaks (2012), but also beech and linden (2003), fully recovered growth and even over-shot (Table A10 in the Appendix). The successful growth recovery of both the mesic and xeric beech populations after the 2003 drought may be judged as an indication of the considerable acclimation and adaptation potential of *F. sylvatica* to drought. This matches Europe-wide dendrochronological analyses that revealed higher drought resistance and recovery rates in beech populations at the southern range edge than in more central provenances, which was interpreted as an indication of successful adaptation of southern populations to warmer and drier climates (Cavin & Jump, 2017; Hacket-Pain et al., 2016; Muffler et al., 2020). How much of this adaptability is due to genetic differences between populations still has to be investigated. Our study on a regional scale demonstrates that the xeric beech populations have a lower resistance, resilience and recovery rate than the mesic stands, displaying the limitations in the adaptive capacity of *F. sylvatica* to drought and heat (questions 2 and 4). It is likely that the genetic differentiation between the neighboring stands in our study region is smaller than in continent-wide studies, and trait plasticity is apparently not sufficient to fully acclimatize to a hotter and drier climate. This was also suggested in other studies of *F. sylvatica* forests close to the species' drought limit (Di Filippo et al., 2007; Dulamsuren et al., 2017; Hartl-Meier et al., 2014b). In western Romania, we expect in the course of climate warming a retreat of beech from its lower drought- and heat-induced distribution limit at the base of the mountains and a replacement by more tolerant tree species, notably oaks. This will happen if beech mortality is higher than that of the oaks. Long-term growth reduction may be an indicator of reduced vitality and an increased mortality risk, as the death of temperate tree species is usually preceded by decades of reduced radial growth (Cailleret et al., 2017). Probably, biologically more important than warming trends alone are the meteorological extremes as exemplified by the three severe summer droughts 2000, 2003 and 2012, in which MST was on average by 2.0 °C higher and MSP 105 mm lower than the long-term average in our study area (1960–2016) (Table A2 in the Appendix). Similar climate change-related shifts in tree species composition have recently been observed in north-eastern Spain (Peñuelas et al., 2007), England (Cavin et al., 2013), Hungary (Berki et al., 2009) and elsewhere. Our findings are support for the more general assessment of European beech as being more drought-susceptible than temperate oaks (Cavin et al., 2013; Friedrichs et al., 2009a; Härdtle et al., 2013; Leuschner, 2020; Leuzinger et al., 2005; Peterken & Mountford, 1996; Scharnweber et al., 2011; Schuldt et al., 2020; Zimmermann et al., 2015). Contrary to our expectation from the distribution range, *Q. cerris* showed a somewhat smaller growth resistance and slightly smaller resilience in the three drought events than *Q. frainetto* and *Q. petraea*, while all three species maintained stable BAIs between 1960 and 2017, despite climate warming. From their growth performance in the three Romanian transects, we conclude that especially *Q. petraea* and *Q. frainetto,* but also *Q. cerris*, are tolerant to the recent warming trend; yet, *Q. frainetto* exhibited a somewhat lower mean BAI than the two other species.

Reductions in BAI may not only result from drought and heat stress, but they could also be a consequence of irregular mast-fruiting, notably in *F. sylvatica* and the *Quercus* species (Dittmar et al., 2003; Müller-Haubold et al., 2013; Nussbaumer et al., 2018). High temperatures and insolation in dry summers likely are triggers of mast-fruiting one or two summers after the drought (Övergaard et al., 2007, Müller-Haubold et al. 2013, Hacket-Pain et al., 2015; Piovesan & Adams, 2001; Vacchiano et al., 2017). Since four of the five studied species are mast-fruiting, it is difficult to test the assumption of a major effect of masting on the observed BAI variation. Yet, *T. tomentosa* showed a similarly strong negative effect of reduced summer precipitation and SWB on BAI as the other species, while not been known as a mast-fruiting species. This suggests that mast fruiting is unlikely the main driver of BAI variation in our stands than are direct drought and heat effects.

3.6 Conclusions

Dendrochronological studies in natural ecotones between two major forest types can be a valuable tool for identifying climatic turning points of tree species and for enabling evidence-based predictions on future species shifts upon climate warming. Moreover, the approach allows comparing the drought sensitivity of different tree species, which is urgently needed in order to support future silvicultural decision-making. *F. sylvatica* and *T. tomentosa* with higher mean individual-based BAIs suffered continued growth declines during the last 10–20 years, while the slower-growing three *Quercus* species maintained growth rate despite deterioration of the climatic water balance, supporting the notion that faster-growing trees are in general more susceptible to drought. Both the negative BAI trend and a lower average resilience to droughts suggest that the slower-growing, better-adapted oaks will eventually outperform beech at its heat- and drought-induced distribution limit. The climate analogy to western Romania suggests that beech forests in large parts of lowland to sub-montane elevation in Central Europe in the core of the species' distribution range may also face vitality and growth reductions in future, if warming continues at the predicted rate. Our results suggest that the climatic turning point of beech is close to 20–21 °C in mid-summer (June–August). The well-documented higher drought tolerance of *Q. petraea* and *Q. frainetto* (and also of *Q. cerris*) recommends these species for silviculture in central and south-eastern European regions, where beech is predicted to lose vitality in future. The replacement of beech by oaks demonstrates that higher drought tolerance usually is linked to lower productivity, as is visible in the lower BAI rates and smaller height of the oak species in our study. This may be an uncomfortable truth for foresters who prefer productive species to increase profitability, but who will face an increasing risk of climate warming-induced forest damage. The search for productive and also drought-tolerant timber species may be a disappointing undertaking, as plants usually trade growth for protection against hazards including drought. Given the uncertain future of climate, it may be wise for silviculture to favor the stress-tolerance over the high-yield option. *Quercus petraea, Q. frainetto* (and also *Q. cerris*) can be considered as relatively safe species that produce highly valued timber.

3.7 Acknowledgements

Our gratitude goes out to all students and field assistants that participated in the field work, as well as all NEMKLIM project partners in Romania and Germany. We further would like to thank the forestry offices in Radna, Caransebeș, Oțelu Roșu and Orșova for their permits and collaboration. Personally, the corresponding author would also like to thank Lara Goldmann for the assistance during the fieldwork.

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3.9 Appendix

Information on forest inventories and soil sampling

To analyze and compare stand structure, vitality and species composition over the three transects and within the four forest types, inventory plots were established systematically in a grid of 200 m x 200 m that had been placed on the transects (Figure A3 and Table A3–A4 in the Appendix). Inventory plots were classified as mesic or xeric beech forests if the relative basal area (BA_{rel}) of *F. sylvatica* was ≥ 66 %, while subhumid-thermophilic oak forests were plots where BA_{rel} of the three oak species (*Q. petraea, Q. cerris, Q. frainetto*) was ≥ 66 %. In the ecotone (subhumid mixed beech–oak and hornbeam forests), the oak species and beech each contributed with about 30 % to the total basal area, while the remainder belonged mostly to *Tilia* and *Carpinus* species. In addition to these four natural forest types, homogenous linden stands (*T. tomentosa* > 85 % of total stem number) were occasionally encountered, which likely are relicts of intensified forest clearing in the past (Dinic et al., 1999; Radoglou et al., 2009). If the BA_{rel} of *T. tomentosa* was ≥ 66 %, these were classified as post-disturbance linden forests; however no tree cores were extracted here. Plots with a total basal area (BA_{tot}) < 10 m^2 ha^{-1} were classified as “no forest” (N=15 for transects A–C) and omitted from analysis of forest types. To assess stand vitality, all trees were classified as: vital (no major deteriorations observable), non-vital (> 25% of tree dead, pathogenic infests observable or major branches / crown broken) and dead (no vitality observable). An overview of the results of forest inventories are presented in Table A4–A6 and vitality results are presented in Table A5 and Figure A10 in the Appendix. To ensure comparability concerning soil physical and chemical properties between the three transects and among the identified forest types, soil samples were systematically extracted following the elevation gradients within the four forest types; samples were taken in proximity to the sampled tree species (Figure A3 and Table A7 in the Appendix). No soil samples were extracted in the post-disturbance linden forests. Details of the forest inventory results (transition of forest structure over elevation) as well as soil analysis are given in Kasper et al. (2021).

Tables

Table A1: Location of the three transects with longitude (Long.) and latitude (Lat.), elevation (Elev.) and climatic characteristics of the highest (top end) and lowest (bottom end) plots. The highest-elevation plots are located in typical beech forests, the lowest plots in typical oak forests. Given are annual mean temperature (Tm), temperature of the warmest month (Tmax), temperature of the coldest month (Tmin), mean temperature of warmest quarter (MST), mean annual precipitation (Pm), precipitation of the wettest month (Pmax), precipitation of the driest month (Pmin), and precipitation of the warmest quarter (MSP) according to data extracted from the CHELSA climate data base (Karger et al., 2017).

Transect locality	County	Transect position	Long.	Lat.	Elev. m	Tm C°	Tmax C°	Tmin C°	MST C°	Pm mm yr^{-1}	Pmax mm	Pmin mm	MSP mm
Milova (A)	Arad	Top end	21.8135	46.1973	759	7.9	23.4	-6.5	18.2	892	125	48	254
		Bottom end	21.8022	46.1290	216	10.8	26.5	-6.5	21.2	690	132	52	248
Maciova (B)	Caraș-Severin	Top end	22.2460	45.5749	719	8.2	23.8	-7.1	18.6	951	100	54	216
		Bottom end	22.2116	45.5248	256	11.1	26.9	-4.0	21.7	791	81	41	157
Eselnita (C)	Orsova	Top end	22.3188	44.7754	907	7.8	23.6	-3.8	18.3	844	106	45	201
		Bottom end	22.3578	44.7173	147	11.9	28.0	-3.5	22.6	598	69	40	137

Table A2: CHELSA climate data (Karger et al., 2017) for: mean summer temperature (MST) in °C, mean summer precipitation (MSP) in mm, and summer water balance (SWB) in mm, calculated for the periods 1960–1979, 1980–1999 and 2000–2016 (a) and for the drought years 2000, 2003 and 2012 for the three transects (A–C) and averaged over the three transects (A+B+C) (b).

a)	Transect A			Transect B			Transect C			Mean (A+B+C)		
Period	**60–79**	**80–99**	**00–16**	**60–79**	**80–99**	**00–16**	**60–79**	**80–99**	**00–16**	**60–79**	**80–99**	**00–16**
MST	18.6	19.0	20.4	18.9	19.4	20.8	19.5	20.0	21.4	19.0	19.5	20.9
MSP	232.4	216.8	229.9	281.6	259.8	274.0	187.0	170.2	180.9	233.7	215.6	228.3
SWB	146.8	139.4	125.6	194.8	180.9	168.5	97.4	88.4	73.0	146.3	136.2	122.4

b)	Transect A			Transect B			Transect C			Mean (A+B+C)		
Year	**2000**	**2003**	**2012**	**2000**	**2003**	**2012**	**2000**	**2003**	**2012**	**2000**	**2003**	**2012**
MST	20.5	21.3	21.9	21.0	21.6	22.4	21.6	22.3	23.0	21.0	21.7	22.4
MSP	100.9	142.5	134.6	116.1	166.5	151.0	65.9	110.5	91.3	94.3	139.8	125.6
SWB	-20.5	-11.3	7.3	-7.4	12.4	21.7	-60.6	-45.1	-41.6	-29.5	-14.7	-4.2

Table A3: Transect length, inventoried forest area, number of inventory plots, sampling intensity (plot area per forest area in %), and total sampled areas in the three transects (A–C). All plots had a size of 314.2 m^2.

Transect	Length [m]	Area [ha]	Plots [n]	Samp. int. [%]	Samp. area [m^2]
A	6694	357.7	90	0.79	28278 m^2
B	6696	352.5	90	0.79	28278 m^2
C	7465	405.0	100	0.76	31416 m^2

Table A4: Basal area in percent of stand total (BA_{rel}), stem density (N_{tot}), mean DBH, mean tree height (H), basal area in absolute figures ($BA_{tot;}$) for each tree species averaged over all plots for transects A–C. Given are also the number of inventory plots (size = 314.2 m²) per transect (n). Coniferous species (*Larix decidua*, *Pinus spp*. and *Picea abies*) and other rarely encountered broadleaf tree species (*Acer tataricum*, *Q. robur, Salix spp*., *T. cordata*) were categorized into the classes Other coniferous or Other deciduous.

	Transect A (n=90)					**Transect B (n=90)**					**Transect C (n=100)**				
Species	**BA_{rel} (%)**	**N_{tot} (ha^{-1})**	**DBH (cm)**	**H (m)**	**BA_{tot} ($m^2\ ha^{-1}$)**	**BA_{rel} (%)**	**N_{tot} (ha^{-1})**	**DBH (cm)**	**H (m)**	**BA_{tot} ($m^2\ ha^{-1}$)**	**BA_{rel} (%)**	**N_{tot} (ha^{-1})**	**DBH (cm)**	**H (m)**	**BA_{tot} ($m^2\ ha^{-1}$)**
A. campestre	0.2	5.0	13.3	16.2	0.1	0.1	1.5	17.7	19.3	0.0	0.3	4.8	14.8	9.7	0.1
A. platanoides	1.4	11.7	22.7	22.6	0.6	0.4	2.9	25.1	25.2	0.2	0.4	2.2	27.9	19.9	0.2
A. pseudoplatanus	1.3	7.8	27.4	21.0	0.5	0.1	0.7	22.5	20.3	0.0	1.3	7.0	28.3	19.9	0.6
Betula spp.						2.2	18.3	24.3	22.4	0.9					
C. betulus	5.7	111.1	15.0	17.0	2.3	11.0	159.9	17.6	18.4	4.5	3.8	70.0	14.7	12.8	1.6
C. orientalis											1.1	44.6	10.8	9.1	0.5
F. excelsior											0.1	1.3	16.9	13.4	0.0
F. ornus											3.0	86.9	12.6	10.4	1.2
F. sylvatica	27.1	128.0	29.7	29.2	10.7	42.5	244.0	26.1	26.2	17.3	35.2	263.6	22.6	22.9	14.7
Other coniferous	1.9	21.2	20.3	23.3	0.8	0.9	17.6	16.1	17.9	0.4	0.0	2.9	8.6	7.3	0.0
Other deciduous	0.3	1.8	19.8	17.1	0.1	0.3	2.6	21.6	20.9	0.1					
P. avium	1.8	18.4	20.1	20.3	0.7	1.4	10.6	24.3	23.8	0.6					
Populus spp.	0.0	1.1	10.5	6.4	0.0	2.9	11.7	32.2	28.5	1.2	0.2	1.9	23.5	18.8	0.1
Q. cerris	3.6	20.5	28.7	22.6	1.4	3.2	9.5	41.0	31.2	1.3	0.7	4.5	26.8	13.5	0.3
Q. frainetto	1.8	11.7	26.7	21.5	0.7	0.7	1.5	44.5	20.6	0.3	2.4	18.1	24.6	14.8	1.0
Q. petraea	26.9	163.0	26.8	25.2	10.6	9.3	46.1	30.5	25.0	3.8	26.0	172.5	26.6	18.3	10.8
R. pseudoacacia						0.5	6.2	20.0	20.1	0.2	0.5	6.0	19.5	12.2	0.2
S. torminalis	0.3	5.0	15.1	12.9	0.1	0.1	1.8	11.2	9.4	0.0	0.5	9.5	15.2	11.5	0.2
T. tomentosa	27.4	316.2	19.1	21.3	10.8	22.7	117.8	29.2	28.2	9.3	24.2	211.7	21.5	19.2	10.1
Ulmus spp.	0.3	3.9	18.0	25.1	0.1	1.7	6.2	28.1	25.0	0.7	0.3	3.5	19.3	14.1	0.1
Totals		**827.3**			**39.4**		**660.8**			**40.8**		**909.7**			**41.8**

Table A5: Basal area in percent of stand total (BA_{rel}), basal area in absolute figures (BA_{tot}), stem density in percent (N_{rel}) and stem density in absolute figures ($N_{tot;}$) for all vitality classes (vital, non-vital and dead) of trees averaged over all inventory plots for transects A–C. Given are also the number of inventory plots per transect (n).

	Transect A (n=90)				**Transect B (n=90)**				**Transect C (n=100)**			
Vitality	**BA_{rel} (%)**	**BA_{tot} ($m^2\ ha^{-1}$)**	**N_{rel} (%)**	**N_{tot} (ha^{-1})**	**BA_{rel} (%)**	**BA_{tot} ($m^2\ ha^{-1}$)**	**N_{rel} (%)**	**N_{tot} (ha^{-1})**	**BA_{rel} (%)**	**BA_{tot} ($m^2\ ha^{-1}$)**	**N_{rel} (%)**	**N_{tot} (ha^{-1})**
Dead	2.1	0.8	5.0	41.0	2.6	1.0	6.2	41.0	4.3	1.8	6.9	62.4
Non-vital	14.3	5.6	13.6	112.8	11.6	4.7	13.7	90.4	21.2	8.9	16.7	151.5
Vital	83.6	32.9	81.4	673.4	85.8	35.0	80.1	529.4	74.5	31.1	76.5	695.8
Total		**39.4**		**827.3**		**40.8**		**660.8**		**41.8**		**909.7**

Table A6: Basal area in percent of stand total (BA_{rel}), stem density (N_{tot}), mean DBH, mean tree height (H) and basal area in absolute figures (BA_{tot}) for all tree species pooled over three transects (A–C) for: moist mesic beech forests & low-elevation xeric beech forests (plots with BA_{rel} of *F. sylvatica* > 66 %), sub-humid / thermophilic oak forests (plots with BA_{rel} of *Quercus* species > 66 %), post-disturbance linden forests (plots with BA_{rel} of *T. tomentosa*: > 66 %), sub-humid mixed beech-oak-hornbeam forests, and all other forests. Given are also the number of inventory plots per forest type (n). Plots with an absolute basal area ($\sum BA_{tot;}$) < 10 m² ha^{-1} were classified as non-forests (n=15) and excluded. Coniferous species (*Larix decidua*, *Pinus spp.* and *Picea abies*) and other rarely encountered broadleaf tree species (*Acer tataricum*, *Q. robur*, *Salix spp.*, *T. cordata*) were categorized into the classes Other coniferous or Other deciduous.

	Moist mesic & "rear-edge" xeric beech forests (n=69)					**Sub-humid mixed beech-oak-hornbeam forests (n=106)**					**Sub-humid / thermophilic oak forests (n=52)**					**Post-disturbance linden forests (n=38)**				
Species	**BA_{rel} (%)**	**N_{tot} (ha^{-1})**	**DBH (cm)**	**H (m)**	**BA_{tot} (m² ha^{-1})**	**BA_{rel} (%)**	**N_{tot} (ha^{-1})**	**DBH (cm)**	**H (m)**	**BA_{tot} (m² ha^{-1})**	**BA_{rel} (%)**	**N_{tot} (ha^{-1})**	**DBH (cm)**	**H (m)**	**BA_{tot} (m² ha^{-1})**	**BA_{rel} (%)**	**N_{tot} (ha^{-1})**	**DBH (cm)**	**H (m)**	**BA_{tot} (m² ha^{-1})**
A. campestre	0.0	0.5	16.8	15.6	0.0	0.3	5.1	17.3	15.5	0.1	0.2	5.5	11.8	10.5	0.1	0.1	5.0	10.1	14.4	0.0
A. platanoides	0.7	4.6	29.4	26.8	0.3	1.0	6.9	24.6	21.6	0.4	0.4	4.9	18.9	19.7	0.1	0.4	5.9	18.9	20.4	0.2
A. pseudoplatanus	0.4	2.8	26.6	24.3	0.2	2.0	10.8	28.1	19.5	0.8	0.1	0.6	33.2	22.8	0.1	0.1	0.8	20.0	21.1	0.0
Betula spp.	0.5	3.7	28.8	28.2	0.2	1.4	11.1	25.3	23.2	0.6	0.0	0.6	15.0	-	0.0					
C. betulus	1.4	20.3	18.3	18.4	0.6	13.3	202.1	16.8	18.0	5.5	3.2	68.6	14.1	13.4	1.2	3.8	117.3	13.3	14.5	1.9
C. orientalis						0.6	19.5	11.5	10.1	0.2	0.9	36.1	10.4	8.1	0.3	0.2	13.4	9.5	8.7	0.1
F. excelsior						0.1	1.2	16.9	13.4	0.0										
F. ornus	0.1	2.3	13.3	10.0	0.0	1.9	50.4	13.2	11.0	0.8	1.4	49.0	11.3	8.8	0.5	0.5	16.8	12.4	12.2	0.2
F. sylvatica	89.1	559.6	26.8	28.1	41.1	23.6	154.7	23.8	24.9	9.7	2.9	40.4	16.0	16.9	1.1	3.3	46.9	18.0	22.5	1.6
Other coniferous						2.3	32.4	18.4	21.5	1.0										
Other deciduous	0.1	0.9	28.5	32.8	0.1	0.2	4.8	14.8	16.3	0.1	0.4	1.2	24.1	21.4	0.1	0.0	0.8	7.0	7.3	0.0
P. avium	0.5	1.8	40.7	29.6	0.3	1.6	16.2	20.5	21.7	0.6	0.5	4.9	16.7	14.0	0.2	1.2	12.6	22.9	23.2	0.6
Populus spp.	0.3	2.3	26.8	22.4	0.1	2.3	8.1	34.6	29.0	1.0	0.2	3.1	16.7	18.2	0.1	0.0	0.8	19.0	20.7	0.0
Q. cerris	0.2	0.5	44.3	31.8	0.1	1.4	8.4	27.2	22.4	0.6	10.6	42.2	33.4	23.4	4.0					
Q. frainetto						1.0	2.4	43.3	20.8	0.4	7.4	52.6	24.6	16.8	2.8					
Q. petraea	3.1	17.1	31.4	25.9	1.4	19.1	119.5	26.9	21.5	7.9	66.2	360.5	27.9	22.4	25.0	7.7	88.0	21.8	21.2	3.7
R. pseudoacacia						1.0	10.5	20.0	14.7	0.4	0.0	0.6	10.0	9.7	0.0					
S. torminalis	0.0	0.5	19.3	12.1	0.0	0.4	6.6	16.1	12.9	0.2	0.5	12.2	13.0	10.4	0.2	0.1	4.2	12.8	11.2	0.1
T. tomentosa	3.3	17.5	30.0	23.6	1.5	24.8	190.7	22.7	22.4	10.2	5.1	49.0	19.9	17.7	1.9	82.4	917.2	21.3	23.7	39.9
Ulmus spp.	0.2	1.8	26.7	26.6	0.1	1.6	8.7	23.6	20.1	0.7						0.2	5.0	16.2	23.4	0.1
Total		**636.2**			**46.2**		**869.3**			**41.3**		**733.3**			**37.8**		**1234.7**			**48.5**

Table A7: Results (means and SD of the pooled data from the three depths 0–10 cm, 10–20 cm and 20–40 cm) of soil physical and chemical analyses in the different forest types in the transects A, B, and C with the corresponding sample size (n). Soil texture (contents of sand, silt and clay) and water storage capacity at a matric potential > -1.5 (pAWC) were only determined for the 20–40 cm layer. Abbreviations: Soil texture = dominant soil texture class, Sand = Sand content [in %], Silt= Silt content [in %], Clay = Clay content [in %], pAWC = Plant-available water capacity in [%], pH= pH in H_2O, B.D.= Bulk soil density [g cm^{-3}], SOC = soil organic carbon concentration [%], STN = soil total nitrogen concentration [%], P_{av} = resin-exchangeable P [µg g^{-1}], C / N = C / N ratio [g g^{-1}], Ca^{+2}_{ex} = $BaCl_2$-exchangeable Ca^{+2} pool [mol_c m^{-2}], K^+_{ex} = $BaCl_2$-exchangeable K^+ pool [mol_c m^{-2}], Mg^{+2}_{ex} = $BaCl_2$-exchangeable Mg^{+2} pool [mol_c m^{-2}], CEC = cation exchange capacity [µmol_c g^{-1}], BS = base saturation [%]. No soil analyses were conducted in the post-disturbance linden forests.

	Moist mesic beech forests			**Low-elevation xeric beech forests**			**Sub-humid mixed beech-oak-hornbeam forests**			**Sub-humid / thermophilic oak forests**		
Transect	**A (n=3)**	**B (n=3)**	**C (n=4)**	**A (n=3)**	**B (n=3)**	**C (n=3)**	**A (n=5)**	**B (n=7)**	**C (n=8)**	**A (n=5)**	**B (n=3)**	**C (n=3)**
Soil texture	sandy silt	sandy silt	high-silty sand / silty-loamy sand	sandy silt	sandy silt	medium loamy sand	sandy silt / silty loam	sandy silt / silty-loamy sand	high-medium silty sand	sandy silt / poor silty sand	silty-loamy sand	high-medium silty sand
Clay	0.02 (0.03)	0.08 (0.04)	0.09 (0.07)	0.01 (0.01)	0.01 (0.02)	0.10 (0.07)	0.07 (0.09)	0.09 (0.10)	0.05 (0.05)	0.06 (0.08)	0.20 (0.09)	0.01 (0.01)
Silt	0.73 (0.08)	0.56 (0.10)	0.44 (0.03)	0.63 (0.07)	0.66 (0.07)	0.21 (0.14)	0.53 (0.14)	0.72 (0.20)	0.41 (0.14)	0.75 (0.11)	0.49 (0.14)	0.38 (0.04)
Sand	0.25 (0.05)	0.36 (0.08)	0.48 (0.06)	0.36 (0.06)	0.33 (0.06)	0.68 (0.09)	0.4 (0.19)	0.19 (0.13)	0.54 (0.11)	0.19 (0.11)	0.31 (0.23)	0.61 (0.03)
pAWC	0.30 (0.01)	0.30 (0.04)	0.29 (0.11)	0.26 (0.03)	0.35 (0.12)	0.25 (0.03)	0.23 (0.04)	0.34 (0.07)	0.27 (0.04)	0.33 (0.06)	0.33 (0.06)	0.27 (0.02)
B.D.	1.15 (0.17)	1.05 (0.18)	0.85 (0.15)	1.20 (0.20)	0.81 (0.23)	0.91 (0.16)	1.36 (0.13)	1.01 (0.22)	0.96 (0.18)	1.24 (0.17)	1.11 (0.13)	1.05 (0.08)
pH	5.20 (0.26)	5.05 (0.42)	5.03 (0.34)	4.96 (0.25)	4.72 (0.15)	4.60 (0.16)	5.19 (0.46)	5.28 (0.4)	5.27 (0.30)	5.03 (0.29)	4.91 (0.17)	5.03 (0.23)
SOC	1.45 (0.70)	1.68 (1.02)	2.16 (0.95)	1.26 (0.70)	1.26 (0.74)	1.56 (0.80)	1.37 (0.67)	1.26 (0.58)	1.53 (0.96)	1.44 (0.90)	1.12 (0.55)	0.99 (0.44)
STN	0.12 (0.06)	0.14 (0.08)	0.16 (0.07)	0.09 (0.05)	0.10 (0.05)	0.07 (0.03)	0.12 (0.06)	0.12 (0.05)	0.11 (0.07)	0.13 (0.07)	0.12 (0.05)	0.07 (0.02)
P_{av}	3.46 (2.16)	2.25 (1.07)	33.36 (22.07)	1.63 (0.92)	0.67 (0.50)	2.49 (1.36)	7.44 (5.64)	8.13 (11.76)	16.44 (18.2)	6.49 (5.46)	1.26 (0.60)	3.08 (1.92)
C/N	11.87 (1.23)	11.60 (2.98)	14.10 (3.12)	13.46 (1.27)	12.77 (1.80)	21.78 (2.36)	10.96 (1.01)	10.31 (2.29)	13.79 (1.74)	10.94 (1.09)	9.29 (0.97)	14.27 (2.15)
Ca^{2+}_{ex}	4.34 (1.35)	4.19 (3.90)	2.92 (1.73)	1.04 (0.54)	0.33 (0.23)	0.24 (0.15)	3.7 (3.38)	6.54 (4.17)	2.32 (2.05)	2.46 (2.44)	2.78 (2.63)	1.22 (0.47)
K^{+}_{ex}	0.18 (0.09)	0.08 (0.02)	0.12 (0.10)	0.12 (0.03)	0.07 (0.03)	0.09 (0.05)	0.20 (0.13)	0.11 (0.07)	0.19 (0.18)	0.23 (0.19)	0.12 (0.06)	0.11 (0.06)
Mg^{2+}_{ex}	1.02 (0.48)	0.63 (0.32)	0.56 (0.43)	0.43 (0.22)	0.18 (0.15)	0.06 (0.03)	0.70 (0.53)	1.83 (1.09)	0.55 (0.39)	0.95 (0.49)	1.28 (1.07)	0.74 (0.36)
CEC	85.7 (23.3)	96.7 (32.6)	86.0 (27.0)	50.2 (14.6)	60.9 (13.0)	34.7 (13.6)	56.1 (21.1)	123.6 (44.8)	58.6 (33.8)	66.5 (16.5)	91.08 (26.0)	51.5 (5.0)
B.S.	58.2 (17.6)	44.5 (31.9)	48.2 (26.0)	28.5 (14.5)	11.6 (6.8)	13.8 (7.2)	52.2 (30.0)	59.3 (29.8)	52.9 (24.6)	41.1 (24.2)	35.62 (22.8)	39.0 (15.6)

Table A8: Climatic conditions in the period 2000–2016 in the three transects A, B and C with mean summer precipitation (MSP) in mm year^{-1}, mean summer temperature (MST) in °C, mean maximum summer temperature (MST_{max}) in °C, mean summer water balance (SWB) in mm year^{-1} as well as the three-month SPEI scores for August (A_3) and summer (pooled SPEI scores for June, July, August (JJA_3)) and six-month SPEI scores for August (A_6), and summer (pooled SPEI scores for June, July, August (JJA_6)). The categorization of drought severity follows the classification scheme of (Nam et al., 2015). Climate data extracted from the CHELSA climate data base (Karger et al., 2017).

	Transect A								**Transect B**								**Transect C**							
	Climate data				**SPEI scores**				**Climate data**				**SPEI scores**				**Climate data**				**SPEI scores**			
Year	MSP	MST	MST_{max}	SWB	A_3	JJA_3	A_6	JJA_6	MSP	MST	MST_{max}	SWB	A_3	JJA_3	A_6	JJA_6	MSP	MST	MST_{max}	SWB	A_3	JJA_3	A_6	JJA_6
2000	**99**	**20**	**26**	**-20**	**-2.09**	**-2.14**	**-1.93**	**-1.98**	**116**	**21**	**27**	**-7**	**-2.16**	**-2.21**	**-2.05**	**-2.07**	**67**	**22**	**27**	**-61**	**-2.14**	**-2.19**	**-2.11**	**-2.01**
2001	296	20	24	163	1.09	0.90	0.88	0.94	355	20	25	221	1.12	1.01	0.94	1.00	213	20	25	74	0.60	0.62	0.49	0.58
2002	244	21	25	103	0.15	-0.69	-0.84	-1.49	282	21	26	141	0.09	-0.70	-0.83	-1.45	195	21	26	53	0.27	-0.58	-0.64	-1.31
2003	**143**	**21**	**27**	**-11**	**-1.73**	**-1.75**	**-1.99**	**-1.84**	**167**	**22**	**27**	**12**	**-1.72**	**-1.79**	**-2.01**	**-1.90**	**110**	**22**	**28**	**-45**	**-1.62**	**-1.62**	**-1.87**	**-1.65**
2004	238	19	24	118	0.19	0.01	0.31	0.34	277	20	25	157	0.11	-0.07	0.26	0.25	188	20	25	65	0.24	0.12	0.27	0.28
2005	332	19	23	247	1.72	0.80	1.68	1.16	397	19	24	312	1.76	0.76	1.63	1.16	288	20	24	202	2.14	1.02	1.70	1.33
2006	299	19	24	235	1.01	0.70	1.50	1.28	349	20	25	284	0.97	0.53	1.46	1.20	240	20	25	173	1.08	0.41	1.32	1.10
2007	205	21	27	161	-0.97	-1.09	-1.02	-0.96	253	22	27	206	-0.82	-1.04	-0.88	-0.85	177	22	28	127	-0.76	-0.93	-0.81	-0.78
2008	257	20	26	221	0.13	0.37	0.29	0.22	300	21	26	264	0.08	0.34	0.32	0.26	185	21	27	141	-0.40	-0.19	-0.15	-0.27
2009	229	20	26	189	-0.29	-0.73	-1.16	-0.97	293	21	26	253	0.05	-0.49	-0.95	-0.76	208	21	27	164	0.19	-0.52	-0.86	-0.70
2010	300	20	25	248	1.09	1.79	1.74	2.09	355	21	26	302	1.07	1.69	1.58	2.00	222	21	26	166	0.80	1.32	1.22	1.76
2011	183	20	25	95	-0.84	-0.81	-1.25	-1.23	230	21	26	140	-0.72	-0.71	-1.18	-1.11	150	21	27	58	-0.71	-0.75	-1.17	-1.10
2012	**135**	**22**	**28**	**7**	**-1.98**	**-1.12**	**-1.61**	**-1.11**	**150**	**22**	**28**	**22**	**-2.05**	**-1.04**	**-1.47**	**-0.88**	**91**	**23**	**29**	**-42**	**-2.12**	**-0.92**	**-1.37**	**-0.66**
2013	154	21	26	12	-1.32	-0.64	-0.02	0.51	192	21	26	52	-1.19	-0.55	-0.04	0.40	136	22	27	-11	-1.02	-0.51	-0.17	0.30
2014	262	20	25	119	0.37	0.70	0.51	0.23	327	20	25	185	0.63	0.97	0.91	0.61	235	21	26	91	0.92	1.33	1.31	0.95
2015	191	22	27	36	-1.20	-1.19	-1.21	-1.16	215	22	28	59	-1.27	-1.21	-1.14	-1.02	137	22	28	-21	-1.37	-1.30	-1.07	-0.83
2016	339	20	26	212	1.28	0.79	0.74	0.87	387	21	26	262	1.23	0.92	0.96	1.04	235	21	27	105	0.67	0.58	0.75	0.90

Drought classification

🟩	no drought (SPEI > 0.0)	🟨	mild drought (0.0 ≥ SPEI > -1.0)	🟧	moderate drought (-1.0 ≥ SPEI > -1.5)	🟥	severe drought (-1.5 ≥ SPEI > -2.0)	🟫	extreme drought (-2.0 ≥ SPEI)

Table A9: Results of Pearson correlation analyses for the relation of RWI for the 1940–2016 period with the climate variables SWB, MST and MSP of the current and previous year, respectively, for the five tree species (and two site types of beech) for all three transects pooled. Species (SP), sampled trees (Trees), Pearson correlation coefficient (r), P-value (P) as well as the lower and upper 95 % confidence interval limits of r (CF-L and CF-U). FM = *F. sylvatica* (mesic), FX = *F. sylvatica* (xeric), QP = *Q. petraea*, TT = *T. tomentosa*, QC = *Q. cerris* and QF = *Q. frainetto*. SWB – soil water balance, MST – mean summer temperature, MSP – mean summer precipitation.

		RWI ~ current SWB				**RWI~ current MST**				**RWI ~ current MSP**			
SP	**Trees**	**r**	**P**	**CF-L**	**CF-U**	**r**	**P**	**CF-L**	**CF-U**	**r**	**P**	**CF-L**	**CF-U**
FM	153	0.41	< 0.01	0.29	0.51	-0.26	< 0.01	-0.38	-0.13	0.38	< 0.01	0.26	0.48
FX	82	0.33	< 0.01	0.21	0.44	-0.25	< 0.01	-0.37	-0.12	0.25	< 0.01	0.13	0.37
TT	94	0.41	< 0.01	0.30	0.51	-0.22	< 0.01	-0.34	-0.09	0.41	< 0.01	0.30	0.51
QC	94	0.30	< 0.01	0.18	0.41	-0.17	< 0.05	-0.29	-0.04	0.32	< 0.01	0.20	0.43
QP	150	0.20	< 0.01	0.07	0.32	-0.11	0.08	-0.24	0.01	0.25	< 0.01	0.13	0.37
QF	92	0.25	< 0.01	0.13	0.37	-0.18	< 0.05	-0.30	-0.05	0.28	< 0.01	0.15	0.39
		RWI ~ previous SWB				**RWI ~ previous MST**				**RWI ~ previous MSP**			
SP	**Trees**	**r**	**P**	**CF-L**	**CF-U**	**r**	**P**	**CF-L**	**CF-U**	**r**	**P**	**CF-L**	**CF-U**
FM	153	0.33	< 0.01	0.21	0.44	-0.21	< 0.01	-0.33	-0.08	0.33	< 0.01	0.21	0.44
FX	82	0.45	< 0.01	0.34	0.55	-0.26	< 0.01	-0.38	-0.14	0.43	< 0.01	0.32	0.53
TT	94	0.25	< 0.01	0.12	0.37	-0.15	< 0.05	-0.27	-0.02	0.27	< 0.01	0.15	0.39
QC	94	0.23	< 0.01	0.11	0.35	-0.13	0.05	-0.25	0.00	0.27	< 0.01	0.15	0.39
QP	150	-0.04	0.57	-0.17	0.09	-0.01	0.93	-0.13	0.12	0.05	0.47	-0.08	0.18
QF	92	0.16	< 0.05	0.04	0.29	-0.10	0.14	-0.22	0.03	0.18	< 0.01	0.05	0.30

Table A10: Number of sampled trees (Trees) averaged over the three transects with mean (SD) basal area increment (BAI in $cm^2\ yr^{-1}$) in the five years reference period (left side) and two years reference period (right side) before and after the 2000, 2003 and 2012 drought periods for the five species (SP) (and two site types of beech). Significant differences between growth in the pre-drought, drought and post-drought periods are indicated with different small letters. Species are abbreviated as: FM = *F. sylvatica* (mesic), FX = *F. sylvatica* (xeric), QP = *Q. petraea*, TT = *T. tomentosa*, QC = *Q. cerris* and QF = *Q. frainetto*.

		5 years reference						**2 years reference**					
SP	**Trees**	**1995–1999**		**2000**		**2001–2006**		**1997–1999**		**2000**		**2001–2002**	
FM	153	30.2 (14.9)	a	16.5 (8.0)	b	22.1 (12.4)	c	31.4 (16.8)	a	16.5 (8.0)	b	15.5 (11.4)	c
FX	80	22.6 (11.4)	a	15.4 (6.7)	b	15.3 (8.1)	b	24.8 (12.3)	a	15.4 (6.7)	b	10.8 (6.8)	c
TT	94	31.5 (14.7)	a	16.0 (7.3)	b	22.7 (11.9)	c	31.3 (16.2)	a	16.0 (7.3)	b	23.5 (14.8)	c
QC	94	20.1 (7.6)	a	15.5 (5.0)	b	15.9 (6.9)	b	20.7 (8.3)	a	15.5 (5.0)	b	15.7 (8.9)	b
QP	150	20.2 (8.5)	a	18.1 (7.7)	b	17.9 (8.4)	b	19.3 (9.1)	a	18.1 (7.7)	a	16.0 (8.6)	b
QF	92	16.0 (7.6)	a	12.9 (5.6)	b	12.9 (6.9)	b	17.0 (8.5)	a	12.9 (5.6)	b	12.5 (8.7)	b
SP	**Trees**	**1998–2002**		**2003**		**2004–2009**		**2001–2002**		**2003**		**2004–2006**	
FM	153	22.1 (11.2)	a	18.6 (11.5)	b	28.9 (14.7)	c	15.5 (11.4)	a	18.6 (11.5)	b	30.5 (16.9)	c
FX	80	17.3 (8.0)	a	14.2 (7.1)	b	22.1 (11.1)	c	10.8 (6.8)	a	14.2 (7.1)	b	20.4 (11.3)	c
TT	94	25.1 (12.8)	a	18.1 (7.6)	b	26.9 (12.4)	a	23.5 (14.8)	a	18.1 (7.6)	b	24.1 (13.0)	a
QC	94	17.7 (7.1)	a	14.8 (4.8)	b	18.3 (6.5)	a	15.7 (8.9)	a	14.8 (4.8)	a	16.5 (7.0)	a
QP	150	17.7 (7.7)	a	16.8 (8.2)	a	19.8 (8.3)	b	16.0 (8.6)	a	16.8 (8.2)	a	20.3 (9.5)	b
QF	92	14.4 (7.5)	a	12.8 (6.1)	a	14.1 (6.2)	a	12.5 (8.7)	a	12.8 (6.1)	a	13.4 (6.5)	a
SP	**Trees**	**2007–2011**		**2012**		**2013–2017**		**2009–2011**		**2012**		**2013–2015**	
FM	153	27.4 (13.6)	a	17.1 (10.0)	b	23.2 (13.0)	c	29.5 (16.8)	a	17.1 (10.0)	b	23.3 (13.8)	c
FX	80	22.8 (12.6)	a	14.1 (9.0)	b	15.6 (8.3)	b	24.0 (15.2)	a	14.1 (9.0)	b	14.7 (8.6)	b
TT	94	24.4 (11.6)	a	20.1 (10.6)	b	20.7 (13.5)	b	24.6 (14.1)	a	20.1 (10.6)	b	19.7 (15.5)	b
QC	94	19.1 (7.2)	a	15.6 (6.0)	b	18.9 (8.6)	a	20.9 (9.2)	a	15.6 (6.0)	b	18.7 (9.4)	ab
QP	150	18.8 (7.8)	a	16.3 (7.8)	b	20.4 (9.3)	a	17.5 (8.1)	a	16.3 (7.8)	a	21.4 (10.9)	b
QF	92	14.8 (6.1)	a	12.0 (5.7)	b	16.6 (7.8)	a	16.3 (7.2)	a	12.0 (5.7)	b	16.5 (9.8)	a

Figures

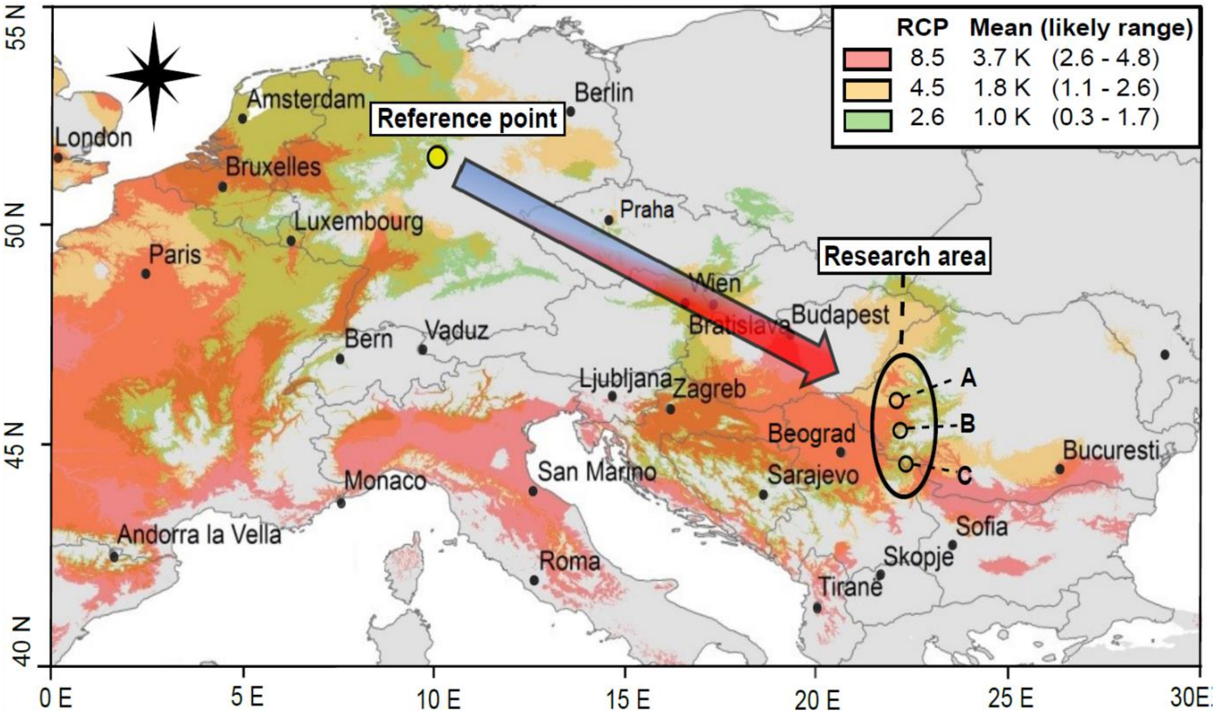

Figure A1: Climate warming projections for a beech forest reference point (German national forest inventory point 19288) in the centre of the distribution range of European beech (Central Germany). The red-, orange- and green-coloured regions of Europe are climate analogue for the climate in 50 years according to the IPCC (2013) scenarios: RCP 2.6, 4.5 and 8.5. They were identified following a principal component analysis representing Europe as a function of mean January temperature, mean summer temperature (June–August) and mean growing season precipitation (May–September). The projected values for these climate variables were matched within the ordination space with locations in Europe currently having these conditions. Depicted are the mean temperature increase (likely range) in Kelvin as well as the location of the study transects in western Romania, where A and B are located within the climate scenario RCP 2.6 and C is within the range of scenario RCP 4.5 (calculations done for the NEMKLIM project by C. Kölling, unpublished). For details on methodology, see Kölling and Zimmermann (2014).

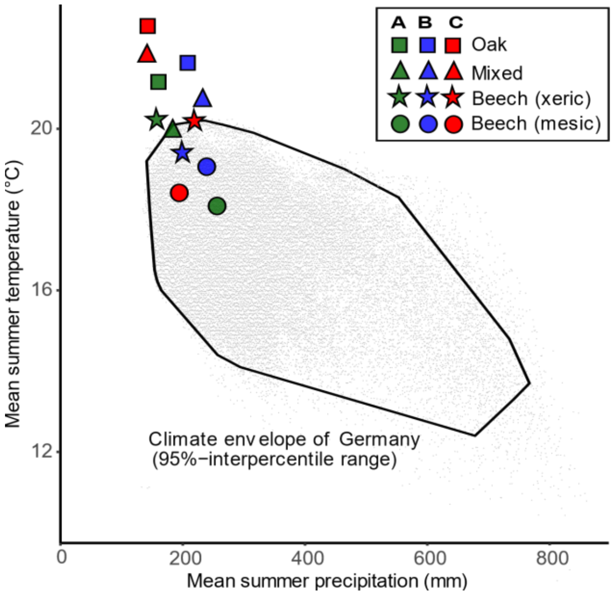

Figure A2: Climatic conditions in the three transects in Romania relative to the climate envelope of Germany in the centre of the distribution range of beech based on mean summer precipitation (June–August, average of 1940–2016) and mean summer temperature (June–August, average of 1940–2016). The symbols represent the climate data extracted for the mean locations of *F. sylvatica* forests in the mesic beech zone (elevation > 600 m), "rear edge" stands of *F. sylvatica* in the low-elevation xeric beech forests (elevation < 400 m), *Q. petraea* and *T. tomentosa* in the mixed forest zone (600 m > elevation > 350 m) and *Q. cerris* and *Q. frainetto* in the thermophilic oak zone (elevation < 350 m), given for the three transects. The depicted envelope gives the 95 % inter-percentile range for the climate stations of Germany. Data: CHELSA-gridded climate data (Karger et al., 2017).

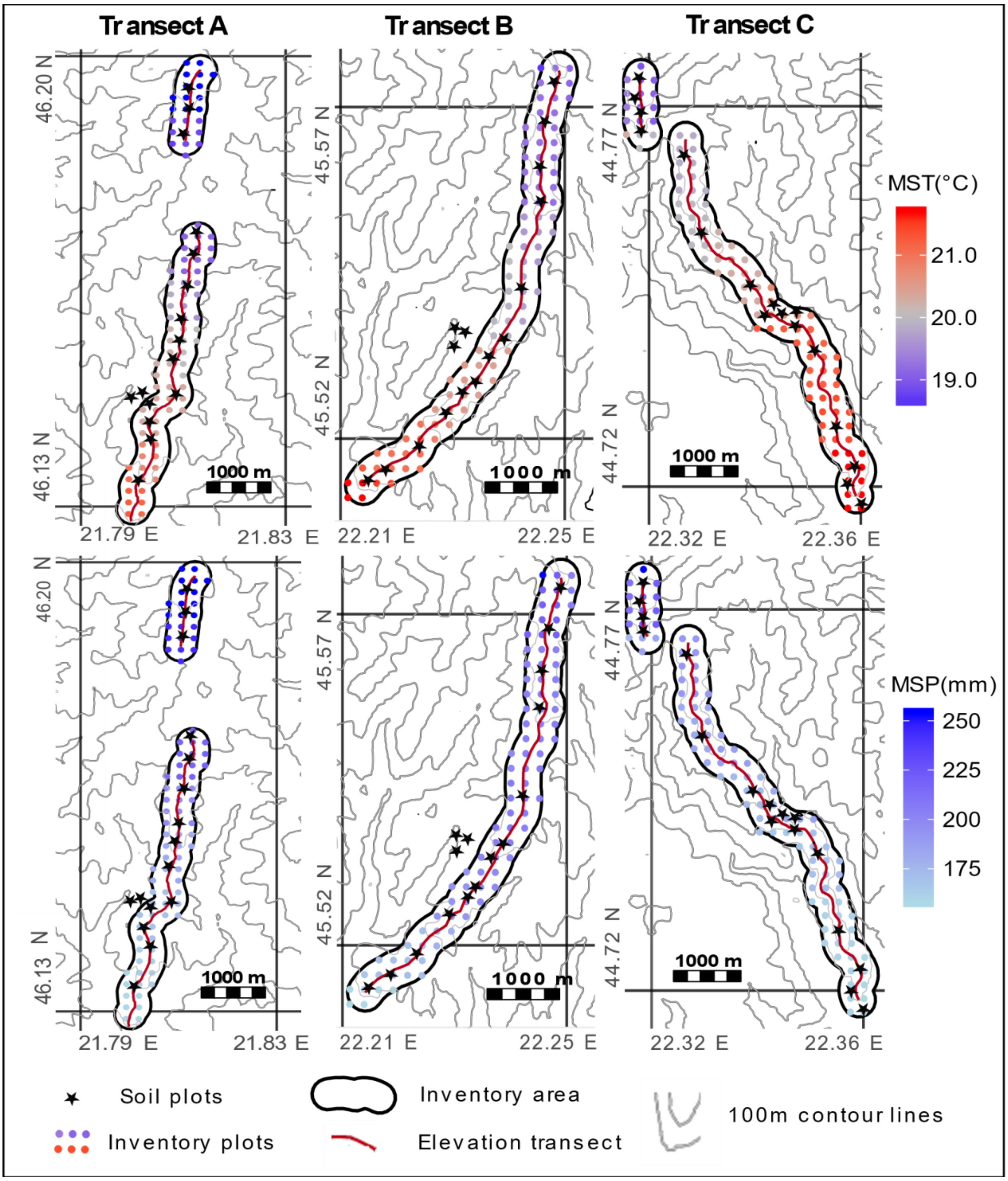

Figure A3: Location of the three elevation transects on the south-exposed slopes with the systematic forest inventory and soil sampling plots. The forest inventory plot symbols were coloured according to MST (top; in °C) and MSP (bottom; in mm year−1). The climatic data (average of 1940–2016) were derived from the CHELSAcruts climate data base (Karger et al., 2017) to display the climate gradient over elevation.

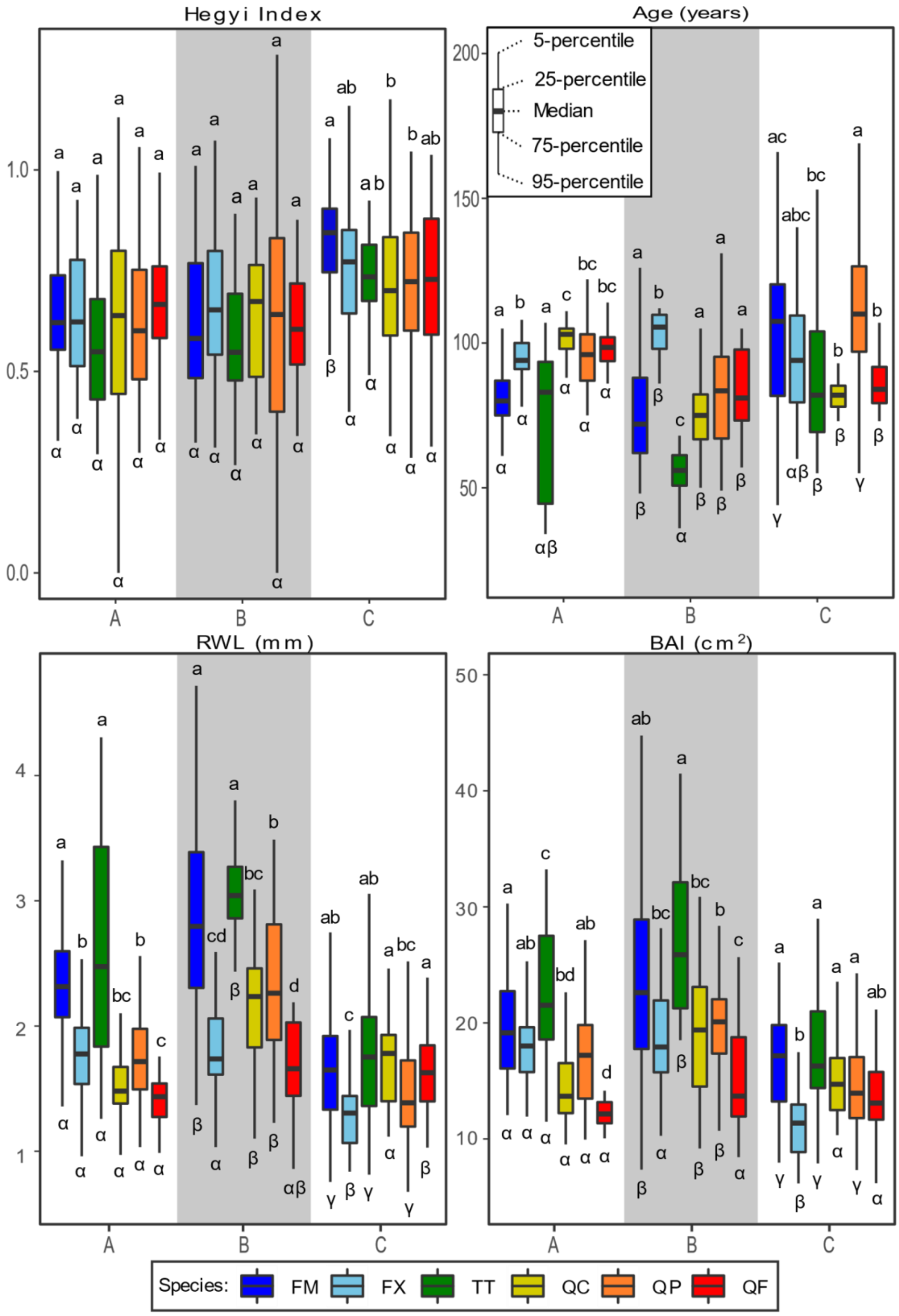

Figure A4: Heygi competition index (CI) (top left panel), stand ages (top right panel), ring width length (RWL) in mm (bottom left panel) and basal area increment (BAI) in cm^2 (bottom right panel) of the five species in the three transects A–C. Differences between species within a transect are indicated with small Latin letters above the boxplots and differences within species across transects with Greek letters below the boxplots. Differences for CI, RWL and BAI were tested with an ANOVA and a post-hoc Tukey test and differences in stand age were tested with a non-parametric K-S test and a post-hoc Wilcoxon Rank Test. All tests were at a 95% confidence level ($p \leq 0.05$). Species are abbreviated as: FM (dark blue) = *F. sylvatica* (mesic), FX (light blue) = *F. sylvatica* (xeric), TT (green) = *T. tomentosa*, QC (yellow) = *Q. cerris*, QP (orange) = *Q. petraea* and QF (red) = *Q. frainetto*.

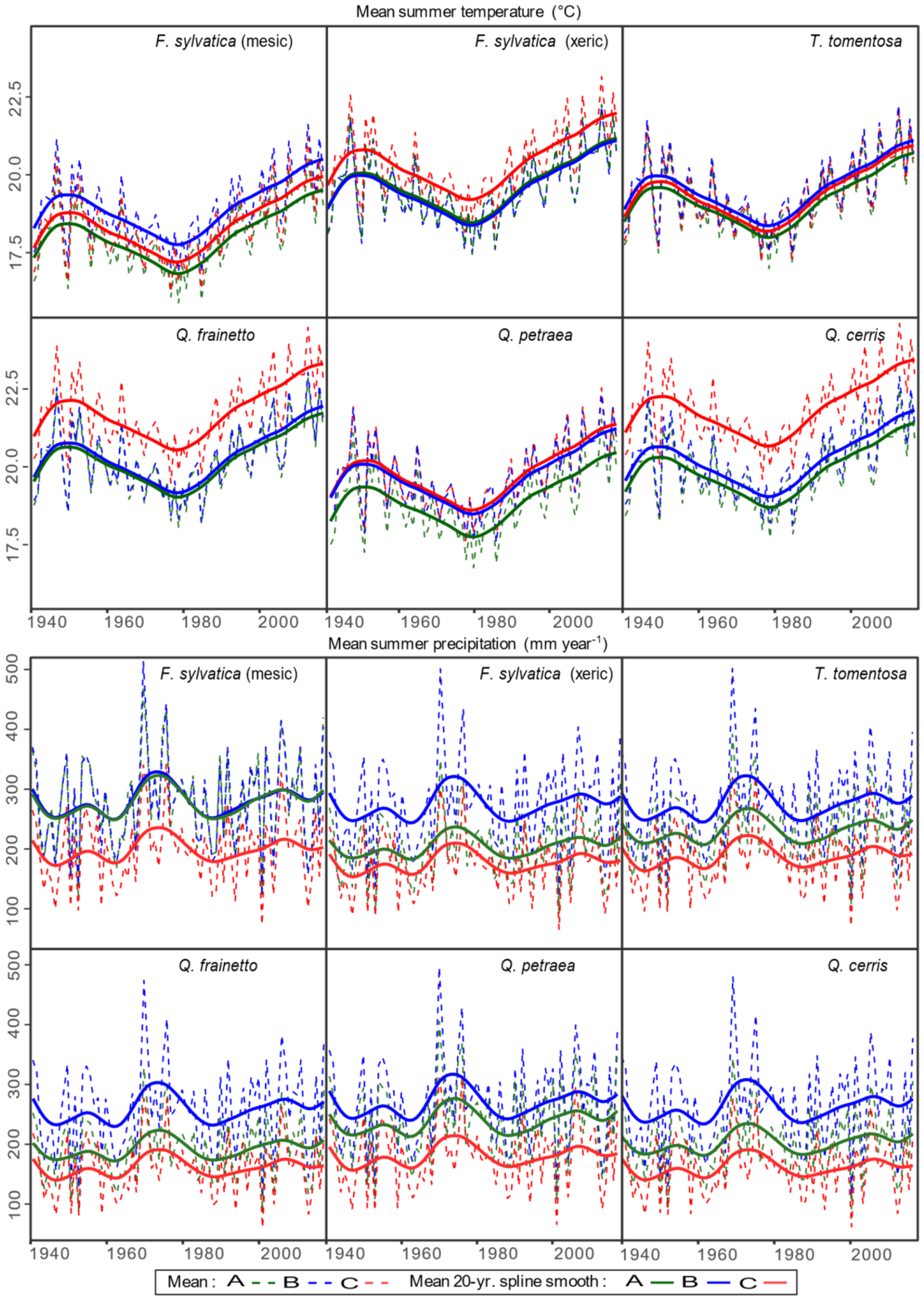

Figure A5: Mean summer temperature (dashed lines) and spline-smoothed (20-yr window) temperature curves (solid lines) (top panel) and mean summer precipitation (MSP, dashed lines) and spline-smoothed (20-yr window) MSP curves (solid lines) (bottom panel) for the stands of the five species (and two site types of beech) in transects A (green), B (blue) and C (red), as calculated from the CHELSAcruts climate data sets (Karger et al., 2017) for the period 1940–2016 using the mean coordinates of the transects as locality.

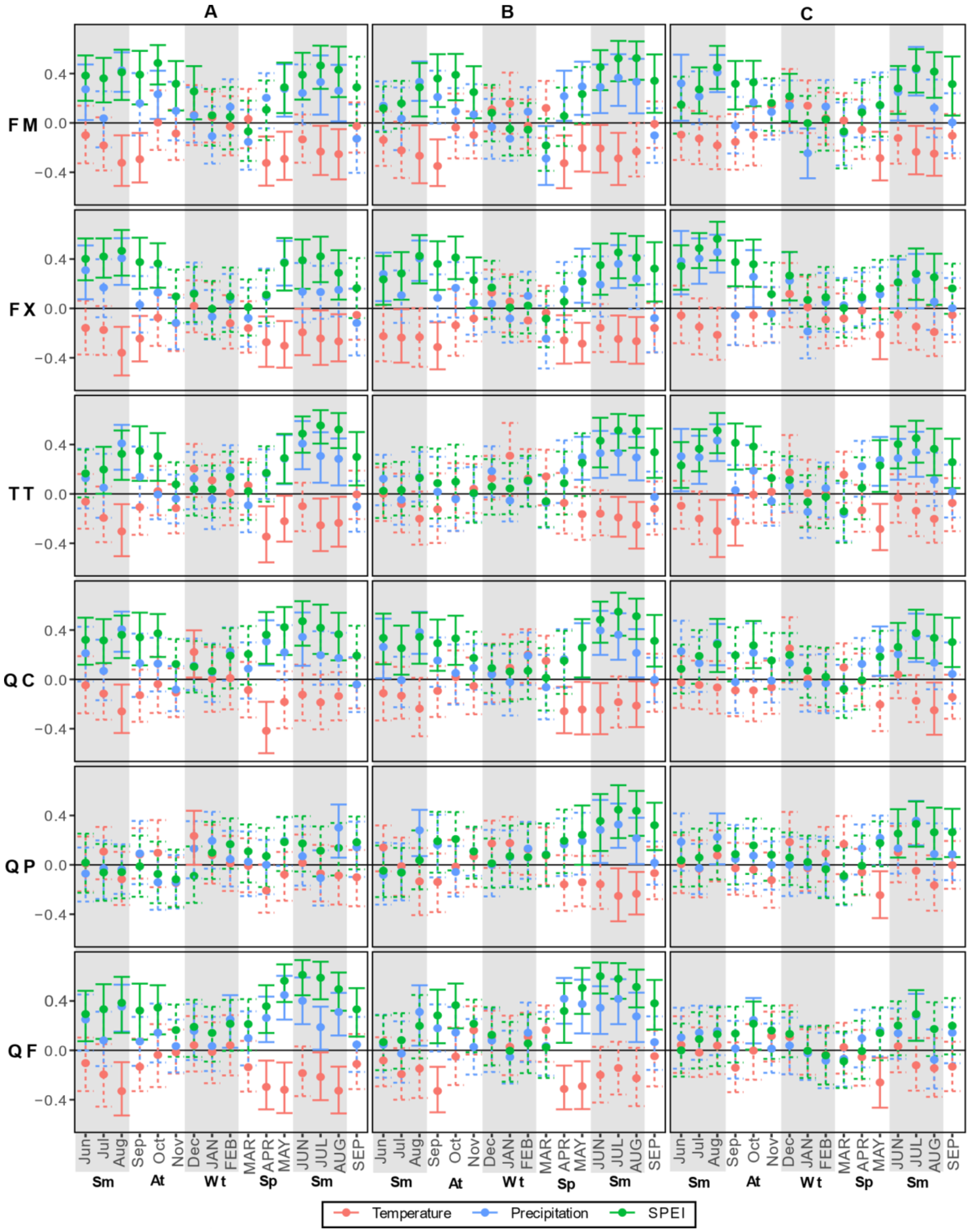

Figure A6: Correlation coefficients (r) of ring-width indices on the y-axis (spline detrending with 30 years moving window and 50 % frequency cut-off) for mean monthly temperature, precipitation and Standard Precipitation Evaporation Index (SPEI at 3-month scale) of the 6 previous-year months (Jun–Dec in minuscule letters) and 9 current-year month (JAN–SEP in capital letters) on the x-axis (averages for 1940–2016). The climate variables are depicted in colour, the transects are sorted from left to right (A–C) and the species sorted from top to bottom. Species are abbreviated as: FM = *F. sylvatica* (mesic), FX = *F. sylvatica* (xeric), TT = *T. tomentosa*, QC = *Q. cerris*, QP = *Q. petraea* and QF = *Q. frainetto*. Significant correlations are shown through solid whiskers for the 2.5% and 97.5% empirical 1000-fold bootstrapped confidence interval. The seasons: winter (Wt, December–February), spring (Sp, March–May) summer (Sm, June–August) and autumn (At, September–November) are also highlighted in the figure.

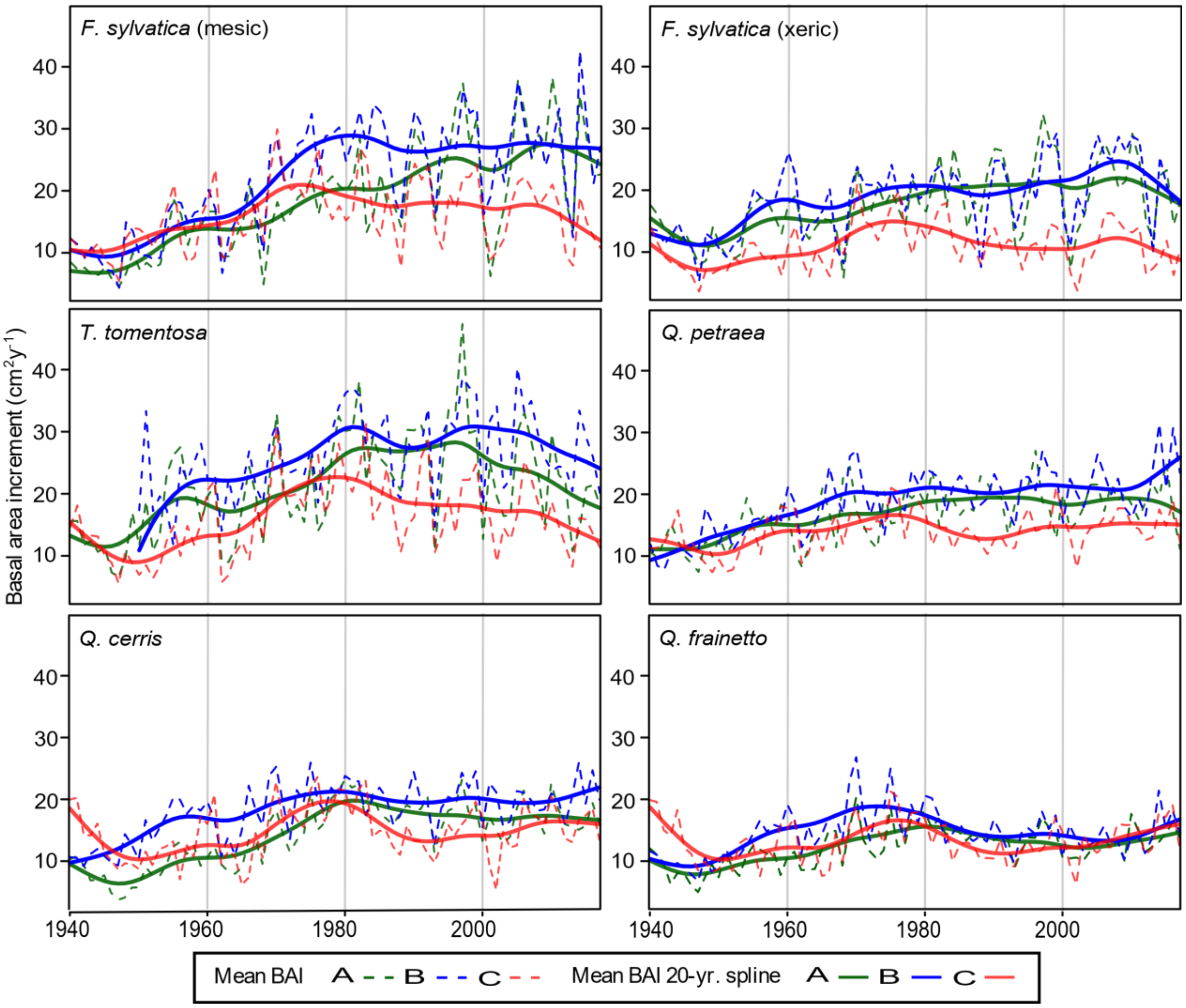

Figure A7: Time series of mean basal area increment (BAI) in cm^2 year^{-1} (dashed line) and smoothed (20-year window) BAI curve (solid line) of the five species (and two site types of beech) in the three transects during the period 1940–2017. *F. sylvatica* mesic: upper-elevation beech forests on south-exposed slope; *F. sylvatica* xeric: lower-elevation beech forests on northern slope.

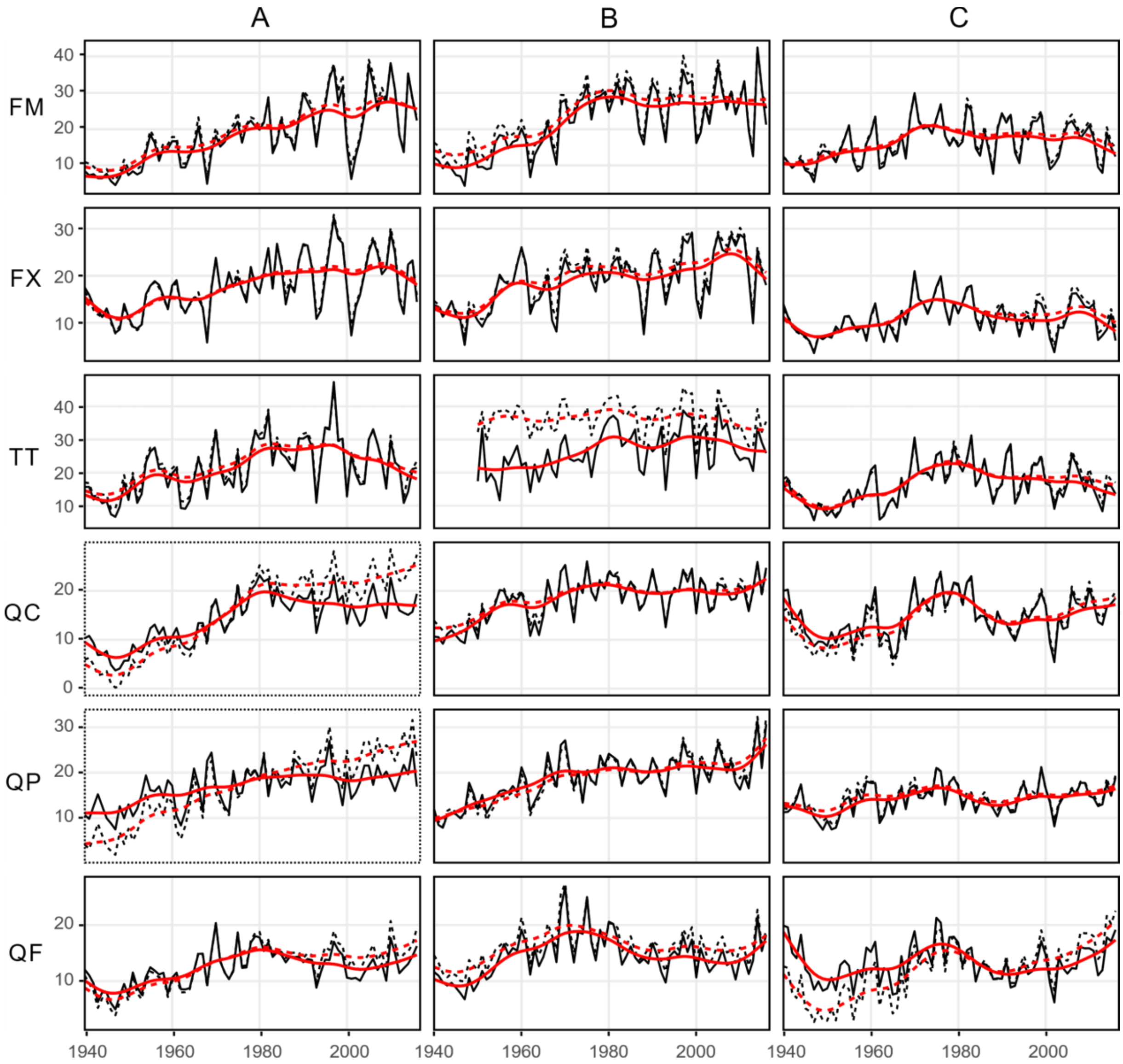

Figure A8: Site chronologies of basal area increment (BAI) in cm² year^{-1} (solid black line) and the smoothed (20-year window) BAI curve (red solid line) of the five species (and two site types of beech) in the three transects (A–C) during the period 1940–2016. Superimposed are the predicted BAI values (also in cm² year^{-1}) from the mixed linear model: BAI ~ SWB + tree-ring age (black dashed line) and the smoothed (20-year window) predicted BAI curve (red dashed line) for transects A–C for the period 1940–2016. Models and predictions were computed per tree individual and then averaged to site chronologies by the same procedure as the measured BAI chronologies (Tukey's bi-weight robust mean). Non-significant effects of SWB are indicated with dotted frames. Species are abbreviated as: FM = *F. sylvatica* (mesic), FX = *F. sylvatica* (xeric), QP = *Q. petraea*, TT = *T. tomentosa*, QC = *Q. cerris* and QF = *Q. frainetto*.

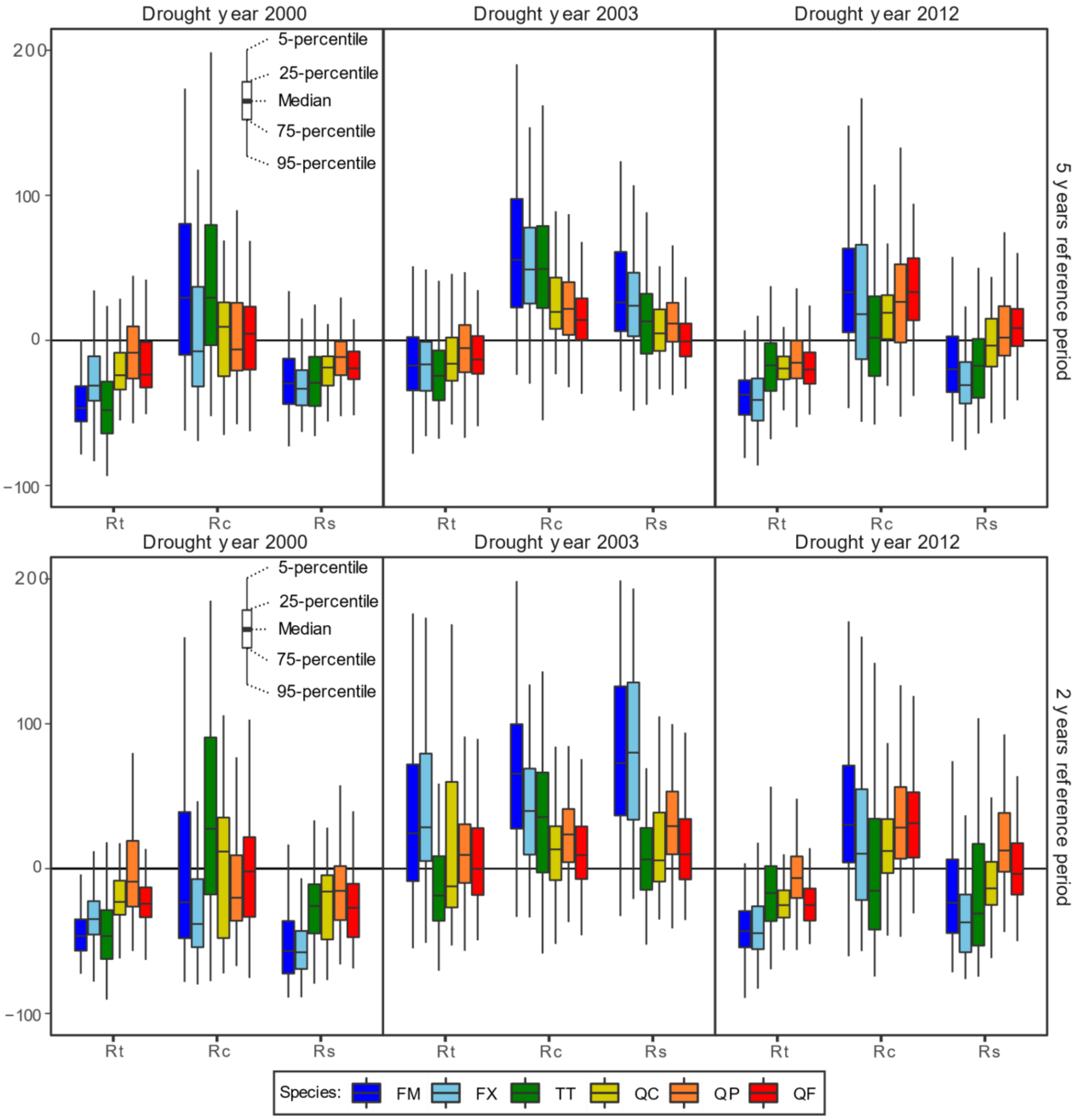

Figure A9: Drought responses: drought resistance (Rt: mean BAI drought / mean BAI pre-drought), drought recovery (Rc, mean BAI post-drought / mean BAI drought) and drought resilience (Rs, mean BAI post-drought / mean BAI pre-drought) for the individual summer-drought events 2000, 2003 and 2012 for the five species (and two site types of beech). The top panel shows the results for an analysis using a 5-year- and the bottom panel the results for a 2-year reference period. Species are abbreviated as: FM (dark blue) = *F. sylvatica* (mesic), FX (light blue) = *F. sylvatica* (xeric), TT (green) = *T. tomentosa*, QC (yellow) = *Q. cerris*, QP (orange) = *Q. petraea*, and QF (red)= *Q. frainetto*.

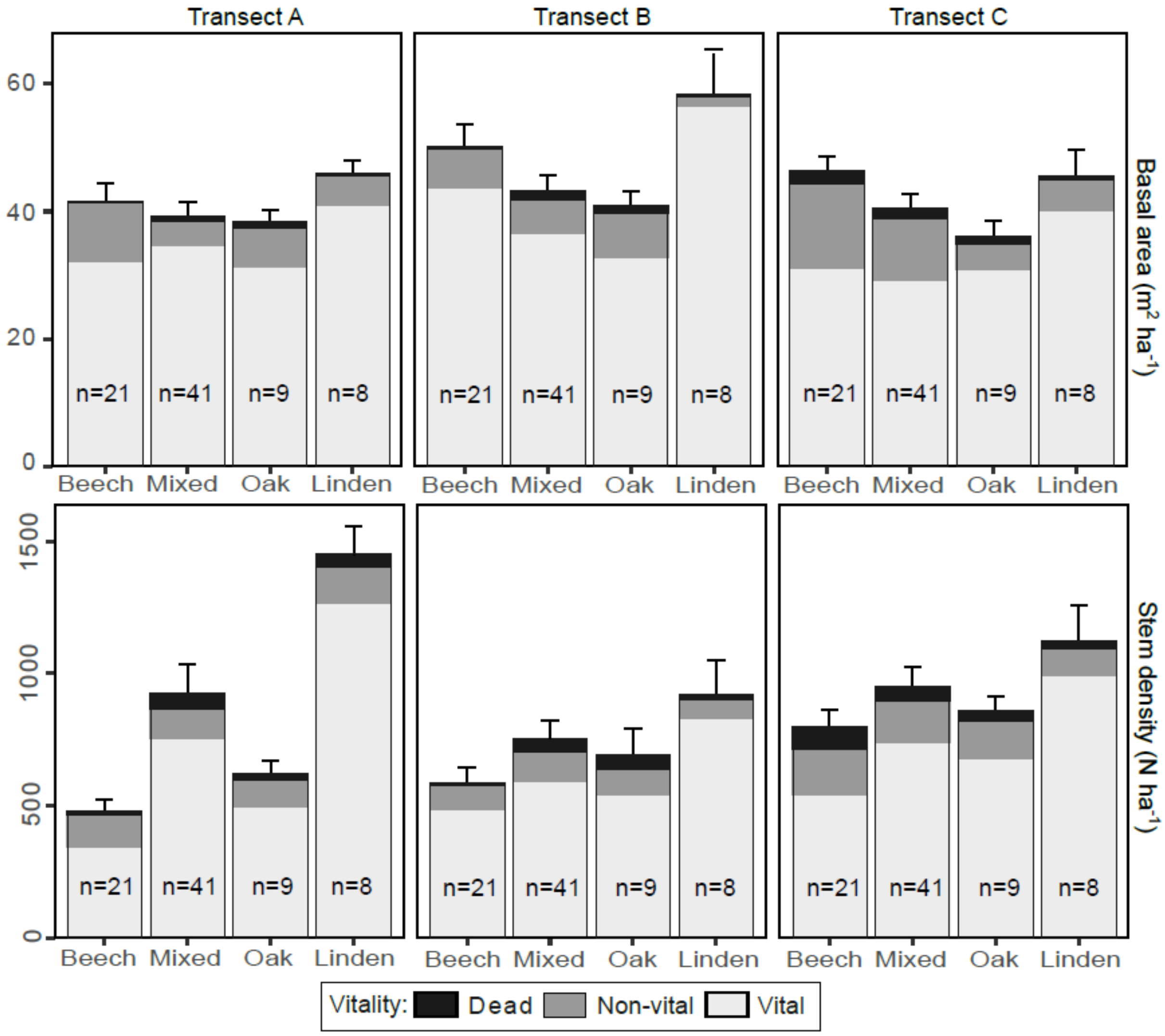

Figure A10: Means (whiskers = standard error) of basal area in m² ha^{-1} (top panels) and stem density in N ha^{-1} (bottom panels) for all vitality classes (vital, non-vital and dead) of trees for each transect (A,B,C) from left to right for: moist mesic beech forests & low-elevation xeric beech forests (plots with BA_{rel} of *F. sylvatica* > 66 %), sub-humid / thermophilic oak forests (plots with BA_{rel} of *Quercus* species > 66 %), post-disturbance linden forests (plots with BA_{rel} of *T. tomentosa*: > 66 %), sub-humid mixed beech-oak-hornbeam forests, and all other forests. Given are also the number of inventory plots per forest type (n). Plots with a total basal area < 10 m² ha^{-1} were classified as non-forests (n=15) and excluded.

CHAPTER IV

HIGHER GROWTH SYNCHRONY AND CLIMATE CHANGE-SENSITIVITY IN EUROPEAN BEECH AND SILVER LINDEN THAN IN TEMPERATE OAKS

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Published in: Journal of Biogeography (2023), 50:209-222

Accepted: 17 October 2022 / Published: 24/11/2022

http://doi.org/10.1111/jbi.14525

4 Higher Growth Synchrony and Climate-Change-Sensitivity in European Beech and Silver Linden than in temperate Oaks

4.1 Abstract

Climate change-induced drought and heat threaten forest health in many regions on earth. Precise predictions of future climate change impacts on forests require a better understanding of how climatic changes are affecting tree growth-climate relationships. We used tree-ring records for the period 1940–2017 to explore the spatio-temporal patterns of climate sensitivity and growth synchronicity of five temperate broadleaf tree species (three ring-porous oak species, and diffuse-porous European beech and silver linden) in the natural beech–oak ecotone in Romania at the dry margin of beech occurrence. In all five species including two Pannonian oak taxa and silver linden, water availability in summer was the most important climatic determinant of radial growth. This factor has gained in importance since the onset of rapid warming after 1980, while the impact of other climate factors in spring and summer has decreased. Within-population growth synchronicity as a measure of overall climatic stress has increased, or remained stable, since 1980 in beech and silver linden, but has decreased in the oak species, matching declining growth trends in beech and linden and increasing (or stable) trends in the oaks. We conclude that patterns of growth synchronicity may provide valuable information on tree species' drought susceptibility in attempts to select suitable tree species for climate change-adapted forestry.

Key words: climate–growth relationship, climate warming, dendrochronology, drought, Quercus cerris, Quercus frainetto, Quercus petraea, radial growth, Romania, tree rings

4.2 Introduction

Widespread occurrence of pre-senescent leaf fall, crown dieback and increased tree mortality have hit Central European forests during the extreme hot droughts of 2003, 2015 and 2018–2020, when heat, a high evaporative demand of the atmosphere and long rainless periods harmed especially fast-growing conifers such as Norway spruce, but hit also broadleaf trees like European beech (*Fagus sylvatica* L.) (Allen, Breshears, & McDowell, 2015; Schuldt et al., 2020; Senf, Buras, Zang, Rammig, & Seidl, 2020). It is almost certain that sensitive timber species will not maintain their productivity during the predicted warming trend until the end of the century and beyond, but our capacity to predict physiological stress responses of temperate forest trees is limited and knowledge of tree species' drought tolerance limits is still poor. The predicted annual temperature increase in Central Europe (Lee et al., 2021) is likely to shift the natural distribution limit of many tree species polewards and upwards to regions with cooler temperatures and higher precipitation (Lenoir, Gégout, Marquet, de Ruffray, & Brisse, 2008; Sykes, Prentice, & Cramer, 1996). For example, climate envelope models predict for the warmer and drier lowlands and lower montane belts of Central Europe a shift from beech-dominated forests to more drought-tolerant, thermophilic forest communities in the course of the 21st century (Fischer, Michler, & Fischer, 2019; Kramer et al., 2010).

The centre of the distribution range of European beech is located in central and southern Germany (Figure S1.1 in Appendix S1 in the Supporting Information), where the species naturally would cover more than 2/3 of the area and is occurring from the lowlands to the montane belt in the mountains (Leuschner & Ellenberg, 2017). Towards southern and south-eastern Europe, hotter summers and higher climatic aridity are shifting the occurrence of beech forests toward higher elevations with cooler and moister climates (Czúcz, Gálhidy, & Mátyás, 2011; Fang & Lechowicz, 2006). In the mountains of south-eastern and southern Europe, beech forests at montane or lower montane elevation usually give way to oak-dominated forest communities at lower elevations, which are linked through a beech–oak ecotone with a mixture of these species (Horvat, Glavač, & Ellenberg, 1975; Mayer, 1984). Various thermophilic deciduous oak species replace beech at its hot and dry distribution limit, in south-eastern Europe mainly *Quercus cerris* Liebl., *Q. frainetto* Ten., *Q, pubescens* L., and various taxa in the species aggregate of *Q. petraea* (Matt.) L. (Figure S1.1 in Appendix S1). They are accompanied by other broadleaf species with assumed higher drought tolerance such as *Carpinus betulus* L. and *C. orientalis* L., *Tilia cordata* L. and *T. tomentosa* Moench., and *Acer tataricum* L. At its south-eastern and southern distribution limit, beech often only persists in small refugia as in deep valleys or on north-exposed slopes with more humid local climate (Coldea, Indreica, & Oprea, 2015; Hohnwald, Indreica, Walentowski, & Leuschner, 2020; Indreica, Turtureanu, Szabó, & Irimia, 2017). These rear-edge populations are well suited for analyzing the adaptive capacity and growth response to climatic changes of beech in comparison to other more drought-tolerant species.

Beech is known to be more drought-sensitive than many co-occurring broadleaf tree species in Central Europe and it suffers from increasing climatic aridity in the course of climate warming especially at the species' drought- and heat-induced range limits (Brinkmann, Eugster, Zweifel, Buchmann, & Kahmen, 2016; Leuschner, 2020; Zang, Hartl-Meier, Dittmar, Rothe, & Menzel, 2014). This is visible in vitality losses at lower elevations, while vitality often increases at higher elevations (Dulamsuren, Hauck, Kopp, Ruff, & Leuschner, 2017; Kasper, Leuschner, Walentowski, Petritan, & Weigel, 2022; Serra-Maluquer et al., 2019) and the distribution range may shift gradually in northern and upward direction (Peñuelas, Hunt, Ogaya, & Jump, 2008). Yet, some studies detected no differences in climate sensitivity of growth between dry marginal and more humid beech populations, which may highlight the species' potential for drought adaptation in dry-marginal populations (Hacket-Pain, Cavin, Friend, & Jump, 2016; Muffler et al., 2020; Tegel et al., 2014).

Dendrochronological and physiological evidence demonstrates that European temperate and submediterranean deciduous oak species are more drought-resistant than beech (Friedrichs et al., 2009; Härdtle et al., 2013; Kasper et al., 2022; Scharnweber et al., 2011) and several other broadleaf species such as linden and hornbeam (Fuchs, Schuldt, & Leuschner, 2021; Köcher, Gebauer, Horna, & Leuschner, 2009; Leuschner, 2020; Zang et al., 2014; Zimmermann, Hauck, Dulamsuren, & Leuschner, 2015). However, most comparative studies cover considerable differences in site conditions, but neglect potential shifts in climate sensitivity over time, in particular possible sensitivity changes after the onset of the rapid warming since the 1980s.

As a consequence of deteriorating climatic growing conditions, trees may show increasingly synchronous radial growth responses to environmental stress (Shestakova et al., 2016; Shestakova, Gutiérrez, & Voltas, 2018; Tejedor et al., 2020). Synchrony here stands for a common temporal variation in a trait among the individuals of a population, or among different species in an ecosystem, which may have implications for ecosystem functioning and stability (Schurman et al., 2019; Shestakova et al., 2016). To quantify the common stress response, we follow the approach of Tejedor et al. (2020) and use the so-called rbar statistic, which is per definition "the common inter-annual variability in tree growth within a defined group", to characterize tree growth synchrony (del Río et al., 2021). Growth synchrony can be assessed spatially by depicting regional to global similarities in growth variation, or temporally by analyzing the response to environmental changes over time. Furthermore, growth synchrony can be investigated at different taxonomical levels, i.e. within populations of the same species or between species (Tejedor et al., 2020). In climate change research, high growth synchrony across populations or across species has been interpreted as an indicator of higher drought susceptibility, whereas lower synchrony was assessed as an indication of higher response diversity (Anderegg & HilleRisLambers, 2019; Camarero, Gazol, Sangüesa-Barreda, Oliva, & Vicente-Serrano, 2015; Pretzsch et al., 2020; Shestakova et al., 2016). A number of studies have reported climate warming-related increases in growth synchrony during the last century, suggesting a causal link to climate change (del Río et al., 2021; Muffler et al., 2020; Shestakova et al., 2016).

In this study, we investigate the climate sensitivity of radial growth and within-population growth synchrony in five co-existing temperate broadleaf tree species, European beech (*F. sylvatica*), hereafter referred to as beech, silver linden (*T. tomentosa;* hereafter linden), and three central to south-east European deciduous oak species (*Q. petraea*, *Q. cerris* and *Q. frainetto*) in western Romania. In this region, the climate conditions are similar to the predicted conditions in the centre of the beech distribution range at the end of the century (Hohnwald et al., 2020; Kasper et al., 2021). For establishing replicates at the landscape scale, we studied three transects across different forest communities with sufficient comparability in terms of thermal and hygric conditions, exposition, bedrock type, tree species composition and management history (Kasper et al., 2021; Kasper et al., 2022; Öder, Petritan, Schellenberg, Bergmeier, & Walentowski, 2021). We analyze correlations between tree growth and climatic factors in the time interval 1940–2016 and split it into the two periods before the pronounced recent temperature increase from ca. 1980 onwards and thereafter. We compare the ring-porous oak species with diffuse-porous beech and silver linden, and further contrast the growth responses of mesic beech stands in a more subhumid climate with xeric beech stands. i.e. rear-edge populations surviving in local humid refugia beyond the drought and heat limit of beech. By selecting western Romania with an about 2.5 K higher annual mean temperature than in central Germany today, this study offers insights into potential responses of beech forests in the species' distribution centre under the Representative Concentration Pathway (RCP) warming scenarios 2.6–8.5 (Lee et al., 2021), which predict by 1.0–3.7 °C warmer climates at the end of the century (Figure S1.2 in Appendix S1).

The following questions guided our research: (1) How do beech, silver linden and the three oak species differ in their climate sensitivity of growth? (2) Did the climate sensitivity of the five species change from the mid-20th century to the period with pronounced warming since the

1980s? (3) Do the five species differ in their within-population growth synchrony and how did the recent warming affect synchrony? (4) Do mesic and xeric (rear-edge) beech populations differ in their climate sensitivity and synchrony of the stress response?

4.3 Methods

Study region, physiography and transect selection

The study was conducted in western Romania on the foothills of the south-western Carpathians (Figure 1a). The climate is temperate sub-continental with warm summers and relatively cold winters and is considered as an analogue for the projected climate in the current centre of the distribution range of European beech in Central Germany around the 2080s. The current climate in the study region thus matches the projected climate in Germany towards the end of the 21st century, as demonstrated by plotting the current and future climates of European regions in an ordination space defined by winter cold, summer warmth and growing season precipitation (Figure S1.2 in Appendix S1, following Kölling & Zimmermann, 2014). Pronounced warming took place at all sites since about 1980, while mean summer precipitation (MSP) has fluctuated in the past decades without a clear trend (Figure S1.3 in Appendix S1). The climatic water balance in summer (precipitation – potential evapotranspiration) has decreased markedly since about 1980 at all sites (Figure S1.4 in Appendix S1, Kasper et al., 2022). Three elevation gradients in downhill direction from submontane/montane to colline elevation were established (Transects A, B and C, Figure 1b, Kasper et al., 2022), which sequentially cover humid beech-dominated forests at >500 m a.s.l., the humid-subhumid ecotone of mixed beech–hornbeam–oak forests at 350–600 m a.s.l., and finally the basal subhumid thermophilic oak-dominated forests at <350 m a.s.l., predominantly on south-west- to south-east-facing slopes (Hohnwald et al., 2020; Indreica et al., 2017; Kasper et al., 2021).

The dominant soils on base-poor bedrock are acidic but eutric Cambisols in all studied forests. The soil is covered at many places by an up to 100 cm thick loess layer (Kasper et al., 2021). All selected stands had roughly similar stem densities and thus comparable competition intensities, were of mature age (> 60 years old), 21–33 m in height and had a closed canopy (Table S1.2 in Appendix S1 and Kasper et al., 2022). While subjected to occasional wood-cutting and low-intensity coppicing in the years before 1960, the forests were afterwards transferred to state-ownership. Previously coppiced stands were allowed to grow into high forests (Öder et al., 2021), and stands were lightly thinned (5–15 % of stand volume) from the pole-wood stage onwards until three quarters of the time till harvest had passed (Ashton & Kelty, 2018). Irregular salvage and sanitary loggings have been conducted at low intensity (removal of < 5% of stand volume). No major harvest operations have occurred in the stands in the last 20 years (Öder et al., 2021).

All three transects were established on predominantly south-west- to south-east-facing slopes. *F. sylvatica* contributed with at least 85 % to total stem numbers in the beech forests, while the thermophilic oak forests were dominated by the three oak species *Q. petraea*, *Q. cerris*, and *Q. frainetto*, which contributed > 85 % of the stem numbers (Table S1.2 in Appendix S1). The remaining stems were contributed by accompanying species such as *Tilia tomentosa*, *Carpinus betulus*, and *Acer campestre* L. In the ecotone, subhumid mixed beech-oak and hornbeam forests were present, with the oak species and beech each contributing with about 30 % to total basal area (except for transect B) and the remaining stems mostly belonging to *T. tomentosa* and *Carpinus* species (Kasper et al., 2021; Kasper et al., 2022).

Species selection and wood core sampling

Five focal species were selected. *F. sylvatica* as the dominant species of the humid beech forests (mesic beech), *Q. petraea, Q. frainetto* and *Q. cerris* as dominants of the thermophilic *submediterranean,* xeric oak forests (oak), and again *Q. petraea* with *T. tomentosa* as co-occurring species in the subhumid mixed beech-oak-hornbeam forests that form the beech–oak ecotone (Figure 1b and Table S1.2 in Appendix S1). In addition, north-facing *F. sylvatica* stands were sampled in extra-zonal beech forests at colline elevation (<400 m a.s.l.; xeric beech) in close proximity to the basal thermophilic oak forest belt.

The wood core sampling in summer 2018 and 2019 resulted in 92 to 153 cores per tree species or forest type (beech mesic vs. xeric). We sampled in most cases dominant individuals of the upper canopy layer with DBH > 40 cm (Table S1.2 in Appendix S1). The sample trees lacked signs of pre-senescent leaf abscission, canopy dieback, or other damage. Tree cores were extracted at breast height (1.3 m) with an increment borer (Haglöf, Langsele, Sweden) in the direction of least tension wood, i.e. perpendicular to any potential tilting direction. Cores with rotten segments were excluded from further analysis. As tree cores were sampled after the beginning of the growing season, the last incomplete annual ring was omitted in the analysis; hence, tree-ring series collectively ended in 2017. For assessing individual tree competition intensity, the Hegyi competition index (CI) was calculated (Hegyi, 1974) and tree age was approximated by counting the number of tree rings.

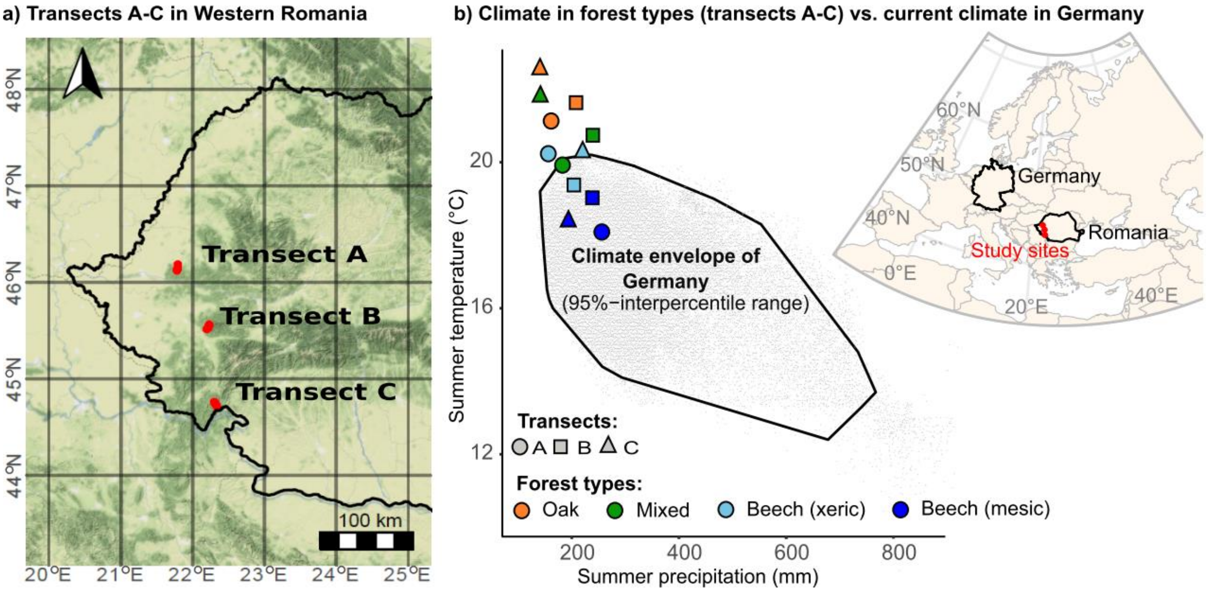

Figure 1: (a) Location of the study transects in the western Romanian Carpathians. (b) Summer climate conditions (June–August CHELSA gridded climate data, Karger et al., 2017, average of 1940–2016) in the study transects in comparison to the centre of beech distribution in Germany. Climate data was extracted for the mean locations of F. sylvatica forests in the mesic beech zone (elevation > 550 m), “rear-edge” stands of F. sylvatica in the low-elevation xeric beech zone (elevation < 400 m), Q. petraea and T. tomentosa in the ecotones (600 m > elevation > 350 m) and Q. cerris and Q. frainetto in the thermophilic oak zone (elevation < 350 m). Local maps are in Mercator projection, the map inset of Europe in azimuthal equal-area projection centred on the North Pole (South, 2011).

Tree-ring data and climate sensitivity analysis

We cross-dated all tree-ring series (TRW, tree-ring width in mm) by relying on the coefficient of agreement (“Gleichläufigkeit” GLK; Eckstein & Bauch, 1969), the cross-dating index (CDI; Dobbertin & Grissino-Mayer, 2004) and Student’s t-value (TVBP; Baillie & Pilcher, 1973). All ring series contributing to the chronologies had a GLK > 65 %, a CDI > 2.0, and a TVBP > 3.0 (Table S1.2 in Appendix S1). To obtain the detrended dimensionless ring width index (RWI), the individual TRW series were divided by the derived 30-year moving-average spline with frequency cut-off at 50 %, with the first-order autoregression removed subsequently (pre-whitening). Master chronologies were calculated for each site and population as the mean value sample (Tukey’s bi-weight robust mean) of individual tree-ring series (RWI) (Figure S1.5 in Appendix S1). As a quality indicator for these chronologies, we considered an expressed population signal (EPS) >0.85, which is an indicator of high growth coherence among neighbouring trees (Wigley, Briffa, & Jones, 1984). Sample sizes were considered sufficient for the period 1940–2017 (except for *T. tomentosa* in transect B: 1950–2017) for analyzing climate sensitivity and growth synchrony.

Monthly and seasonal (winter: previous December–current February; spring: March–May; summer: June–August; autumn: September–November) temperature and precipitation time series of the period 1940–2016 for the studied forest stands were computed from high-resolution gridded climate data (30 arcsec, ~1 km^2) that were downloaded from the CHELSA (CHELSAcruts) climate database (Karger et al., 2017). To investigate the effect of droughts, we calculated the Standardized Precipitation-Evapotranspiration Index (SPEI) (Vicente-Serrano, Beguería, & López-Moreno, 2010) for 3-month time intervals at monthly and seasonal scales. Climate data were compiled for each individual tree before being averaged to population or transect means.

The effect of climate variables on annual radial increment (climate sensitivity) was assessed by correlating RWI chronologies with mean monthly temperature, the monthly precipitation sums, and drought exposure (3-month SPEI value), spanning the meteorological conditions from previous year's June to current year's September. This was done for the common observation period (1940–2016) and separately for the periods before (1940–1979; earlier period) and after the onset of the recent warming trend (1980–2016; later period) (Figure S1.3 in Appendix S1). We assessed the statistical significance at $p \leq 0.05$ in all analyses using a 1000-fold bootstrapping procedure in the R-package 'treeclim' v2.0.5.1 (Zang & Biondi, 2015).

Growth synchronicity

Synchronous inter-annual variability in tree-ring series is usually estimated through the mean inter-series correlation (rbar = 0: no synchrony to rbar = 1: totally synchronized growth dynamics) value, which is the average Pearson correlation among all tree-ring series within a given chronology (Wigley et al., 1984). We calculated running synchrony values (rbar) in a 20-year moving window using the R package 'dplR' v1.7.1 (Bunn, 2008). Significance of trends during the observation period was assessed using the Mann-Kendall trend test.

When computing synchrony values among different populations of a species, the associated random error structure, which may change over time, must be carefully selected. We followed the approach of Shestakova et al. (2016; 2018), using a mixed model approach ('DendroSync' v0.1.3 R package; Alday, Shestakova, Resco de Dios, & Voltas, 2018) to analyze spatial patterns of radial growth (RWI) synchrony in tree-ring networks at species level (and for beech mesic vs. xeric). First, mixed models allowing for different variance–covariance (VCOV) structures among grouping variables (homoscedastic vs. heteroscedastic versions) were estimated to select the best VCOV structure based on Akaike's Information Criterion (AIC) and Bayesian Information Criterion (BIC) (Burnham & Anderson, 2004). Species synchronicities were then estimated from the VCOV models, where synchrony values again range from 0 (no regional synchronization across populations) to 1 (total regional synchronization) (Alday et al., 2018;

Shestakova et al., 2018). We also calculated moving averages in a 30-year window with individual fitting of the best VCOV model in lag periods of 5 years (del Río et al., 2021; Shestakova et al., 2016), where for each 5-year period the best VCOV model was selected following the above-mentioned criteria.

Means (± SD) are presented throughout the paper and differences between means depicted in the graphs and tables were tested for statistical significance with a Wilcoxon Rank test and with a t-test in case of pairwise comparisons. All statistical procedures were performed in R v4.0.3 (R Core Team, 2020).

4.4 Results

Climate sensitivity

Radial growth was limited by high summer temperatures in most species and transects (and additionally by high spring temperatures in transect A), while we found no hints on low-temperature limitation in winter and autumn (Figure 2; similar patterns are visible in Figure S1.6 in Appendix S1 which were derived from correlations with monthly climate data). Interestingly, negative temperature-growth correlations were generally weaker in the driest transect C (Figure 2). High summer precipitation enhances growth in all stands (except for Q. petraea in transect A and Q. frainetto in transect C), while spring precipitation was only sporadically influential (Q. frainetto (A and B), Q. cerris (A), T. tomentosa (A and B), and F. sylvatica xeric (A)), and winter and autumn precipitation variability had no effect (Figure 2). Previous year's summer precipitation seemed to be less important for the three oak species than for F. sylvatica and T. tomentosa, especially in the driest transect C (Figure S1.6 in Appendix S1). Local variability in summer water availability (SPEI 3-months aggregation period) was the most limiting climate factor for stem growth in all species and all transects (except for Q. petraea in transect A), while spring SPEI was influential only in Q. cerris (transect A) and Q. frainetto (transects A and B), and autumn SPEI was only influential in F. sylvatica (transect B), Q. cerris (transect C) and Q. frainetto (transect B) (Figure 2). Previous year's SPEI of the summer months was not influential in Q. petraea, while it influenced Q. cerris and Q. frainetto and, in particular, F. sylvatica and T. tomentosa (Figure S1.6 in Appendix S1).

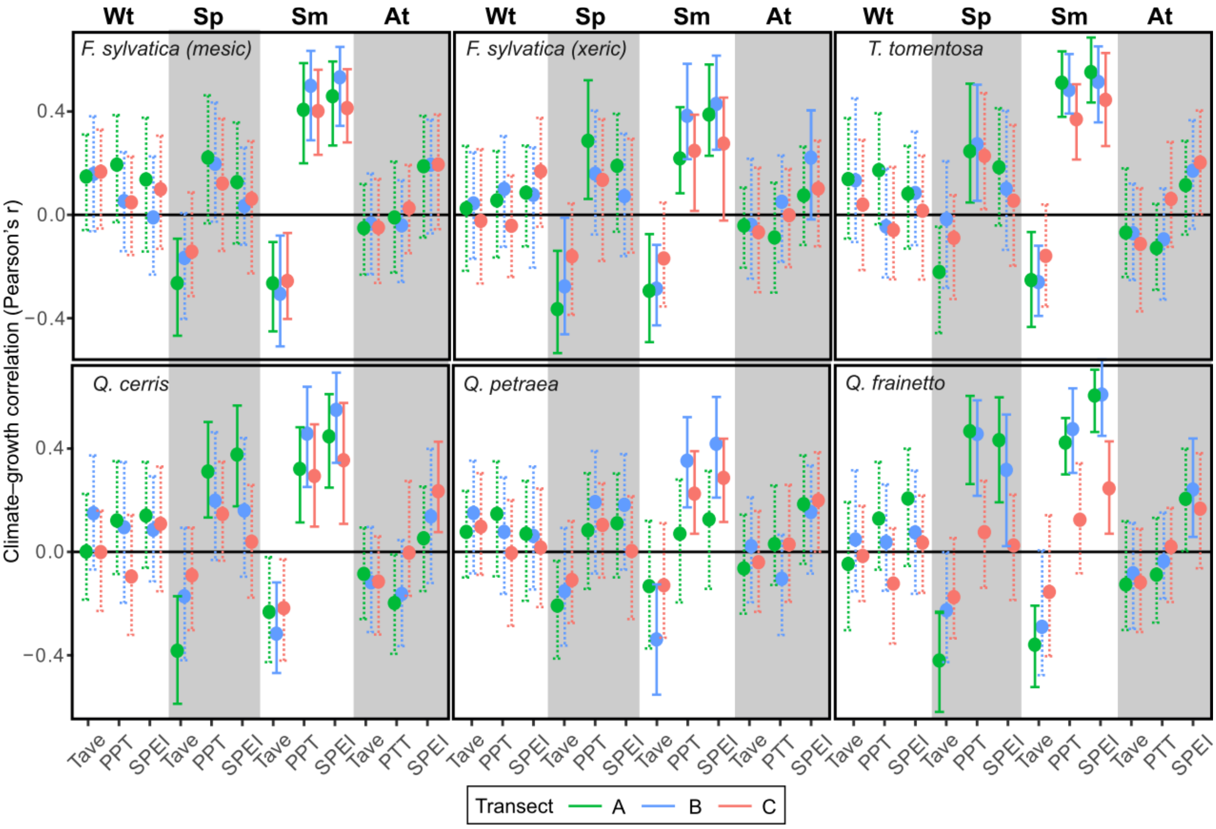

Figure 2: Climate–growth relationships (Pearson's r on the y-axis) for the correlation of tree-ring index chronologies with winter (Wt: previous December–February), spring (Sp: March–May), summer (Sm: Jun–Aug) and autumn (At: September–November) averages/sums of climate variables (Tave – average temperature, PPT – precipitation sum, SPEI – average Standardized Precipitation–Evapotranspiration Index) for the period 1940–2016 at the study transects A–C in the western Romanian Carpathians. Significant correlations are shown through solid whiskers for the 2.5% and 97.5% empirical 1000-fold bootstrapped confidence interval.

After the onset of recent warming at around 1980, most species (except for *Q. frainetto* in transects A and B) showed a weakening of the summer high-temperature signal (Figure 3). All species became more sensitive to higher summer precipitation with notable exceptions in the driest transect C, where the influence of summer precipitation declined in *Q. cerris*, *Q. frainetto*, and the xeric *F. sylvatica* stands (Figure 3, Figure S1.7 in Appendix S1). There was no consistent decline or increase of the summer SPEI signal across species and transects, whereas the influence of climate conditions in spring declined especially in beech and linden (Figure 3). Differences also existed between transects, with an overall increase of the influence of summer precipitation toward the later period in the moister transects A and B, but no consistent change over time in the driest transect C, and a reduced negative influence of summer temperature in the driest transect C, but less so in the moister transects A and B (Figure S1.7).

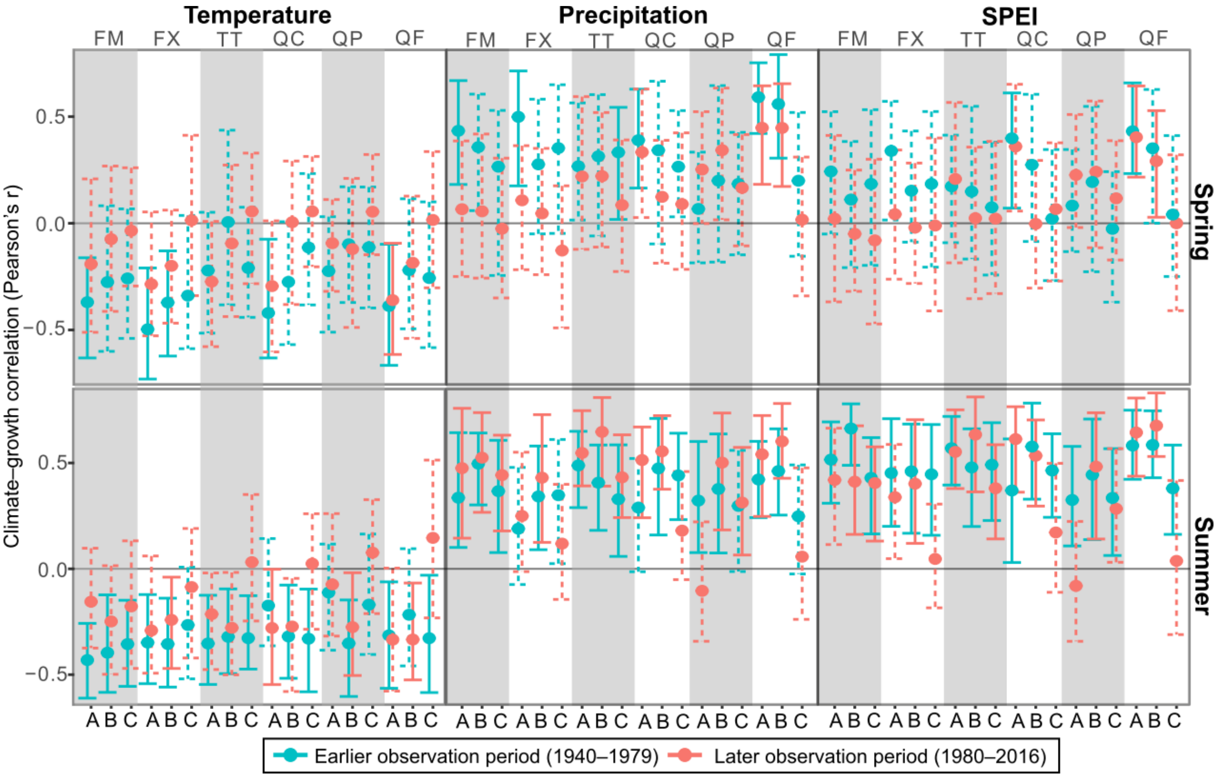

Figure 3: Shift of climate–growth correlations (Pearson's r on the y-axis) with spring (March–May) and summer (June–August) averages (temperature and SPEI) or sums (precipitation) of climate variables between the earlier observation period (1940–1979) and the recent climate warming (later) period (1980–2016). Significant correlations are shown through solid whiskers for the 2.5% and 97.5% empirical 1000-fold bootstrapped confidence interval. Species are abbreviated as: FM = F. sylvatica (mesic), FX = F. sylvatica (xeric), QP = Q. petraea, TT = T. tomentosa, QC = Q. cerris and QF = Q. frainetto at the study transects A–C in the western Romanian Carpathians. SPEI is the Standardized Precipitation–Evapotranspiration Index.

Within-population growth synchronicity

Growth synchrony (rbar) among the trees of a stand was in most species lowest in the moistest transect B. Overall, highest synchrony was recorded for Q. cerris and Q. petraea in the moderately moist transect A, while lowest rbar values were found for Q. petraea in the moistest transect B (Figure 4a). Compared to the other species, F. sylvatica was characterized by medium rbar values at both the mesic and xeric sites. The five species also differed in their synchrony change from the earlier to the later period (Figure 4b). Synchrony of F. sylvatica increased in transect A (mesic and xeric) and C (xeric) and declined for T. tomentosa in transect B (Figure 4b). All three oak species showed large declines in growth synchrony toward the later period in transects A and C; the synchrony of Q. cerris declined also in transect B (Figure 4b).

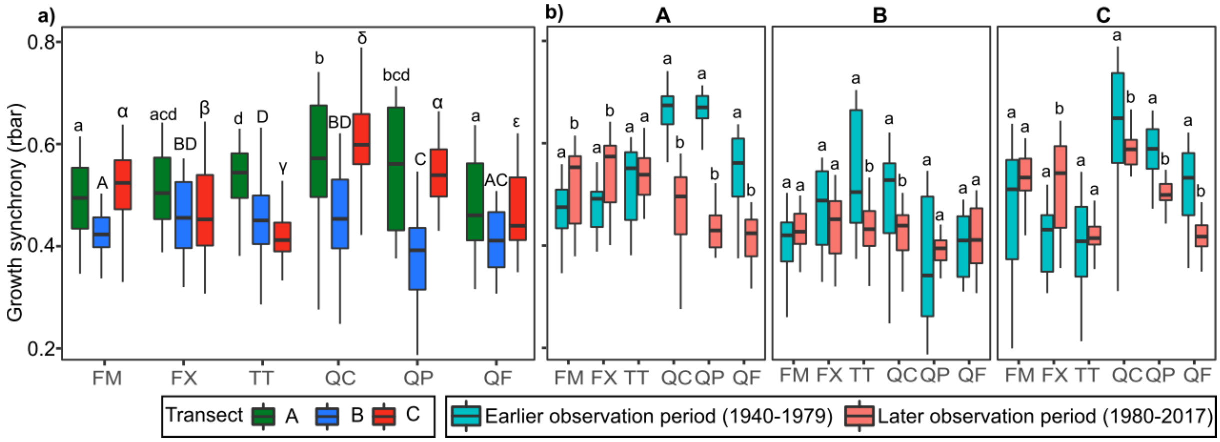

Figure 4: a) Growth synchrony ("rbar": the mean correlation between all tree-ring index series in a chronology) for the five species (and two site types for beech) for the period 1940–2017 in the three transects in the western Romanian Carpathians. For each transect, significant differences between the species (and two site types for beech) are marked with different lowercase letters (transect A), uppercase letters (transect B), and Greek letters (transect C). b) Growth synchrony (rbar) of the five species in the three transects in the earlier observation period before the onset of warming (1940–1979, light blue) and in the later period (1980–2017, red) during warming. Significant changes between the two periods are marked with different lowercase letters. Species are abbreviated as: FM = F. sylvatica (mesic), FX = F. sylvatica (xeric), QP = Q. petraea, TT = T. tomentosa, QC = Q. cerris and QF = Q. frainetto. Whiskers extend over the 5–95% confidence intervals.

Within-stand synchrony (rbar) significantly increased for F. sylvatica in all transects (except transect B for xeric beech) and for T. tomentosa in transect A and C in the long term, which was linearly related to long-term increases in mean summer temperature (Figure 5). In both species, synchrony dropped temporarily in the 1970s, which coincided with temporarily high summer precipitation. When precipitation decreased again in the early 1980s (Figure S1.3), synchrony continuously increased (Figure 5). Both Q. frainetto and Q. petraea showed a significant synchrony decline in the drier transects A and C, and an increase in the moistest transect B. For Q. cerris, a significant decrease of growth synchrony was only observed in transect A (Figure 5). In contrast to beech and silver linden, the synchrony within the oak populations of the two driest transects (A and C) was inversely related to mean summer temperature during the last decades (Figure 5).

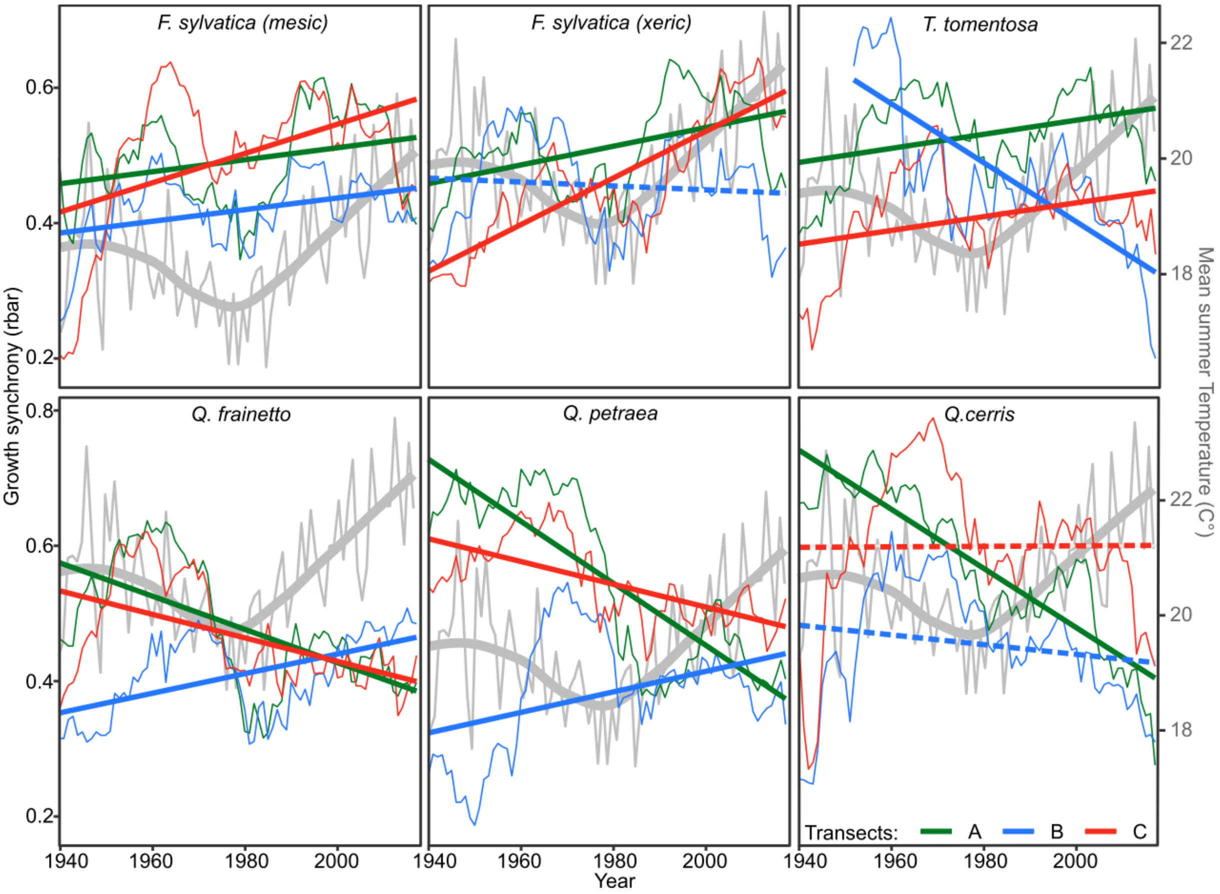

Figure 5: Change in growth synchrony ("rbar": the mean correlation between all tree-ring index series in a chronology) in the five species (and two site types for beech) in the three transects in the western Romanian Carpathians from 1940 to 2017 (in case of T. tomentosa in transect B: 1950–2017). Pooled over the three transects (A–C) per species on the second y-axis is the mean summer (June–August) temperature (raw data: fine grey line and trends: depicted through spline smoothing as thick grey line). Linear regression models predicting rbar depending on the calendar year were computed for every transect and species (and two site types for beech) and are depicted as solid lines, if a significant temporal trend was detected in a Mann-Kendall trend test. For detailed results of the Mann-Kendall trend tests see Table S1.3 in Appendix S1.

Between-species growth synchronicity and temporal trends

The best variance–covariance (VCOV) models for assessing growth synchrony among the five species were homoscedastic unstructured models (mUN) that allowed for heterogeneous variances and co-variances. The obtained results were similar for RWI data with and without pre-whitening (Table S1.4 in Appendix S1), showing lower growth synchronicities in the Quercus species as compared to F. sylvatica (mesic and xeric) and T. tomentosa (Figure S1.8 in Appendix S1). Split into two periods (before and after the temperature increase), the results of the best VCOV models (Table S1.4 in Appendix S1) show a synchrony increase for F. sylvatica (mesic and xeric) and T. tomentosa in comparison to decreases in the Quercus species (Figure S1.8c in Appendix S1), again with similar results for non-pre-whitened RWI data (Figure S1.9a in Appendix S1). The best VCOV models for assessing temporal synchrony trends for pre-whitened RWI data until 1975 were broad evaluation models (mBE), suggesting homogenous growth responses among the species (Figure 6 and Table S1.5 in Appendix S1). After 1975, homoscedastic unstructured models (mUN) showed the best fit, with bifurcations in synchrony patterns for each species. Following the VCOV models, synchrony then increases for F. sylvatica (mesic and xeric) and T. tomentosa, whereas it remains stable or decreases for the Quercus species (Figure 6) with again similar results for non-pre-whitened RWI values (Figure S1.9b and Table S1.5 in Appendix S1).

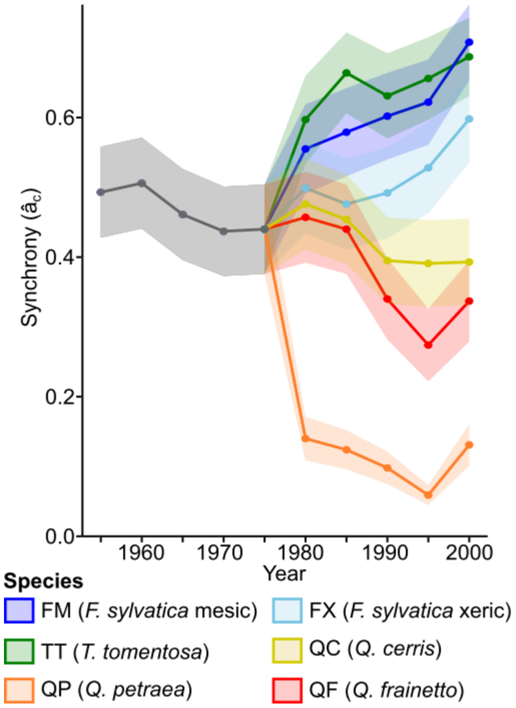

Figure 6: Temporal trends of synchrony estimates ("âc" ranging from 0 (no regional synchronization) to 1 (total regional synchronization) calculated with a mixed model approach, Alday et al., 2018) for the five species (and two site types of F. sylvatica) in the western Romanian Carpathians for pre-whitened ring-width index (RWI) chronologies calculated with the best-fit variance–covariance model for 30 year-wide moving intervals by 5-year steps over the period 1940–2017. The x-axis shows the central year of the moving time interval. Shadows are 1 standard error (SE).

4.5 Discussion

Climatic drivers of radial growth in the five species

In agreement with our results from the beech–oak ecotone in Romania, low summer water availability and high summer temperatures have been identified as limiting factors for temperate Central and Southern European beech and oak forests in numerous other studies (Bose et al., 2021; Bosela et al., 2018; Fuchs et al., 2021; Hacket-Pain et al., 2016). The key role for atmospheric and/or edaphic water limitation is further underpinned by the observation that the growth rates of all five species were generally lower in transect C with highest stress exposure than in the other transects and the generally more productive beech and linden suffered greater growth reductions than the oak species during the extreme dry years 2000, 2003, and 2012 (Kasper et al., 2022). In our study, the strong influence of local variability of the climatic water balance (SPEI) suggests that primarily atmospheric vapour pressure deficit (for which long-term stand-level data are missing), together with soil water availability during summer is controlling growth instead of temperature and precipitation alone (Fuchs et al., 2021; Kasper et al., 2022; Scharnweber et al., 2011). Physiological mechanisms leading to reduced stem growth during dry summers may include lowered carbon gain due to partial stomatal closure and turgor loss in stem cambial cells caused by a reduction in the tree's hydraulic capacity (Bréda, Huc, Granier, & Dreyer, 2006; Müller-Haubold, Hertel, Seidel, Knutzen, & Leuschner, 2013; Salomón et al., 2022). Other factors leading to reduced stem growth could be enhanced C investment in the fine root system to compensate for increased root mortality during drought, as well as the formation of thicker pit membranes and a reduction of xylem conduit cross-sectional area to enhance hydraulic safety at the cost of hydraulic efficiency (Fonti, Heller, Cherubini, Rigling, & Arend, 2013; Fuchs, Hertel, Schuldt, & Leuschner, 2020; Hertel & Leuschner, 2002). Thus, smaller annual growth rings to increase hydraulic safety might alternatively be interpreted as an acclimation to drought rather than a response to drought-impairment of the tree's carbon and water relations (Bréda et al., 2006; Gessler, Bottero, Marshall, & Arend, 2020; Lloret, Keeling, & Sala, 2011). Physiological measurements on hydraulic safety margins and the C and water balance of the trees would be needed to separate between active (adaptive) and passive (drought impairment) responses to water deficits.

The ring-porous oaks complete most of their radial growth during a short period during or after leaf-out, when large vessels are formed that allow high photosynthetic rates, while stored carbohydrates seem to play a smaller role than in diffuse-porous beech and linden (Di Filippo et al., 2007; Fuchs et al., 2021; Lebourgeois, Bréda, Ulrich, & Granier, 2005; Müller-Haubold et al., 2013). In accordance, our data show not only a minor influence of previous year's weather on the growth of oaks (all three species in transect C, and Q. petraea in all transects), but also support the evidence of a generally lower climate susceptibility of oak growth (Friedrichs et al., 2009; Mérian, Bontemps, Bergès, & Lebourgeois, 2011; Scharnweber et al., 2011). This is visible both in a higher drought resistance of oak radial growth to individual drought events and in a higher resilience to recover to pre-drought growth levels in comparison to beech and linden, as detected earlier in our stands (Kasper et al., 2022). Furthermore, Q. petraea seems to maintain a smaller fine root system than the other species and its fine roots apparently are less drought-sensitive (Fuchs et al., 2020; Hertel & Leuschner, 2002). Temporal shifts in the carbohydrate allocation to the root system might therefore be less important for Q. petraea than for the studied diffuse-porous species.

Drought stress in spring has been identified as the main climatic factor constraining the radial growth of temperate oaks due to their early onset of wood formation during bud burst in contrast to the diffuse-porous species, which have a later onset of growth (Barbaroux & Bréda, 2002; Bose et al., 2021; Fuchs et al., 2021). In our study region with hot and dry summers, however, summer drought was in most cases at least equally, or even more, important for oak radial growth than spring water availability, suggesting that this picture may need adjustment in continental climates.

Temporal changes in climate sensitivity

Our results demonstrate a marked decadal shift in the climate sensitivity of growth, confirming non-stationarity of climate responses as discussed by Wilmking et al. (2020). This bases on the observation of D'Arrigo, Wilson, Liepert, and Cherubini (2008) that high-latitude forests lose track of their temperature signal, because climate factors other than low temperatures have recently become more growth-limiting. In our study in the southeast European beech–oak ecotone, non-stationarity in climate-growth relationships was detected, although summer heat and drought, and not low temperatures, are the main growth-limiting climatic factors. Surprisingly, the summer heat limitation of tree growth weakened in the observation period in this region especially in beech and linden, despite a rising evaporative demand of the atmosphere with climate warming, in a similar manner as has been observed in some Central and Western European forests during the last decades (Fuchs et al., 2021; Mérian et al., 2011). Instead, summer water deficit and summer precipitation became more important growth-controlling factors over time especially in the diffuse-porous species, as has been observed in other studies on beech and also oak species at their dry limits (Bosela et al., 2018; Friedrichs et al., 2009; Roibu et al., 2020). Probably as a consequence of increasing limitation by summer water deficits, the influence of spring weather on growth has decreased. It appears that non-stationarity is greater in beech and linden than in the oaks, and higher sensitivity to summer water availability has partly replaced sensitivity to summer heat in the diffuse-porous species.

While tree age is known to affect climate-growth relationships, climate sensitivity of growth should rather stabilize when trees reach maturity (Carrer & Urbinati, 2004; Konter, Büntgen, Carrer, Timonen, & Esper, 2016). Tree size may also affect climate sensitivity (Trouillier et al., 2019), as trees often become more sensitive to xylem embolism when growing tall (Olson et al., 2018; Ryan, Phillips, & Bond, 2006). Changes in dominance (Mérian & Lebourgeois, 2011) or competition intensity in the stand over time might also change climate sensitivity (Piutti & Cescatti, 1997; Rozas, 2001). Although we took great care to extract all cores from dominant, vital trees of the top canopy layer (Kraft classes 1 or 2) that were exposed to similar Hegyi-competition intensities across the study plots (except for one mesic beech stand in transect C), we naturally cannot precisely conclude on the competitive pressure the sample trees were exposed to in the past.

Surprisingly, the driest transect C showed the largest share (3 of 5) of species with recently declining precipitation signal in the tree-ring series. A plausible explanation is acclimation of the local tree populations during the last decades to increasing water deficits in an already drought-limited environment (Bréda et al., 2006; Gessler, Bottero, Marshall, & Arend, 2020; Lloret, Keeling, & Sala, 2011; Muffler et al., 2020). Possible mechanisms are increasingly deeper root penetration and increases in hydraulic safety through the production of smaller xylem conduits.

Climate warming effects on growth synchrony

In temperate and boreal forests, increased climate variability or shifts in the climate sensitivity of growth have been found to be linked to increasing synchronisation of tree growth patterns, suggesting the amplification of common climatic stressors for tree growth (del Río et al., 2021; Muffler et al., 2020; Shestakova et al., 2016). This happens when climatic conditions become more stressful, local factors such as competition intensity and small-scale edaphic conditions become less influential on tree growth, and the common ring width variance due to the effect of macroclimatic drivers increases (Shestakova et al., 2016; Tejedor et al., 2020). It is highly likely that the recent temporal increase in growth synchrony of more drought-sensitive beech and linden is attributable to the species' higher vulnerability to summer water deficits, as evidenced by both their recent simultaneous increase in precipitation sensitivity and growth synchrony in contrast to the oak species in our study area. Moreover, the more pronounced growth reductions in extreme drought years of beech and linden as compared to the oak species, as found in Kasper et al. (2022) is another strong hint of the former species' greater vulnerability. Shifting phenological patterns due to climate warming likely do not explain this recent synchrony divergence, as experimental warming of beech and oak saplings led to similar phenological responses in both genera (Fu et al., 2014; Zohner, Rockinger, & Renner, 2019). The most plausible explanation is a better drought adaptation of the oaks. In support of this conclusion, we observed generally positive growth trends in the three oak species, but declining trends (notably in the transects A and C) in beech and linden since the 1980s (Kasper et al., 2022).

It is reasonable to expect that growth coherence in the more drought-sensitive tree species beech and linden will further increase with increasing climate variability and drought stress in the future. Since our Romanian study area was chosen as a climate analogue site for the projected climate change during this century in the distribution centre of beech (which is located in Germany), our findings of recently increasing growth synchrony together with the evidence of lower drought resilience (Kasper et al., 2022) suggest that central beech populations will suffer in the next decades more from increasing climate stress than the ring-porous oak species. Certainly, the genetic constitution differs between central beech populations in Germany and Romanian dry-marginal populations (Magri et al., 2006), which complicates extrapolating from Romania to Germany. In any case, central beech provenances were found to be less drought-adapted than dry-marginal populations (Thiel et al., 2014), suggesting that the results from Romania should underestimate rather than exaggerate the expected growth response to future climate change in German beech forests.

Our results further suggest that the analysis of growth synchrony may represent a better measure for comparing the climate sensitivity of tree species than the more conventional analysis of climate-growth relationships, since the former may capture the joint influence of various climatic stressors on tree growth dynamics better. In fact, climate sensitivity analysis might fail to capture climate change-related stressors due to the ‘divergence problem’ (D'Arrigo et al., 2008) of shifting importance between different growth-influencing climate factors.

4.6 Conclusions

From the start of rapid warming since the 1980s onwards, growth synchrony in the western Romanian beech–oak ecotone has increased in beech and, to a lesser extent, in silver linden, while marked decreases were observed in the three oak species. This can be interpreted as a sign of recently increasing climatic limitation of beech and linden vitality in contrast to the less affected oak species. We conclude that the analysis of climate change impacts on temperate forest growth, which often alter climate–growth relationships, may profit from the interpretation of growth synchrony patterns, as these patterns should provide an integrative picture of long-term change in the climate sensitivity of tree growth. Our results further suggest that water deficits in summer are a main determinant of the observed changes in synchrony, as water limitation was identified as key determinant of radial growth rates. Our results of climate warming-induced impairment of tree growth in the natural beech–oak ecotone of South-eastern Europe may support predictive modelling of the fate of Central European forests under advancing climate warming. Various lines of evidence suggest that productive but vulnerable species such as beech will face increasing risks of climate warming-induced vitality loss and possible future dieback also in some regions in the range centre, while the more drought-resistant oak species will be advantaged, if drought happens in summer and not in spring. To increase climate change resilience in forests, it may be wise to favour more stress-tolerant over high-yield timber species in vulnerable regions. The three studied oak species, which produce highly valued timber, would be a promising option for the transition to climate change-adapted forests.

4.7 Acknowledgements

Our gratitude goes out to all students and field assistants who participated in the field work, as well as all NEMKLIM project partners in Romania and Germany. We further would like to thank the forestry offices in Radna, Caransebeș, Oțelu Roșu and Orșova for their permits and collaboration. No other permits were needed for this research. Personally, the corresponding author would also like to specially thank Lara Goldmann for the assistance during the fieldwork and publication process.

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4.9 Appendix

Tables

Table S1.1: Location of the three transects with longitude (Long.) and latitude (Lat.), elevation (Elev.) and climatic characteristics of the highest (top end) and lowest (bottom end) plots. The highest-elevation plots are located in typical beech forests, the lowest plots in typical oak forests. Given are annual mean temperature (T), mean temperature of the warmest month (Tmax), mean temperature of the coldest month (Tmin), mean temperature of warmest quarter (MST), annual precipitation sum (P), precipitation sum of the wettest month (Pmax), precipitation sum of the driest month (Pmin), and precipitation sum of the warmest quarter (MSP) according to data extracted from the CHELSA climate data base (Karger et al., 2017).

Locality	**County**	**Transect position**	**Long.**	**Lat.**	**Elev.** [m]	**T** [C°]	**Tmax** [C°]	**Tmin** [C°]	**MST** [C°]	**P** [mm yr^{-1}]	**Pmax** [mm]	**Pmin** [mm]	**MSP** [mm]
Milova (Transect A)	Arad	Top end	21.8135	46.1973	759	7.9	23.4	-6.5	18.2	892	125	48	254
		Bottom end	21.8022	46.1290	216	10.8	26.5	-6.5	21.2	690	132	52	248
Maciova (Transect B)	Caraș-Severin	Top end	22.2460	45.5749	719	8.2	23.8	-7.1	18.6	951	100	54	216
		Bottom end	22.2116	45.5248	256	11.1	26.9	-4.0	21.7	791	81	41	157
Eselnita (Transect C)	Orsova	Top end	22.3188	44.7754	907	7.8	23.6	-3.8	18.3	844	106	45	201
		Bottom end	22.3578	44.7173	147	11.9	28.0	-3.5	22.6	598	69	40	137

Table S1.2: Descriptive variables characterizing stand structure and growth of the five tree species (and two site types for beech) in the three transects in western Romania. Transect (T), species (Sp), number of sampled trees (Trees), tree age (Age), elevation (Elev.), diameter at breast height (DBH) tree height (H), Hegyi competition index (CI), mean ring width (MRW) for the 1940–2017 period (except T. tomentosa, transect B: 1950–2017), mean "Gleichläufigkeitswert" (GLK, (Eckstein & Bauch, 1969)) and mean first-order auto-correlation (AC1). TRW = tree ring width. Given is also the expressed population signal (EPS, Wigley, Briffa, & Jones, 1984) calculated from the detrended (30-year moving average standardization with frequency cut-off at 50 %) ring width series. Species are abbreviated as: FM = *F. sylvatica* (mesic), FX = *F. sylvatica* (xeric), QP = *Q. petraea*, TT = *T. tomentosa*, QC = *Q. cerris* and QF = *Q. frainetto*.

			Stand structural data					**RWL and RWI data (1940–2017)**			
T	**Sp**	**Trees**	**Age**	**Elev.**	**DBH**	**H**	**CI**	**MRW**	**GLK**	**AC1**	**EPS**
			years	m a.s.l.	cm	m		mm			
A	FM	54	82 (14)	648 (72)	44.4 (5.7)	31.0 (3.1)	0.43 (0.20)	2.38 (0.52)	0.69 (0.06)	0.55 (0.12)	0.98
B	FM	55	75 (17)	574 (105)	47.6 (9.1)	31.6 (3.7)	0.42 (0.24)	2.88 (0.76)	0.67 (0.08)	0.56 (0.17)	0.97
C	FM	44	105 (32)	721 (113)	45.3 (5.8)	27.0 (3.1)	0.72 (0.24)	1.63 (0.43)	0.67 (0.07)	0.53 (0.11)	0.98
A	FX	29	93 (11)	368 (40)	46.0 (5.1)	32.4 (3.4)	0.43 (0.20)	1.78 (0.33)	0.69 (0.06)	0.55 (0.10)	0.97
B	FX	26	102 (20)	412 (26)	48.1 (8.0)	33.5 (3.5)	0.49 (0.26)	1.85 (0.44)	0.66 (0.06)	0.58 (0.13)	0.96
C	FX	27	94 (28)	397 (40)	37.6 (6.1)	21.7 (4.9)	0.58 (0.25)	1.30 (0.33)	0.69 (0.07)	0.53 (0.10)	0.96
A	QC	32	102 (10)	382 (69)	42.9 (5.9)	28.6 (4.2)	0.45 (0.30)	1.56 (0.34)	0.70 (0.06)	0.63 (0.10)	0.98
B	QC	32	76 (15)	377 (44)	44.0 (6.1)	31.5 (3.8)	0.44 (0.30)	2.14 (0.49)	0.70 (0.07)	0.61 (0.20)	0.97
C	QC	30	82 (12)	225 (16)	41.2 (5.2)	22.0 (3.9)	0.53 (0.29)	1.78 (0.49)	0.71 (0.06)	0.61 (0.09)	0.98
A	QF	32	99 (10)	321 (30)	39.7 (4.0)	27.0 (3.6)	0.47 (0.22)	1.44 (0.30)	0.70 (0.06)	0.49 (0.12)	0.98
B	QF	30	83 (15)	365 (19)	42.4 (7.7)	28.3 (3.7)	0.40 (0.27)	1.75 (0.63)	0.68 (0.06)	0.65 (0.13)	0.96
C	QF	30	84 (13)	233 (15)	40.2 (5.7)	18.7 (3.9)	0.56 (0.28)	1.76 (0.59)	0.69 (0.06)	0.64 (0.12)	0.97
A	QP	49	95 (11)	521 (118)	45.0 (6.2)	28.5 (3.3)	0.40 (0.24)	1.79 (0.47)	0.71 (0.06)	0.51 (0.16)	0.98
B	QP	42	82 (18)	455 (82)	44.3 (5.6)	29.2 (4.1)	0.50 (0.40)	2.33 (0.61)	0.68 (0.06)	0.61 (0.18)	0.96
C	QP	59	113 (29)	520 (201)	44.3 (7.1)	22.7 (4.0)	0.53 (0.25)	1.44 (0.40)	0.68 (0.06)	0.56 (0.13)	0.98
A	TT	36	72 (26)	492 (90)	45.3 (9.2)	27.7 (4.4)	0.34 (0.22)	2.64 (0.94)	0.70 (0.08)	0.56 (0.15)	0.97
B	TT	28	56 (10)	485 (88)	46.9 (9.5)	30.6 (4.2)	0.38 (0.24)	3.17 (0.55)	0.65 (0.08)	0.54 (0.25)	0.93
C	TT	30	89 (26)	561 (164)	45.3 (6.2)	22.4 (2.8)	0.56 (0.20)	1.76 (0.59)	0.67 (0.07)	0.56 (0.13)	0.96

Table S1.3: Results from the linear regression models predicting synchrony ("rbar": the mean correlation between all tree-ring index series in a chronology) for the detrended tree-ring series (RWI) (30-year moving-average standardization and frequency cut-off at 50 %) depending on calendar year (rbar ~ year) for each species (and two site types for beech) in the transects A–C. Synchrony trends were additionally tested with the Mann-Kendal Trend Test. All significant results are printed in bold.

		Rbar ~ Year			**M-K Test**	
Transect	**Species**	**Adj. R^2**	**F-value**	**P-value**	**Tau**	**P-value**
A	*F. sylvatica* (mesic)	**0.10**	**9.3**	**<0.01**	**0.20**	**<0.05**
A	*F. sylvatica* (xeric)	**0.24**	**24.4**	**<0.001**	**0.30**	**<0.001**
A	*Q. cerris*	**0.80**	**313.6**	**<0.001**	**-0.68**	**<0.001**
A	*Q. frainetto*	**0.69**	**171.2**	**<0.001**	**-0.50**	**<0.001**
A	*Q. petraea*	**0.37**	**45.1**	**<0.001**	**-0.40**	**<0.001**
A	*T. tomentosa*	**0.16**	**15.0**	**<0.001**	**0.23**	**<0.01**
B	*F. sylvatica* (mesic)	**0.13**	**12.8**	**<0.01**	**0.18**	**<0.05**
B	*F. sylvatica* (xeric)	-0.01	0.3	0.587	-0.06	0.463
B	*Q. cerris*	0.01	1.7	0.193	**-0.25**	**<0.01**
B	*Q. frainetto*	**0.16**	**15.0**	**<0.001**	**0.20**	**<0.05**
B	*Q. petraea*	**0.27**	**29.3**	**<0.001**	**0.40**	**<0.001**
B	*T. tomentosa*	**0.56**	**81.8**	**<0.001**	**-0.50**	**<0.001**
C	*F. sylvatica* (mesic)	**0.22**	**22.9**	**<0.001**	**0.23**	**<0.01**
C	*F. sylvatica* (xeric)	**0.72**	**192.1**	**<0.001**	**0.63**	**<0.001**
C	*Q. cerris*	-0.01	0.1	0.710	-0.05	0.518
C	*Q. frainetto*	**0.42**	**55.9**	**<0.001**	**-0.43**	**<0.001**
C	*Q. petraea*	**0.27**	**28.6**	**<0.001**	**-0.37**	**<0.001**
C	*T. tomentosa*	**0.13**	**11.8**	**<0.01**	**0.19**	**<0.05**

Table S1.4: Homoscedastic variance–covariance model comparison (VCOV) for a) pre-whitened, detrended (30-year moving-average standardization and frequency cut-off at 50 %) tree-ring chronologies (ring width index, RWI) and b) detrended RWI chronologies according to restricted log-likelihood (LogLik) statistics: Akaike's Information Criterion (AIC), corrected AIC (AICc) and Bayesian Information Criterion (BIC). AIC, AICc and BIC are in smaller-is-better form. n is the number of observations used in the model fit and df is the degrees of freedom related with the number of predictors in the fitted model. The models of choice are shown in bold. Model abbreviations: Broad Evaluation model (mBE); Narrow Evaluation model (mNE); Compound Symmetry model (mCS); Unstructured model (mUN).

a) RWI pre-whitened							**b) RWI**						
Total observation period: 1940–2017							**Total observation period: 1940–2017**						
VCOV	**n**	**df**	**AIC**	**AICc**	**BIC**	**LogLik**	**VCOV**	**n**	**df**	**AIC**	**AICc**	**BIC**	**LogLik**
mBE	1392	20	-1124	-1123	-1019	-1164	mBE	1392	20	-763	-762	-658	-803
mNE	1392	25	-867	-866	-736	-917	mNE	1392	25	-492	-491	-361	-542
mCS	1392	22	-1125	-1125	-1010	-1169	mCS	1392	22	-776	-775	-661	-820
mUN	**1392**	**40**	**-1201**	**-1199**	**-992**	**-1281**	**mUN**	**1392**	**40**	**-876**	**-874**	**-667**	**-956**
Earlier period: 1940–1979							**Earlier period: 1940–1979**						
VCOV	**n**	**df**	**AIC**	**AICc**	**BIC**	**LogLik**	**VCOV**	**n**	**df**	**AIC**	**AICc**	**BIC**	**LogLik**
mBE	708	20	-537	-535	-446	-577	mBE	708	20	-328	-327	-237	-368
mNE	708	25	-334	-332	-221	-384	mNE	708	25	-117	-115	-347	-167
mCS	708	22	-533	-532	-433	-577	mCS	708	22	-324	-323	-224	-368
mUN	**708**	**40**	**-527**	**-522**	**-346**	**-607**	**mUN**	**708**	**40**	**-331**	**-326**	**-150**	**-411**
Later period: 1980–2017							**Later period: 1980–2017**						
VCOV	**n**	**df**	**AIC**	**AICc**	**BIC**	**LogLik**	**VCOV**	**n**	**df**	**AIC**	**AICc**	**BIC**	**LogLik**
mBE	684	20	-464	-463	-374	-504	mBE	684	20	-315	-314	-225	-355
mNE	684	25	-413	-411	-300	-463	mNE	684	25	-268	-266	-155	-318
mCS	684	22	-475	-474	-376	-519	mCS	684	22	-340	-339	-241	-384
mUN	**684**	**40**	**-532**	**-527**	**-352**	**-612**	**mUN**	**684**	**40**	**-416**	**-411**	**-236**	**-496**

Table S1.5. Temporal trends in synchrony patterns ("âc" ranging from 0 (no regional synchronization) to 1 (total regional synchronization) calculated in a mixed model approach, Alday, Shestakova, Resco de Dios, & Voltas, 2018) and SE for the five species for a) pre-whitened, detrended (30-year moving-average standardization and frequency cut-off at 50 %) tree-ring chronologies (ring width index, RWI) and b) detrended RWI chronologies estimated from the best homoscedastic variance–covariance models (VCOV) for 30 year-wide intervals moving by 5-year steps over the period 1940–2017. Year gives the central year of the moving time interval. Model abbreviations: Broad Evaluation model (mBE); Compound Symmetry model (mCS); Unstructured model (mUN).

a) RWI pre- whitened					b) RWI				
VCOV	**Year**	**Species**	**$\hat{a}_c$**	**SE**	**VCOV**	**Year**	**Species**	**$\hat{a}_c$**	**SE**
mBE	1955	FM; FX; TT; QC; QP; QF	0.49	0.07	mUN	1955	FM	0.65	0.06
mBE	1960	FM; FX; TT; QC; QP; QF	0.51	0.07	mUN	1955	FX	0.64	0.06
mBE	1965	FM; FX; TT; QC; QP; QF	0.46	0.07	mUN	1955	QC	0.57	0.06
mCS	1970	FM; FX; TT; QC; QP; QF	0.44	0.06	mUN	1955	QF	0.54	0.07
mBE	1975	FM; FX; TT; QC; QP; QF	0.44	0.06	mUN	1955	QP	0.43	0.06
mUN	1980	FM	0.56	0.06	mUN	1955	TT	0.70	0.06
mUN	1980	FX	0.50	0.07	mBE	1960	FM; FX; TT; QC; QP; QF	0.54	0.07
mUN	1980	QC	0.48	0.07	mBE	1965	FM; FX; TT; QC; QP; QF	0.48	0.07
mUN	1980	QF	0.46	0.07	mBE	1970	FM; FX; TT; QC; QP; QF	0.44	0.06
mUN	1980	QP	0.14	0.03	mUN	1975	FM	0.62	0.06
mUN	1980	TT	0.60	0.06	mUN	1975	FX	0.59	0.06
mUN	1985	FM	0.58	0.06	mUN	1975	QC	0.50	0.07
mUN	1985	FX	0.48	0.07	mUN	1975	QF	0.47	0.07
mUN	1985	QC	0.45	0.06	mUN	1975	QP	0.31	0.06
mUN	1985	QF	0.44	0.06	mUN	1975	TT	0.63	0.06
mUN	1985	QP	0.12	0.03	mUN	1980	FM	0.59	0.06
mUN	1985	TT	0.66	0.06	mUN	1980	FX	0.59	0.06
mUN	1990	FM	0.60	0.06	mUN	1980	QC	0.48	0.07
mUN	1990	FX	0.49	0.07	mUN	1980	QF	0.47	0.07
mUN	1990	QC	0.40	0.06	mUN	1980	QP	0.24	0.05
mUN	1990	QF	0.34	0.06	mUN	1980	TT	0.62	0.06
mUN	1990	QP	0.10	0.02	mUN	1985	FM	0.63	0.06
mUN	1990	TT	0.63	0.06	mUN	1985	FX	0.60	0.06
mUN	1995	FM	0.62	0.06	mUN	1985	QC	0.48	0.07
mUN	1995	FX	0.53	0.07	mUN	1985	QF	0.49	0.07
mUN	1995	QC	0.39	0.06	mUN	1985	QP	0.23	0.05
mUN	1995	QF	0.27	0.05	mUN	1985	TT	0.69	0.06
mUN	1995	QP	0.06	0.01	mUN	1990	FM	0.70	0.06
mUN	1995	TT	0.66	0.06	mUN	1990	FX	0.64	0.06
mUN	2000	FM	0.71	0.05	mUN	1990	QC	0.43	0.06
mUN	2000	FX	0.60	0.06	mUN	1990	QF	0.38	0.06
mUN	2000	QC	0.39	0.06	mUN	1990	QP	0.17	0.04
mUN	2000	QF	0.34	0.06	mUN	1990	TT	0.65	0.06
mUN	2000	QP	0.13	0.03	mUN	1995	FM	0.71	0.05
mUN	2000	TT	0.69	0.06	mUN	1995	FX	0.68	0.06
					mUN	1995	QC	0.45	0.06
					mUN	1995	QF	0.32	0.06
					mUN	1995	QP	0.14	0.03
					mUN	1995	TT	0.69	0.06
					mUN	2000	FM	0.77	0.05
					mUN	2000	FX	0.72	0.05
					mUN	2000	QC	0.44	0.06
					mUN	2000	QF	0.36	0.06
					mUN	2000	QP	0.21	0.04
					mUN	2000	TT	0.71	0.05

Figures

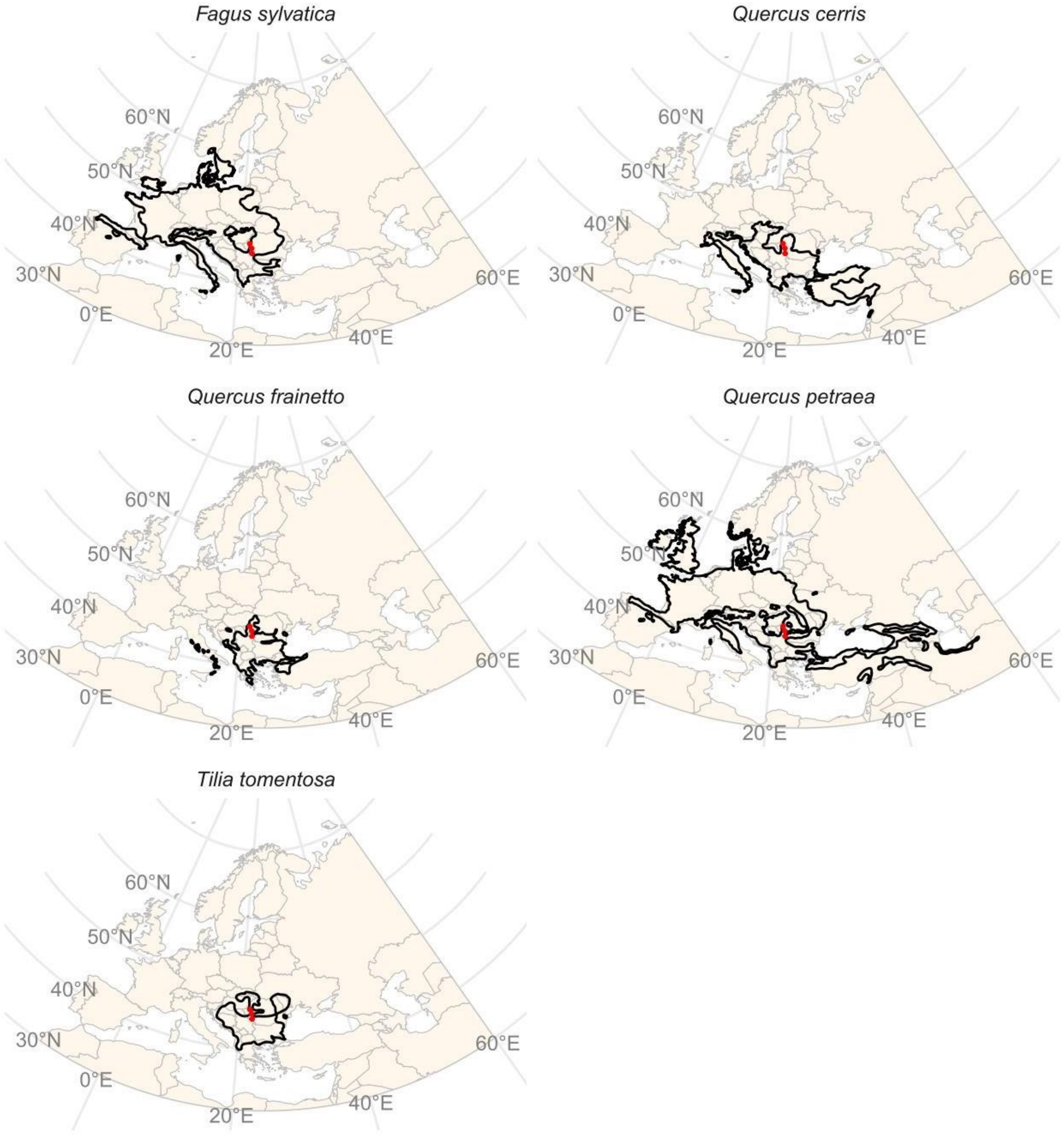

Figure S1.1: Situation of the study sites (red dots) in the closed natural distribution ranges of the studied tree species (black outlines according to Caudullo, Welk, & San-Miguel-Ayanz, 2017). Generated with Natural Earth data (South, 2011) in azimuthal equal-area projection centred on the North Pole.

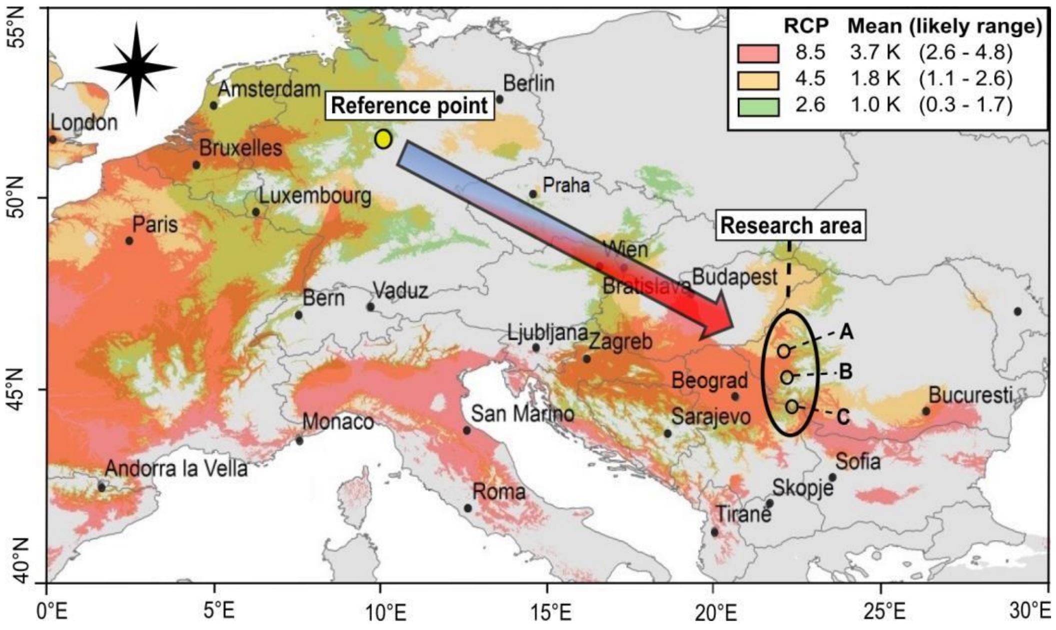

Figure S1.2: Climate warming projections for a beech forest reference point (German national forest inventory point 19288) in the centre of the distribution range of European beech (Central Germany). The red, orange and green coloured regions of Europe are climate analogue for the climate around the 2080s according to the IPCC (2013) scenarios: RCP 2.6, 4.5 and 8.5. The regions were defined following a principal component analysis representing Europe as a function of mean January temperature, mean summer temperature (June–August) and mean growing season precipitation (May–September). The climate values projected for Germany were matched within the ordination space with locations in Europe currently resembling these climate conditions. Depicted are the mean temperature increase (likely range) in Kelvin as well as the location of the study transects in western Romania, where A and B are located within the climate scenario RCP 2.6 (moderate warming) and C is within the range of scenario RCP 4.5 (strong warming) (calculations done for the NEMKLIM Project by C. Kölling, unpubl.). For more details on the methodology, see Kölling and Zimmermann (2014).

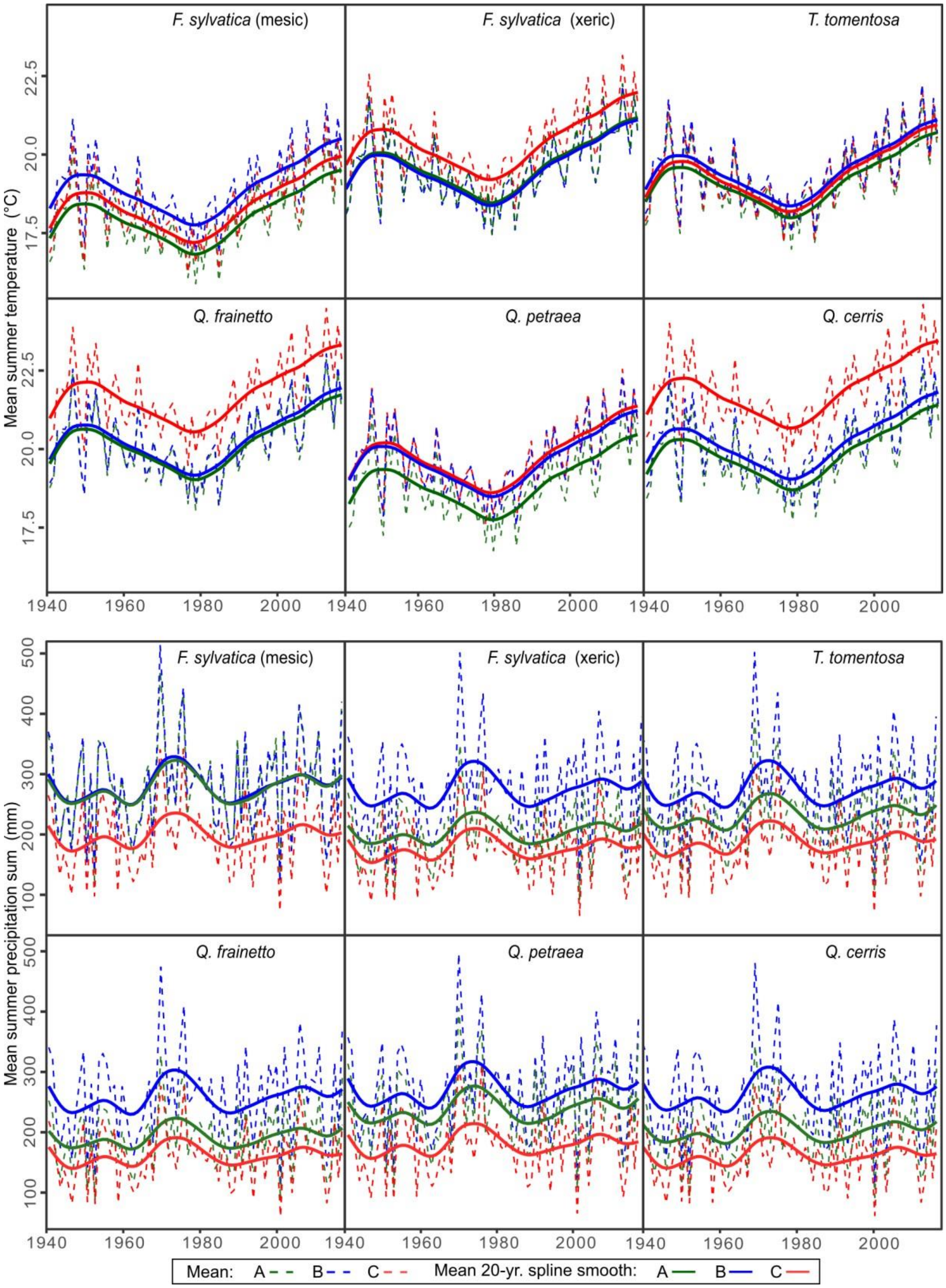

Figure S1.3: Mean summer temperature (dashed lines) and spline-smoothed (20-yr moving window) temperature curves (solid lines) (top panel) and mean summer precipitation sum (MSP, dashed lines) and spline-smoothed (20-yr window) MSP curves (solid lines) (bottom panel) for the stands of the five species (and two site types of beech) in transects A (green), B (blue) and C (red) in the western Romanian Carpathians, as calculated from the CHELSAcruts climate data sets (Karger et al., 2017) for the period 1940–2016 using the mean coordinates of the sampled populations as locality.

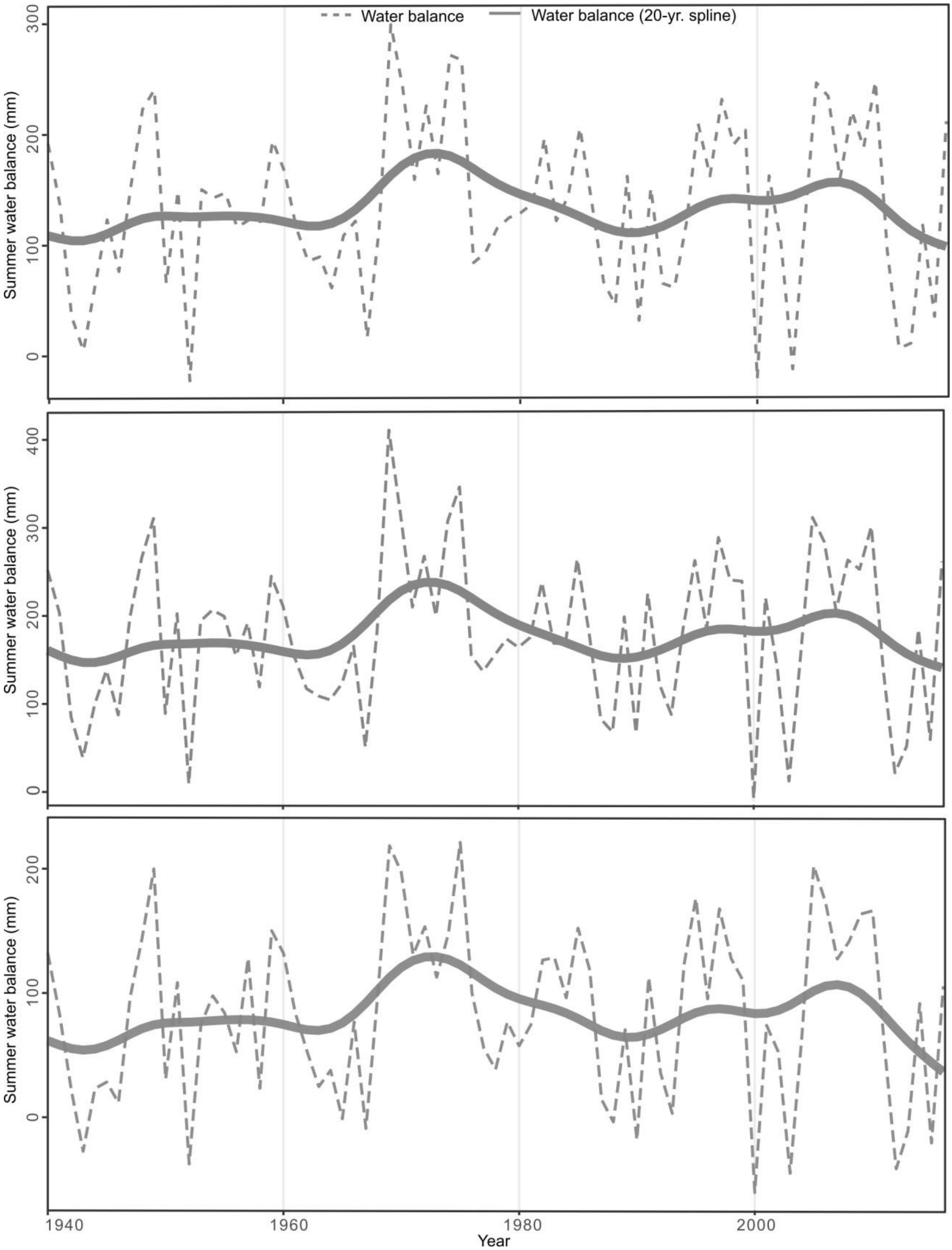

Figure S1.4: Summer water balance (and smoothing spline in a 20-yr moving window) on average in transects A, B, and C in the western Romanian Carpathians, as calculated from the CHELSAcruts climate data sets (Karger et al., 2017) for the period 1940–2016 using the mean coordinates of the transects as locality.

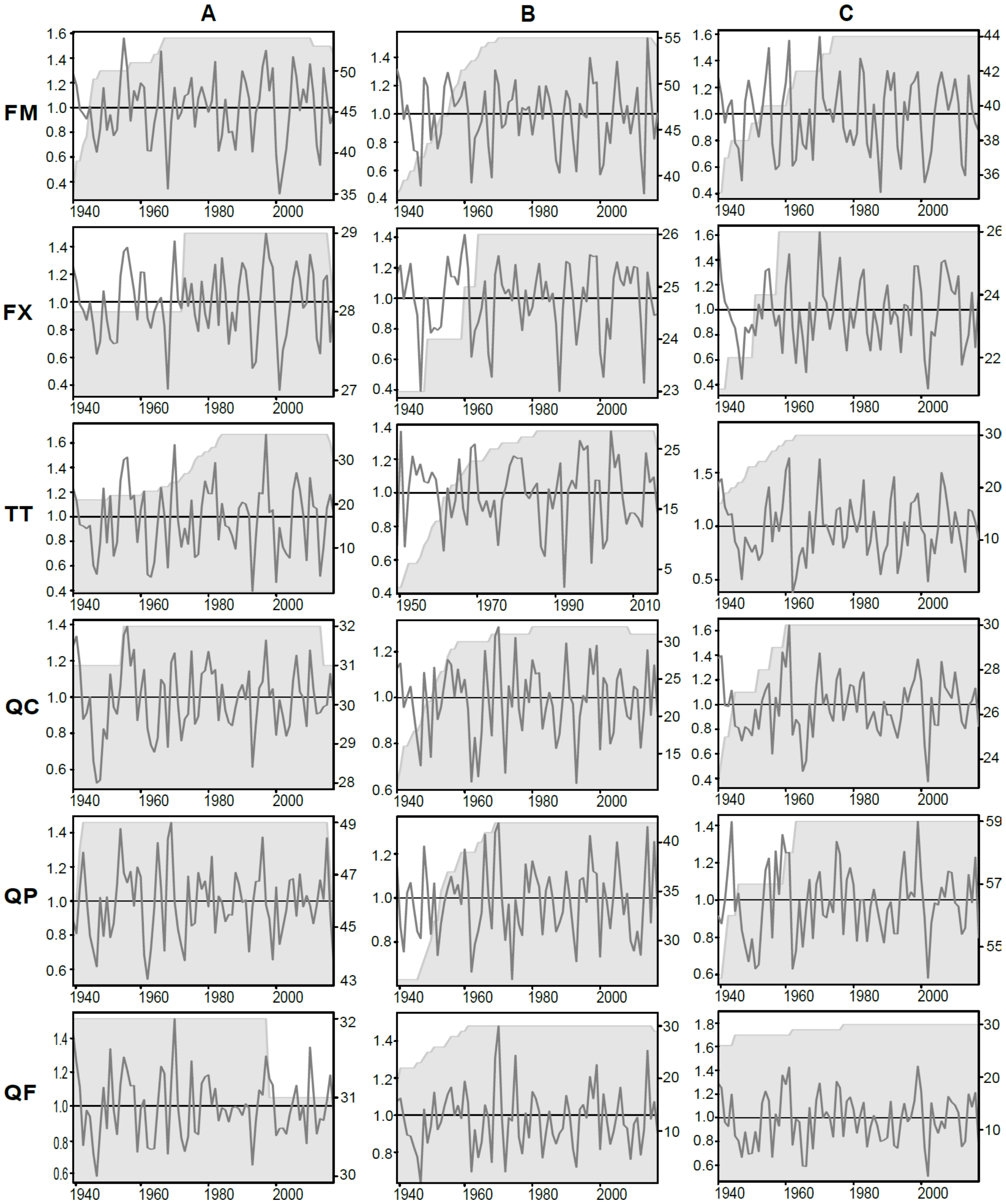

Figure S1.5: Detrended tree-ring series (ring width index, RWI) of the five species (and two sites for F. sylvatica) for the transects A, B and C in the western Romanian Carpathians generated with a 30-year moving average standardization and a frequency cut-off at 50 % for the time period 1940–2017 (except for *T. tomentosa* transect B: 1950–2017). Sample size for RWI series is depicted on the second y-axis and species abbreviations are: FM = *F. sylvatica* (mesic), FX = *F. sylvatica* (xeric), TT = *T. tomentosa*, QC = *Q. cerris*, QP = *Q. petraea* and QF = *Q. frainetto*.

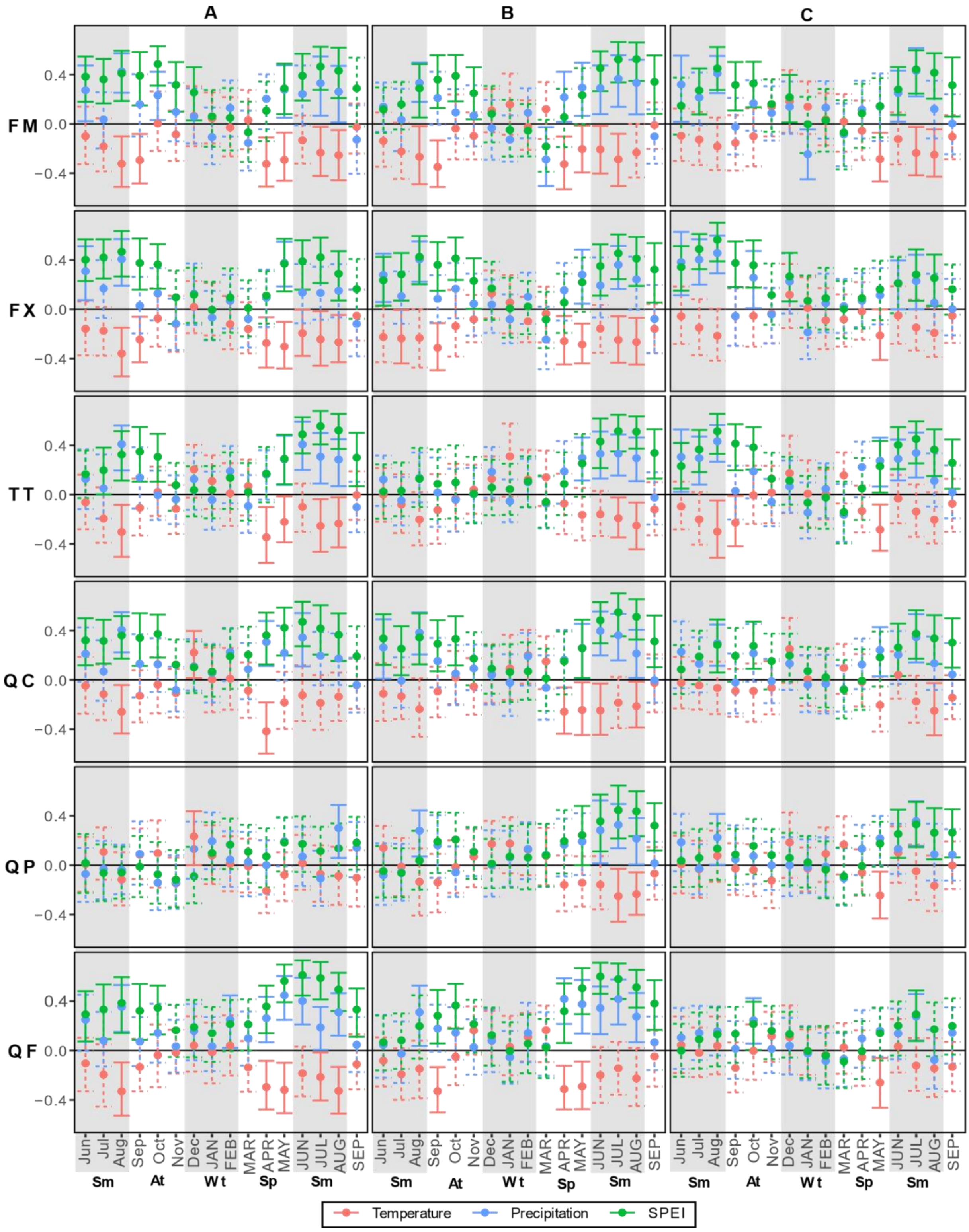

Figure S1.6: Climate–growth relationships (Pearson's r on the y-axis) for the correlation of tree-ring index chronologies with mean monthly temperature, precipitation and Standard Precipitation Evaporation Index (SPEI at 3-month scale) of the 6 previous-year months (Jun–Dec in lowercase letters) and 9 current-year months (JAN–SEP in uppercase letters). The climate variables are depicted in colour, the transects in the western Romanian Carpathians are sorted from left to right (A–C) and the species sorted from top to bottom. Significant correlations are shown through solid whiskers for the 2.5% and 97.5% empirical 1000-fold bootstrapped confidence interval. The seasons: winter (Wt), spring (Sp) summer (Sm) and autumn (At) are highlighted. Species are abbreviated as: FM = *F. sylvatica* (mesic), FX = *F. sylvatica* (xeric), TT = *T. tomentosa*, QC = *Q. cerris*, QP = *Q. petraea* and QF = *Q. frainetto*.

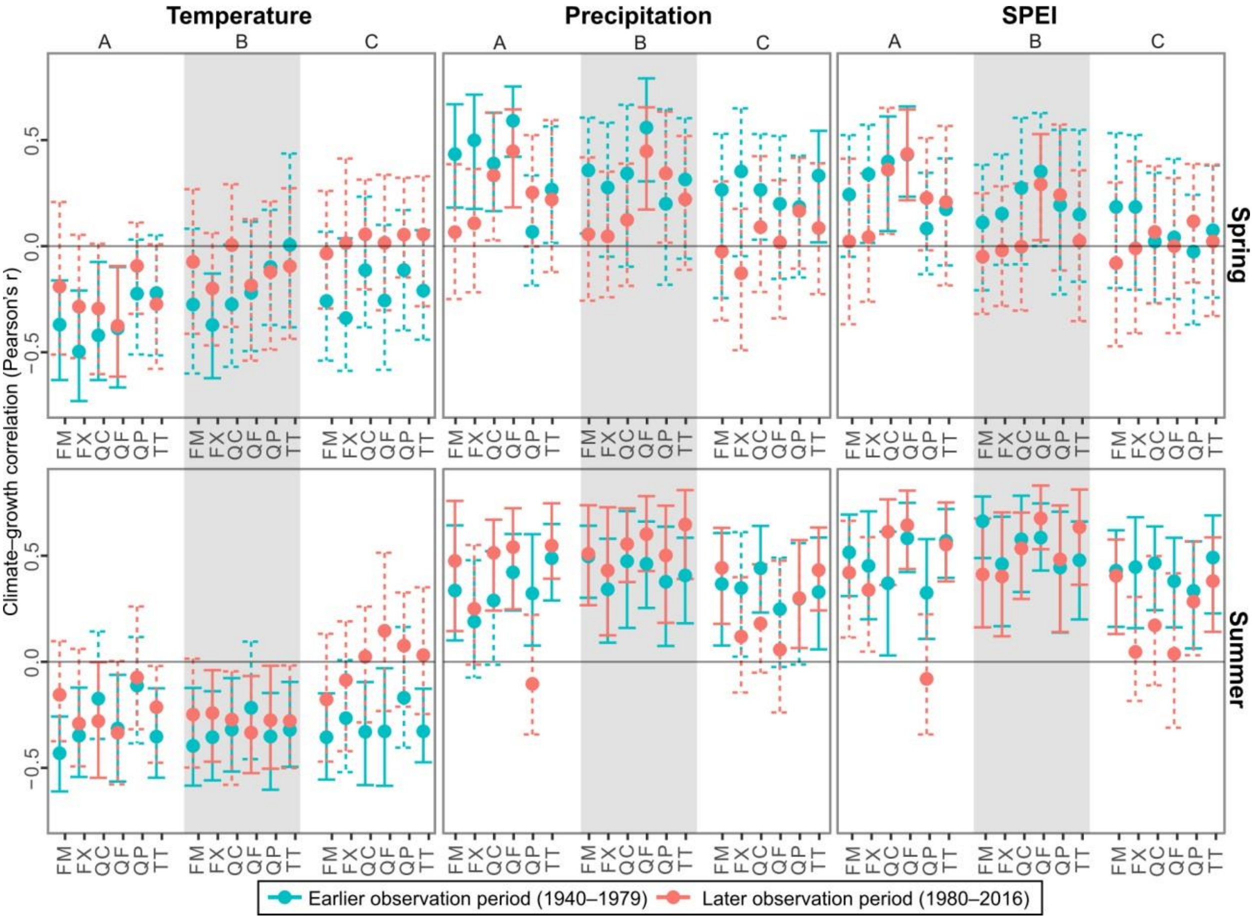

Figure S1.7. Shift of climate–growth correlations (Pearson's r on the y-axis) in the western Romanian Carpathians with spring and summer climate variables between the earlier observation period (1940–1979) and the recent climate warming (later) period (1980–2016). The five species are grouped by transects along the x-axis. Significant correlations are shown through solid whiskers for the 2.5% and 97.5% empirical 1000-fold bootstrapped confidence interval. Species are abbreviated as: FM = F. sylvatica (mesic), FX = F. sylvatica (xeric), QP = Q. petraea, TT = T. tomentosa, QC = Q. cerris and QF = Q. frainetto.

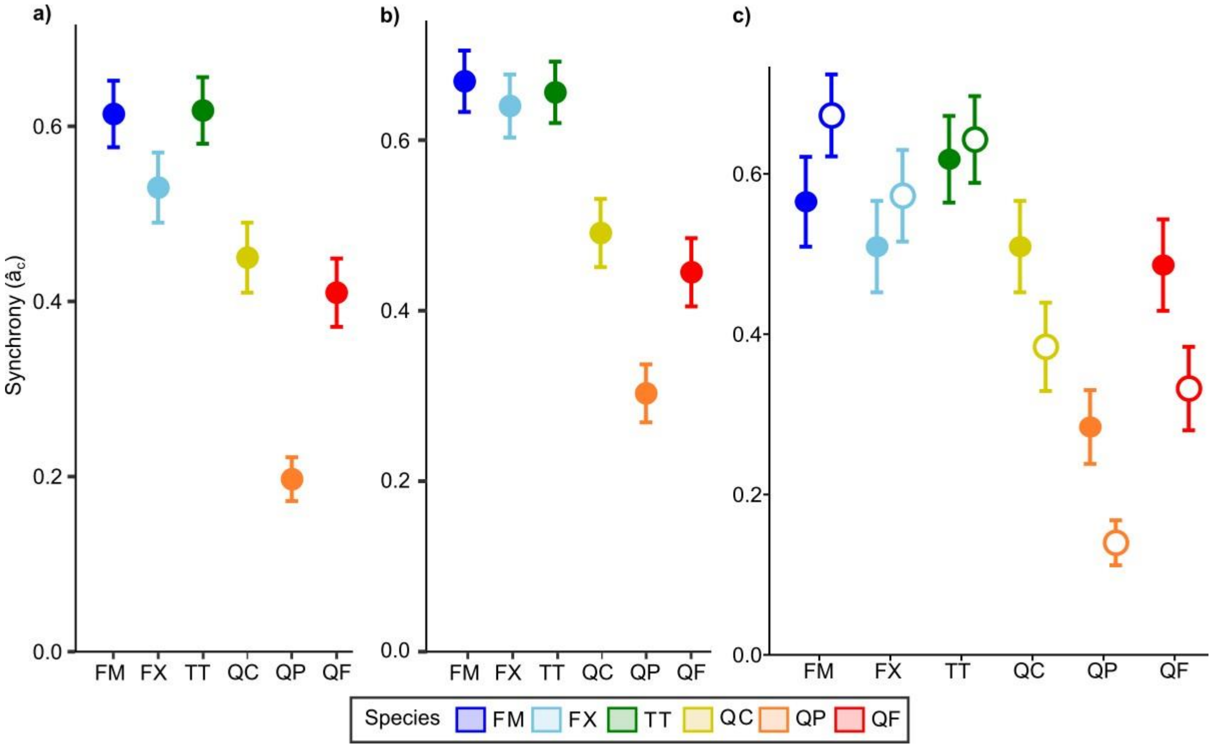

Figure S1.8. Synchrony estimates ("âc" ranging from 0 (no regional synchronization) to 1 (total regional synchronization) calculated with a mixed model approach, Alday et al., 2018) for the five species and two site types of F. sylvatica in the western Romanian Carpathians in the period 1940–2017 for a) pre-whitened, detrended RWI chronologies, b) not pre-whitened, detrended RWI chronologies, and c) for pre-whitened, detrended RWI chronologies for the periods 1940–1979 (filled circles) and 1980-2017 (circles)calculated for the best variance–covariance model. Error bars depict 1 standard error (SE). Species are abbreviated as: FM = *F. sylvatica* (mesic), FX = *F. sylvatica* (xeric), TT = *T. tomentosa*, QC = *Q. cerris*, QP = *Q. petraea* and QF = *Q. frainetto*.

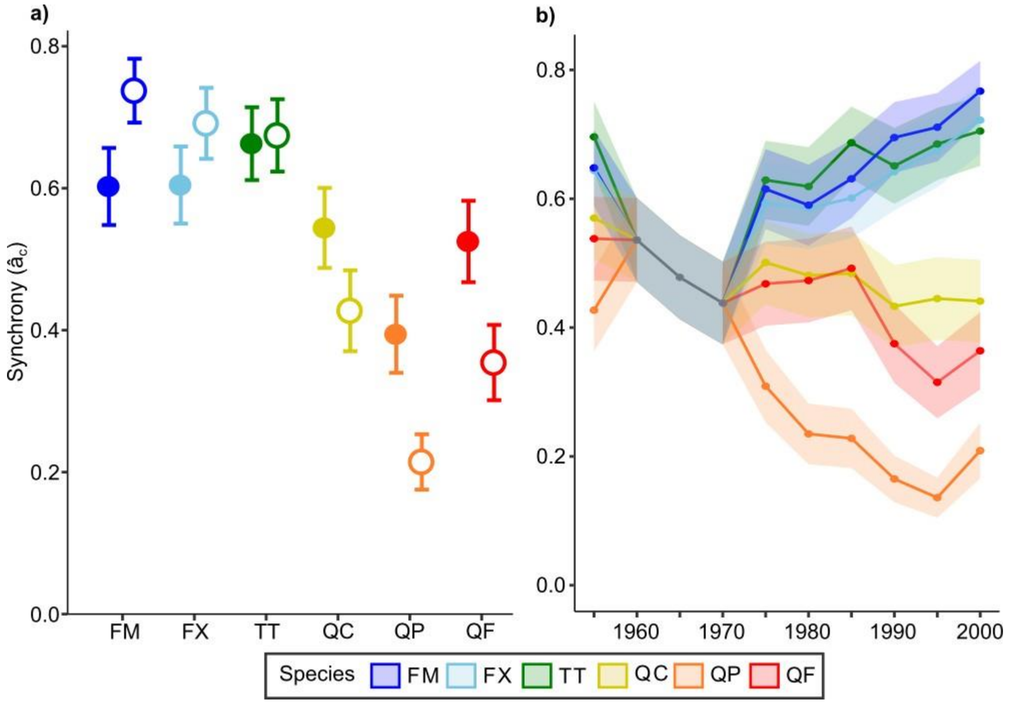

Figure S1.9: a) Synchrony estimates (“âc” ranging from 0 (no regional synchronization) to 1 (total regional synchronization) for the five species (and two site types for F. sylvatica) for non-pre-whitened, detrended tree-ring series (ring width index, RWI) chronologies calculated for the best variance–covariance model for the periods 1940–1979 (filled circles) and 1980–2017 (circles). Error bars depict 1 standard error (SE). b) Temporal trends in Synchrony patterns (âc) for the five species for non-pre-whitened and detrended RWI chronologies estimated from the best variance–covariance model for 30-year moving intervals lagged by 5 years over the period 1940–2017. The x-axis shows the central year of the moving time interval. Shadows are 1 standard error (SE). Species are abbreviated as: FM = *F. sylvatica* (mesic), FX = *F. sylvatica* (xeric), TT = *T. tomentosa*, QC = *Q. cerris*, QP = *Q. petrae*a and QF = *Q. frainetto*.

CHAPTER V

SYNOPSIS

5 Synopsis

5.1 Loss of carbon stocks with the replacement of beech by oak forests

With a projected warming by 2–3 K over the 21st century (IPCC, 2021), silvicultural adaptation measures and natural succession may lead to the replacement of European beech forests by thermophilic oak forests for large parts of central and south-eastern Europe (Hohnwald et al., 2020; Chapter 2 and Chapter 3 in this thesis). This replacement of beech by oak may considerably reduce carbon storage in aboveground biomass and soil due to shifts in tree species and forest composition (Binkley and Giardina, 1998; Burschel et al., 1993; Grüneberg et al., 2019 and Chapter 2). Our study of stand structure and ecosystem carbon pools in the beech–oak ecotone demonstrates possible consequences of this climate change-driven forest transformation. From the cooler, more humid beech forests to the warmer, xeric oak forests, which are 1–2 K warmer, above ground carbon and soil organic carbon pools decreased by about 22 % (40 Mg C ha^{-1}) and 20 % (17 Mg C ha^{-1}), respectively (see Chapter 2). If drought- and heat-affected beech forests in Central Europe are replaced by thermophilic oak forests in future, this will lead to carbon losses of ~ 50–60 Mg ha^{-1}, thus reducing ecosystem carbon storage substantially. In our model's size of biomass and soil carbon pools was clearly related to a beech–oak abundance gradient, confirming that, despite a marked effect of region, the decrease in ecosystem C storage is significant thus underpinning the general validity of our findings. While the biomass C difference is mainly caused by tree species and related management effects, it is likely that the soil organic carbon difference is largely a consequence of the elevation difference and temperature change. Our results demonstrate that carbon inventories across forest ecotones along temperature and/or precipitation gradients are one option for scientists and foresters to explore putative changes in biomass and soil C stores that result from man-made or natural tree species shifts.

5.2 Declining growth and increasing synchronicity in fast growing beech and linden in comparison to oaks

Dendrochronological studies in natural ecotones between two major forest types can be a valuable tool for identifying climatic turning points of tree species (Mette et al., 2013) and for enabling evidence-based predictions on future species shifts upon climate warming (Jump et al., 2006; Penuelas and Boada, 2003). Moreover, the approach allows comparing the drought sensitivity of different tree species, which is needed to support future silvicultural decision-making (Fuchs et al., 2021; Knutzen et al., 2017; Kunz et al., 2018). Climate sensitivity, resilience to drought of radial growth, and long-term growth trends of mesic and rear-edge populations of beech (*F. sylvatica*), the three oak species (*Q. petraea, Q. frainetto, Q. cerris*) and silver linden (*T. tomentosa)* in natural beech–oak ecotones showed that radial growth of all species was positively influenced by summer precipitation and low drought intensity, and negatively by high summer temperatures. However, beech and silver linden with higher mean individual-based basal area increments, suffered continued growth declines during the last 10–20 years, while the slower-growing oak species maintained stable growth rates despite a deterioration of the climatic water balance. Growth reductions during three severe 21st century summer drought events were stronger, and growth resilience lower, in beech and silver linden than in the oak species, pointing at a thermal limit for stable beech growth rates close to 20–21 °C in mid-summer (see Chapter 3). Both the negative BAI trend and a lower average resilience to droughts support conclusions that faster-growing trees such as beech and linden are more susceptible to drought and the slower-growing, better-adapted oaks will eventually outperform beech at its heat- and drought-induced distribution limit (Dolos et al., 2016; Fuchs et al., 2021; Kunz et al., 2018 and Chapter 3).

Precise predictions of climate change impacts on forests also require a better species-specific and site-specific understanding of how tree growth-climate relationships are affected. Spatiotemporal patterns of climatic sensitivity and growth synchronicity patterns can provide valuable information on this (D’Arrigo et al., 2008; Stine and Huybers, 2017; Wilmking et al., 2020). We observed that tree ring increment was mostly limited by summer water availability with the importance of summer precipitation increasing after the onset of climate warming (after 1980), while other climate factors in spring and summer became less important. Accordingly, the growth synchronicity, as a measure of common climatic stress among tree individuals, increased or remained constant for the drought sensitive beech and silver linden. In contrast, growth synchrony decreased in the past decades for the more drought resilient oak species (see Chapter 4). These findings for beech coincide with results from other studies (del Río et al., 2021; Muffler et al., 2020) and show that also in temperate ecosystems, climate change impacts can be analysed through the interpretation of synchrony patterns of tree-ring networks (Black et al., 2018; Shestakova et al., 2014; Tejedor et al., 2020 and Chapter 4). Growth synchronicity can thus provide insights on growth dynamics in “rear edge” tree populations, where due to climatic constraints the analysis of climate growth relationships fails to disclose the information (Shestakova et al., 2019, 2018). Our results also show that tree growth for all species was consistently linked to water availability, which is also declining and is the main factor inhibiting tree growth thus effecting synchrony patterns.

Since the climate of the studied ecotones in Romania is similar to the predicted climate at colline / submontane elevation in Central Europe in about 50 years, a decline in beech growth and vitality is also likely in the distribution centre of beech. The well-documented higher drought tolerance of *Q. petraea* and *Q. frainetto* (and also of *Q. cerris*) (Friedrichs et al., 2009; Härdtle et al., 2013 and Chapter 3 and 4) recommends these species for silviculture in central and south-eastern European regions, where beech is predicted to lose vitality. The replacement of beech by oaks also demonstrates that higher drought tolerance usually is linked to lower productivity, as is visible in the lower growth rates and smaller height of the oak species in this doctoral study (see Chapter 3). Given the uncertain future of climate, it may be wise for silviculture to favor the stress-tolerance over the high-yield option, where oaks can be considered as more secure species that produce highly valued timber.

5.3 Consequences for Central European beech forests at their "climatic edge"

Significant changes in forest dynamics are taking place since the late 20th century and consequently productive species, such as beech may face an increasing risk of warming-induced forest damage. When beech dominance at mesic sites declines, accompanying tree species will start outperforming it, especially as most deciduous trees species in Central Europe have their ecological optimum in the center of the beech distribution range (Leuschner and Ellenberg, 2017). This retreat of beech as dominant element of mesic forest stands can be either temporary as "short-term" effect (e.g. after large-scale windthrows or calamity events) or permanent as "long-term" effect after a climatic threshold is exceeded. As we are expecting an increase in frequency of windstorms and weather extreme events, disturbance ecology will thus play an increasing role in central European forest dynamics. According to Senf et al. (2018) tree canopy affected by mortality has already doubled in the last 30 years and climate warming associated increases in heat and drought periods have led to severe vitality loss and mortality in many temperate European forest ecosystems (Allen et al., 2015; Schuldt et al., 2020; Senf et al., 2020). When the "climatic turning point" for beech forest ecosystems is surpassed, long-term effects of beech replacement become apparent and more stress-tolerant and / or more regenerative tree species successively establish themselves. Here our results show that a system change from mesic beech forests over submesic mixed oak forests to mixed deciduous oak forests is a possible scenario for large parts of Central Europe (see Chapter 1). Other associated effects with this system change could be increased tree mortality and higher deadwood supply, increased vertical stratification of stands and altered competitive conditions for forest regeneration (Heinrichs et al., 2016; Öder et al., 2021; Petritan et al., 2012). Although a warming in the near future will generally increase both forest productivity and decomposition rates, if other factors such as drought or nutrient deficiency are not limiting, empirical findings suggest that temperate forest soils will respond by decreasing the soil organic carbon pool (Hopkins et al., 2012; Melillo et al., 2017). Also may shifts in tree species composition accelerate carbon losses, as more drought-tolerant species are typically less productive in biomass accumulation (Fuchs et al., 2021; Walentowski et al., 2017 and Chapter 2). Our examination of stand structure and ecosystem carbon pools along the semi-natural beech–oak ecotones support this theory and reveal some potential consequences of changes in forest vegetation. However, scientists and foresters concerned with tree species selection and the effects on forest carbon storage in the face of global warming will still need to improve their understanding of the consequences of future tree species shifts.

5.4 Assisted migration on an ecological basis as a strategy

In view of increases in frequency and intensity of natural hazards, rising winter and summer temperatures and intensifications of droughts (IPCC, 2021; Kornhuber et al., 2019; Lesk et al., 2016; Mitchell et al., 2016) the question of appropriate mitigation strategies for forest management arises. As forest ecosystems are controllable through forest management, climatic “short term” effects can for example be mitigated by promoting fast-growing tree species with pioneer characteristics, whereas long term effects can be reduced by implementing species with higher drought resilience. In this context, increasingly adopted in Central Europe, is the cultivation of conifer tree species such as Douglas fir (*Pseudotsuga menziesii* [Mirbel] Franco) or Corsican pine (*Pinus nigra* J.F. Arnold) (Eilmann and Rigling, 2012; Isaac-Renton et al., 2014), however, regarding the ecological effects of introduced species on biodiversity (Felton et al., 2016), there is a strong drive towards the use of more native trees to adapt forests drought resistance (Brang et al., 2008; Vitali et al., 2017).

Here, the possibility of “assisted migration” strategies, aiming to enrich forests with selected tree species or species provenances, based on analysis of origin and destination are one option (Kreyling et al., 2011; Williams and Dumroese, 2013), especially in areas that are susceptible to increasing drought severity and frequency. Towards the warm-dry edge of beech dominance in Central Europe, secondary and companion tree species are becoming more and more relevant for climate-adaption and a whole range of native tree species can play an increased role in future forest management (Fuchs et al., 2021; Kunz et al., 2018; Walentowski et al., 2017). In our warmest regions in Germany forest management could already include tree species that are now sub-Mediterranean in distribution and whose climatic envelopes very well can be realized in the future (Kölling and Zimmermann, 2014; Mellert et al., 2016, 2015 and Chapter 3 and 4).

The forests of Romania offer a spectrum of possible tree species, where a controlled, assisted migration could ensure habitat continuity in the future (e.g. introducing drought adapted beech provenances or thermophile oak species). The idea of implementing native secondary tree species into silviculture is not a new insight – however, has this in commercial forests so far been predominantly discussed in connection with economic risk diversification, rather than as guarantors of ecological biotope and habitat continuity. Assisted migration must comprehensively take into account concerns of biodiversity conservation, economic aspects and forest protection and therefore must be done cautiously as it is also associated with risks and certainly does not offer a sole solution to the problems (Vitt et al., 2010; Williams and Dumroese, 2013). Concerning our research area in western Romania for example, bioclimatic requirements such as the oceanic gradient must also be considered.

Ecological forest conversion towards deciduous forests adapted to climate warming requires a broader thinking and other measures to reduce anthropogenic pressure on forests must be considered. A guiding principle here should be to consider what nature offers as an ecological response to climatic shifts and increasing disturbance regimes. However, this will not work without trade-offs between economic and ecologic objectives and the price for higher stress tolerance and regeneration capacity of for example oak species compared to beech, is lower volume increment, lower mass yield and a lower C storage in biomass (see Chapter 3). Choosing stress-tolerant species may be an uncomfortable truth for foresters who are facing an increasing risk of forest damages and forest managers will need to decide on which ecosystem services to prioritize.

5.5 Future directions and final words

Future studies must consider that tree species resisting drought has different implications on their growth performance and mortality risks. Clearly, retrospective analyses of radial growth rates, as described in Chapter 3 and 4, are limited to living trees and the results might be biased, as they only represent the surviving part of the populations. To fully capture the impact of increasing drought exposure on a species, both, growth reactions and mortality rates, must be addressed. However, to record drought-driven mortality rates, information on mortality of unmanaged stands is required, which is difficult to obtain in regions such as Central Europe. A comprehensive analysis of drought-induced mortality including physiological measurements, would help identify lethal stress levels in the species' drought responses. Additionally, short term growth reductions in response to drought should be supplemented with wood anatomical and physiological research in the post-drought phase to measure, whether growth reductions are an expression of vitality loss, or are part of a drought response due acclimation and thus an expression of increased drought tolerance.

Generally, field studies across climatic gradient transects as “space-for-time substitutions” are a valid method in forest ecology to derive climatic limits of changes in increment, physiological tree responses, and stress indicators of tree growth in the face of climate change. Here, the present dissertation provides insights to drought responses of two key deciduous tree species in European forests (beech and sessile oak) along a climatic gradient and closes a knowledge gap for three lesser-known timber species (*Q. cerris*, *Q. frainetto* and *T. tomentosa*). However, there are large differences for observed and predicted impacts of climate change on forest ecosystems, which not only depend on future climates but also on geographical scales, forests predispositions, land-use legacies, disturbance regimes and most importantly management schemes. The preceding analysis and descriptions of some major climate change effects shows that addressing them at larger level remains difficult and that most environmental impacts are interconnected at multiple ecological levels making precise predictions difficult. However, the results also clearly show that climate change impacts are a current reality and must be investigated at all forest ecosystem levels to address their full magnitude and thus find adequate solutions for mitigation.

5.6 References

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CHAPTER VI

GENERAL APPENDIX

Acknowledgements

First of all, I would like to thank God Almighty for creating trees and climate.

I thank Veronika Öder for her cooperation and Stefan Hohnwald for his organisational capacities facilitating my field stays in Romania and giving me scientific advice. Special thanks also to my Thesis Advisory Committee for the scientific supervision during my doctoral time. I also appreciate the comprehensive, quick replies from Dirk Gansert advising me administratively. Special thanks also to the examination board in taking time to review my dissertation and being available for its defence.

Several people supported me writing this thesis and finishing it would not have been possible without the help of these colleagues and friends. My severe gratitude goes out to all technical assistants working at the institute and all students that participated in the field, laboratory and analytical work, notably: Anja Gröning, Jonas Haber, Leon Schmidt, Mathias Rümping, Charlotte Loris and the rest of the NEMKLIM field students crew for staying motivated after long working days.

My thanks go to the NEMKLIM project partners in Romania and Germany, especially Any Mary Petritan. I further would like to thank the forestry offices in Radna, Caransebeș, Oțelu Roșu and Orșova for their permits and uncomplicated collaboration. My severe gratitude goes to Prof. Dr. Helge Walentowski for the technical and financial support of the HAWK as well as proof reading and editing. I am very grateful to Dr. Robert Weigel for his efforts in scientific analyses, co-authorships and his major advice in any R-related questions. Thank you for real Robert!

I would also particularly like to thank Prof. Dr. Christoph Leuschner for a challenging PhD project, for advice, support and constant trust over the last four years.

Most importantly, my greatest thank goes to my closest family and friends for the encouragement and especially to Lara for her patience and perseverance of my moods, for the help in the field, editing work, e-mail correspondence and mental support and for simply being the best – together with Jakob, who makes me smile every single day since he is born.

Erklärungen

1. Hiermit erkläre ich, daß diese Arbeit weder in gleicher noch in ähnlicher Form bereits anderen Prüfungsbehören vorgelegen hat. Weiter erkläre ich, daß ich mich an keiner anderen Hochschule um einen Doktorgrad beworben habe.

2. Hiermit erkläre ich eidesstattlich, daß diese Dissertation selbständig und ohne unerlaubte Hilfe angefertigt wurde.