RESEARCH PAPER

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

Jan Kasper[1] · Robert Weigel[1] · Helge Walentowski[2] · Anja Gröning[1] · Any Mary Petritan[3] ·
Christoph Leuschner[1]

Abstract

Key message **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.**

Context 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 twenty-first 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.

Aims 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).

Methods 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.

Results 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 the case of AGC, but direct temperature effects for SOC.

Conclusion 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.

Keywords Beech-oak ecotone · Climate turning point · *Fagus sylvatica* · *Quercus petraea* · Above ground carbon · Soil carbon · Soil nutrient pools

---

Handling Editor: Shuguang (Leo) Liu

✉ Jan Kasper
jan.kasper@uni-goettingen.de

Extended author information available on the last page of the article

1 Introduction

Climate warming-related heat waves and droughts have the potential to destabilise 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; Horvat et al. 1974), 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, 2008), 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 2080 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 twenty-first 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 year^{-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 have 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 twenty-first 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; Doniţă, 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 (Doniţă, 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 determined not only 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: (i) tree species diversity increases with the transition from beech to oak dominance, as beech dominance suppresses light- and warmth-loving species. (ii) The aboveground biomass C storage decreases from beech to oak dominance, as drought-affected forests accumulate less biomass. (iii) Soil organic carbon (SOC) storage decreases from beech to oak dominance, as higher temperatures favour mineralization. (iv) The C stock decrease in biomass is primarily a tree species effect, while the decrease in SOC is mainly a climatic (elevation) effect.

2 Methods

2.1 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 (Fig. 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 (Fig. 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 Eşelniţa (C; 44.7° N/22.3° E) west of Orşova close to river Danube (Fig. 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 (Fig. 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.

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 have 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).
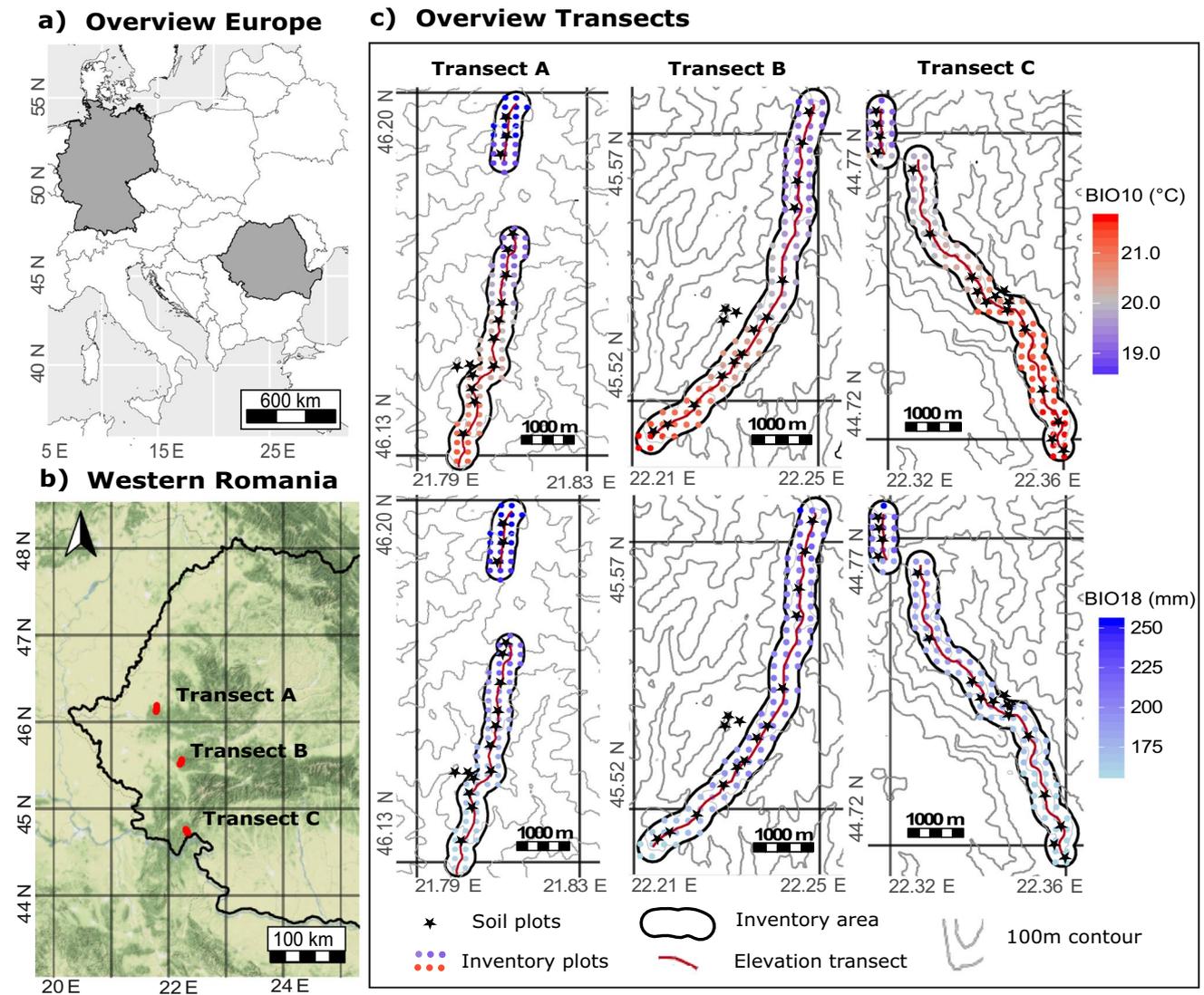
a) Overview Europe

c) Overview Transects

Fig. 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)

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 4, in the Appendix). The lapse rate of annual precipitation was assumed to be $+45$ mm year^{-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).

$$EQm = \left(\frac{BIO10}{BIO18} \right) \times 100$$

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.

2.2 Climate data

High-resolution gridded climate data with a grain of 30 arcsec (~ 1 km^2) 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 characterise the three gradients with respect to thermal and hygric conditions (Fig. 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 centre of the beech distribution range (Fig. 2).

2.3 Forest inventories and dominant tree species

We obtained forest structure data through systematic sampling in a squared grid of 200 m $\times$ 200 m along the studied 500 m-wide north–south oriented transects (Fig. 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 5, in the Appendix). For each grid point, the starting point was accessed in the field with a GPS (Garming 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) $\geq$ 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 $\alpha > 9°$ (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 (Kasper
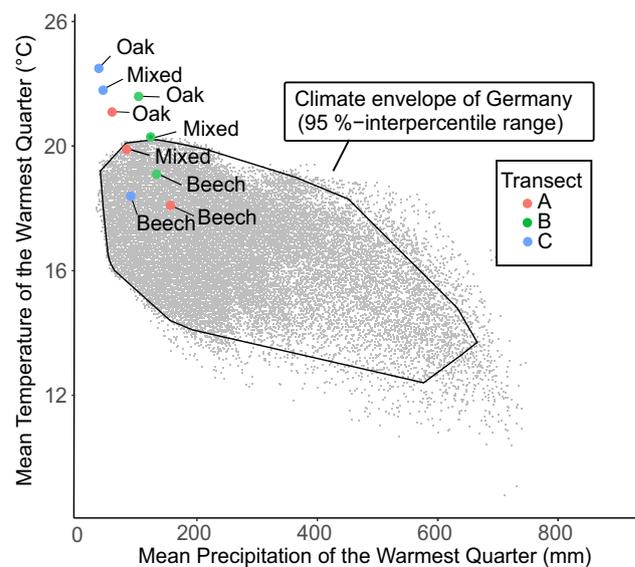

Fig. 2 Location of the oak, mixed forest and beech plots of the three transects (red: transect A, green: transect B, blue: transect C) in a biplot of mean temperature of the warmest quarter (BIO10) and mean precipitation of the warmest quarter (BIO18), relative to the climate stations of Germany (grey 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)

et al. 2021). 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):

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

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 6 (in the Appendix).

2.4 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
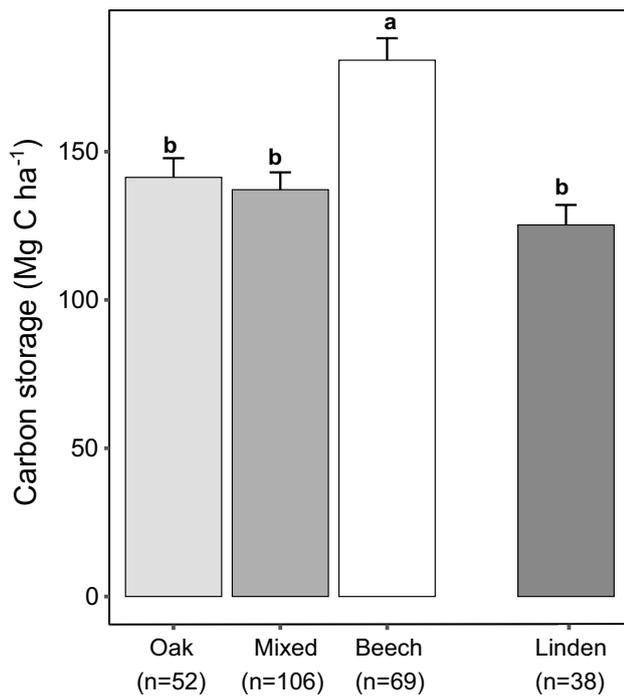
INRAE   Springer

Fig. 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)

elevation steps (13–15 pits per transect; black stars in Fig. 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 cm^3 volume for 48 h at 70 °C and weighing them (Kasper et al. 2021).

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$_2$O, the organic fraction was dissolved with 30 mL H$_2$O$_2$ (30%) and the soil particles were subsequently dispersed with a solution of 60 g Na$_4$P$_2$O$_7$ per 1.0 L H$_2$O (for details see www.meter group.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$_2$O) was measured in a suspension of 10.0 g fresh sieved soil (2.5 g for the organic layer) in 25 mL deionised 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 μmol$_c$ 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 × 8–50. P$_{av}$ was then re-exchanged from the resin with NaCl and
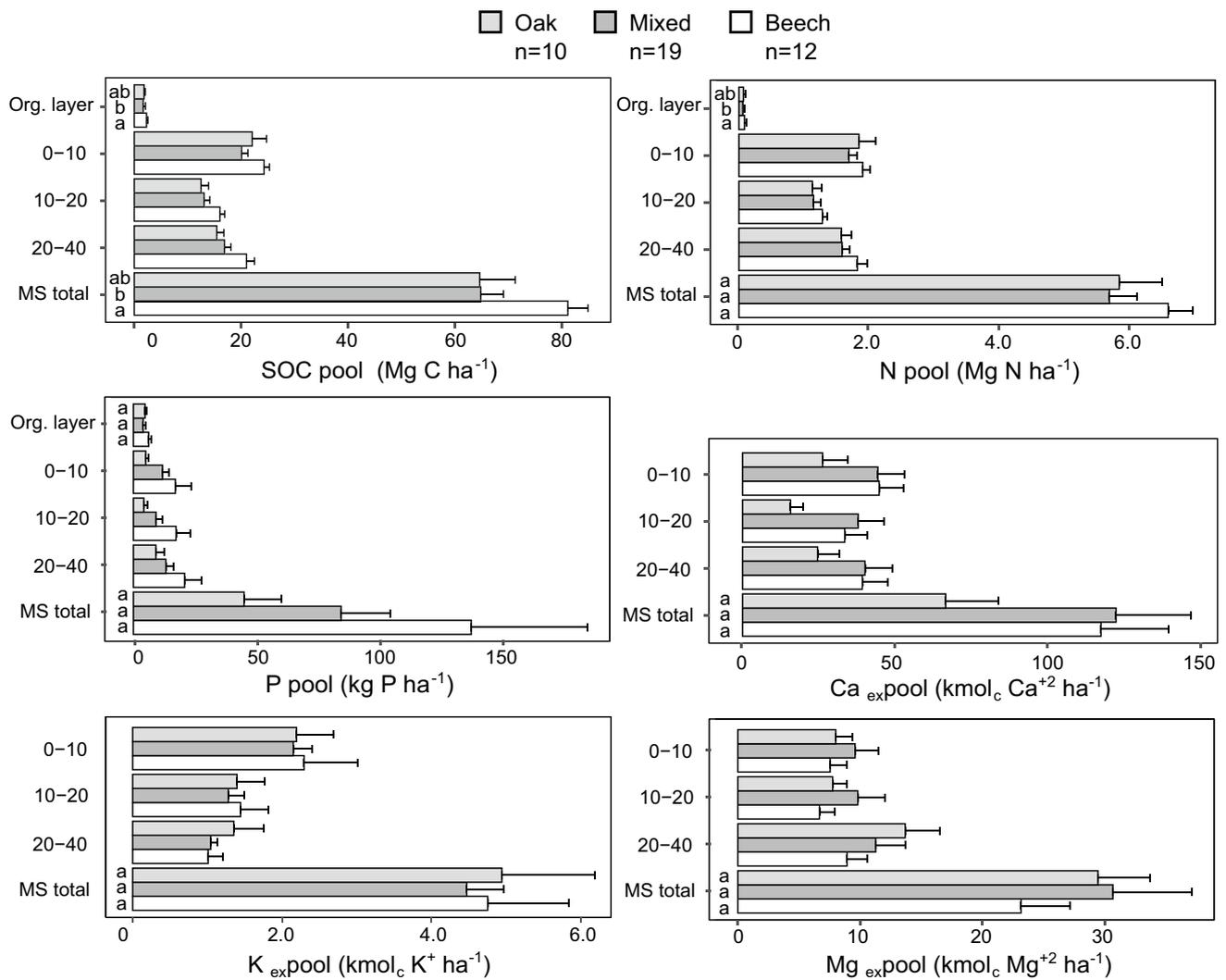
Fig. 4 Means (and SE) of C, N, P and cation pools in organic layer and mineral soil of the beech, mixed (beech-oak) and oak stands (n = number of plots). In the case of SOC and N, total pools are given for organic layer and mineral soil. P_{av} is resin-extractable P in the mineral soil and total P in 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

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 amongst 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 7 in the Appendix)

2.5 Data analysis

All data was analysed 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

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

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 m^2 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 multi-collinearity 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). Furthermore, 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).

Furthermore, 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 ($y \sim$ transect × index). If the interaction was non-significant, the interaction was removed to simplify the model ($y \sim$ 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.

3 Results

3.1 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; Fig. 3 and Appendix Table 8). 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) (Fig. 4 and Appendix Table 9). 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 (Fig. 4 and Appendix Table 9). The difference in AGC between beech forests and oak-, mixed oak-beech- and linden-dominated forests was found in all three transects (Fig. 7, in the Appendix), whereas the trend to higher SOC contents in the beech forests was only observed in transects B and C (Fig. 8, in the Appendix).

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$_2$O]	−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 10–20 cm [mg g^{-1}]	**−0.98**	**−0.20**	**0.16**	**< 0.01**
SOC 10–20 cm [mg g^{-1}]	**−0.76**	**−0.65**	**0.16**	**< 0.01**
STN 0–10 cm [mg g^{-1}]	**−0.98**	**−0.20**	**0.15**	**< 0.01**
SOC 0–10 cm [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 20–40 cm [mg g^{-1}]	**−0.57**	**−0.82**	**0.09**	**< 0.01**
STN 20–40 cm [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}$10–20 cm [mg kg^{-1}]	**−0.48**	**−0.88**	**0.04**	**< 0.05**
C/P 0–10 cm [g g^{-1}]	−0.85	−0.53	0.04	0.09
N/P 0–10 cm [g g^{-1}]	−0.82	−0.57	0.03	0.17
P$_{av}$ 0–10 cm [mg kg^{-1}]	−0.26	−0.97	0.03	0.05
pH [H$_2$O]	**−0.66**	**0.75**	**0.03**	**< 0.05**
C/N 0–10 cm [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$_{av}$ 20–40 cm [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 10–20 cm [g g^{-1}]	−0.17	0.98	0.02	0.67
N/P 10–20 cm [g g^{-1}]	−0.18	0.98	0.01	0.73
C/N 10–20 cm [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 20–40 cm [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 20–40 cm [g g^{-1}]	0.38	−0.93	0.00	1.00
C/P 20–40 cm [g g^{-1}]	0.72	0.69	0.00	1.00

The nitrogen pool in the organic layer of the mixed stands and the oak forests was smaller than in the beech forests (Fig. 4; difference significant only to beech forests), while the differences in the mineral soil N pools were not significant (Fig. 4 and Appendix Fig. 8). The significant trends between forest types were more pronounced in the transects B and C than in A (Fig. 8 in Appendix). Soil C/N ratio and base saturation did not differ between the three forest types (Table 9 in 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 (Fig. 4 and Appendix Fig. 8). 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 (Fig. 4 and Appendix Table 9). For the Mg and K pools, no clear patterns across the three forest types were found.

3.2 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 6,
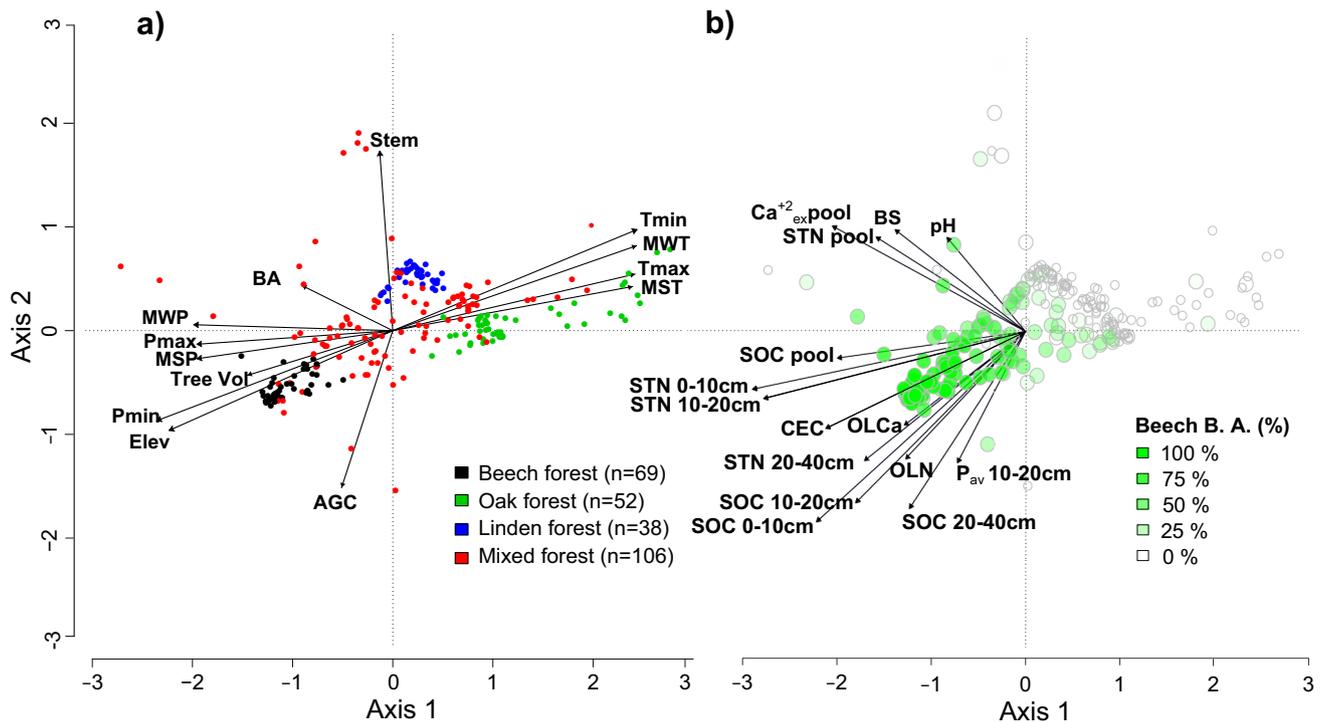
INRAE ⌂ Springer

Fig. 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 %) 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 11 in 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

in the Appendix) and of the two less abundant thermophilic oak species (*Q. cerris* and *Q. frainetto*, Table 6, 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 amongst 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 (Fig. 10, in the Appendix).

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 the 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 (Fig. 5a, Table 2a).

Amongst the soil variables, the association with the ordination axes was the 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 (Fig. 5b, 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 (Fig. 5b, 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).
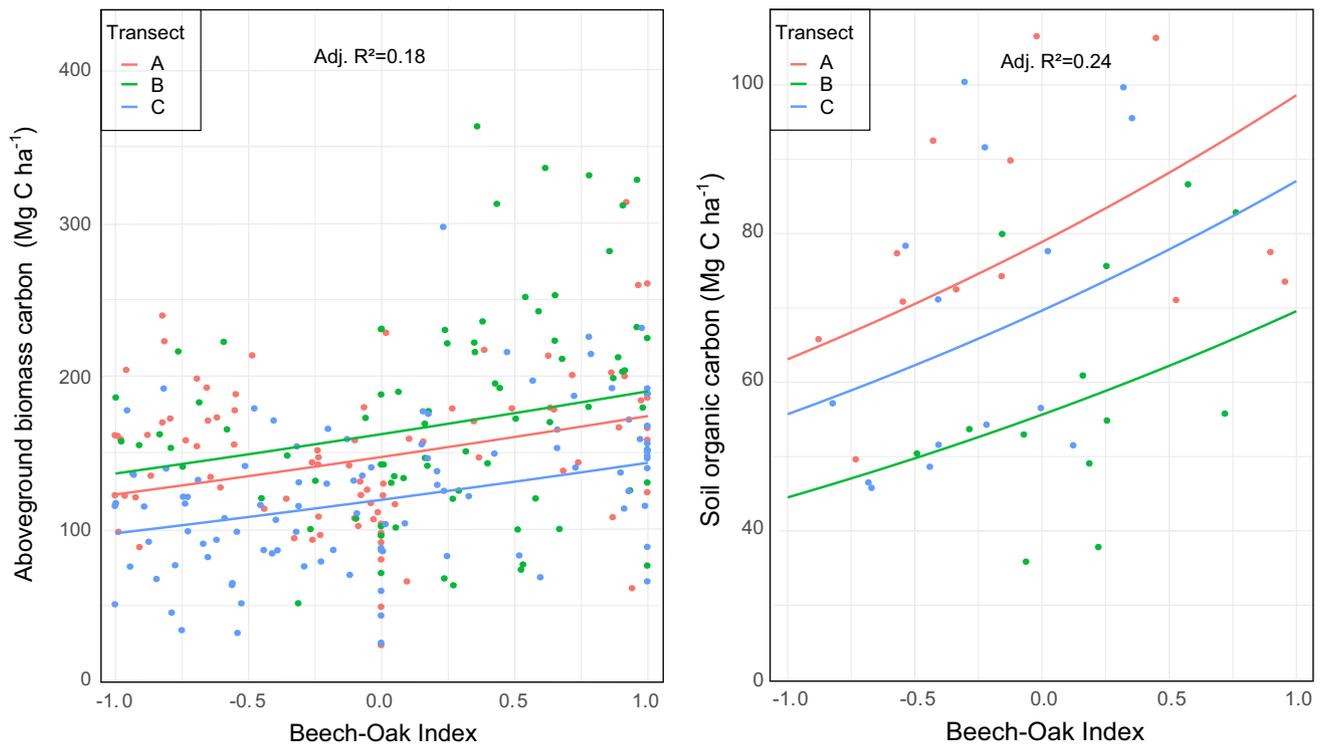
Fig. 6 Left panel: aboveground carbon (Mg C ha^{-1}) and right panel: soil organic carbon (Mg C ha^{-1}) in dependence of the beech-oak index (-1 for 100% oak to 1 for 100% Beech relative basal area) for the three transects according to the model predictions. The adjusted R^2 of the model fit is also given. The abundance of plots near an index value of 0 is caused by plots in which *T. tomentosa* forms pure stands

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 (Fig. 5a, Table 2a).

3.3 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) and 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 $y \sim$ transect $\times$ index. None of the variables was related to the interaction between transect and beech-oak index, yet when a simplified ANCOVA model of the form $y \sim$ transect $+$ index was run, numerous soil and climate variables showed a significant transect effect, revealing regional differences between the three study sites (Table 10, 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 (Fig. 6, Table 3), and the organic layer Ca pool (results of the ANCOVA modeling in Table 10, 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 $\sim$ 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 (Fig. 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 (Fig. 6).

4 Discussion

4.1 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 amongst 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).

4.2 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 characterise 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 colonise forest gaps and form nearly pure stands (Dinic et al., 1999; Radoglou et al., 2009).

4.3 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 year^{-1}/100 m in the study region, which results in an estimated precipitation increase of 90–140 mm year^{-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 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 the 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, was 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.

4.4 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 ($\approx$ 40 Mg ha^{-1}) in aboveground biomass and 25% more C ($\approx$ 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-year-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 compared to the oak forests coincides with a larger SOC pool: 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.

4.5 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, have 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 species pools (Meusel and Jager 1992; 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 and 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.

5 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.

6 Appendix

[Edit]

Table 4 Location of the three transects with longitude (Long.) and latitude (Lat.), elevation (Elev.) and climatic characteristics of the highest (top end) and the 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 (MAT), 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]	MAT [C°]	Tmax [C°]	Tmin [C°]	BIO10 [C°]	Pm [mm year⁻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)	Caraş-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 5 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 m²

Transects	Length [m]	Area (ha)	No. of plots (n)	Sampling intensity (%)	Sampled area (m²)
Transect A	6694	357.7	90	0.79	28278 m²
Transect B	6696	352.5	90	0.80	28278 m²
Transect C	7465	405.0	100	0.76	31416 m²

Table 6 Results (means and SD in brackets) of the forest inventories (trees with DBH ≥ 7 cm) 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 in Mg in DM. (Bio). Coniferous species (*Larix decidua*, *Pinus* spp. and *Picea abies*) occurring on single plots as well as additional deciduous broad-leaf species (*A. tataricum*, *Q. robur*, *Salix* spp., *T. cordata*) were grouped to the classes *Other coniferous* and *Other deciduous*

Species	Transect A (n=90)							Transect B (n=90)							Transect C (n=100)						
	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	0.0	1.1	10.5 (0.5)	6.4 (0.9)	0.0	0.0	0.0								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.								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 7 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 the 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), total 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]				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}] / Bulk density [g cm^{-3}]	2.7 (0.9)	1.6 (0.9)	4.1 (1.0)		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)
(Mass row organic)	10.3 (4.7)	3.5 (2.1)	3.8 (1.4)										
pH (H$_2$O)	5.8 (0.4)	5.5 (0.3)	5.4 (0.4)		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}] / SOC [%]	292.4 (68.0)	404.0 (52.0)	407.6 (24.7)		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}] / STN [%]	11.5 (2.0)	11.8 (1.3)	12.2 (2.4)		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)		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}] / P$_{av}$ pool [mg P$_{av}$ kg^{-1}]	0.78 (0.38)	0.23 (0.16)	0.37 (0.21)		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}] / Ca$_{ex}$ pool [kmol$_c$ Ca^{+2} ha^{-1}]	136.2 (83.6)	47.3 (29.7)	57.6 (22.2)		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}] / K$_{ex}$ pool [kmol$_c$ K$^+$ ha^{-1}]	31.8 (15.6)	10.3 (8.3)	12.8 (3.8)		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}] / Mg$_{ex}$ pool [kmol$_c$ Mg^{+2} ha^{-1}]	30.0 (26.3)	7.3 (5.9)	6.9 (2.7)		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 8 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 9 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 the 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), total pools of the organic layer and BaCl$_2$-exchangeable pools of the mineral soil are given. Pools of SOC, STN an 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 10 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

Dependent variable	Transect		Beech-oak index	
	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

INRAⓔ ⓹ Springer

Table 11 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			(c) Mineral soil variables		
Abbreviation	Explanation	Unit	Abbreviation	Explanation	Unit
Tmin	Average temp. of coldest month	°C	Sand [%]	Sand content in 20–40 cm	%
Tmax	Average temp. of hottest month	°C	Silt [%]	Silt content in 20–40 cm	%
Pmin	Average prec. of driest month	mm	Clay [%]	Clay content in 20–40 cm	%
Pmax	Average prec. of wettest month	mm	pAWC [%]	Plant available water capacity in 20–40 cm	%
MST (BIO10)	Mean summer (Jun, Jul, Aug) temp	°C	pH	Mean soil pH (in H_2O) from all 3 depths	
MWT	Mean winter (Dec, Jan, Feb) temp	°C	Ca^{+2}_{ex} pool	$BaCl_2$-exchangeable Ca^{+2} pool in 0–40 cm	$kmol_c\ ha^{-1}$
MSP (BIO18)	Mean summer (Jun, Jul, Aug) prec	mm	Mg^{+2}_{ex} pool	Total $BaCl_2$-exchangeable Mg^{+2} in 0–40 cm	$kmol_c\ ha^{-1}$
MWP	Mean winter (Dec, Jan, Feb) prec	mm	K^+_{ex} pool	Total $BaCl_2$-exchangeable K^+ in 0–40 cm	$kmol_c\ ha^{-1}$
Elev	Elevation above sea level	m	CEC	Cation exchange capacity	$mol_c\ kg^{-1}$
Slope	Plot slope angle	°	BS	Base saturation	%
Exposition	Plot exposition	°	SOC 0–10 cm	SOC concentration in 0–10 cm	$mg\ g^{-1}$
Stem	Mean number of stems	ha^{-1}	SOC 10–20 cm	SOC concentration in 10–20 cm	$mg\ g^{-1}$
BA	Mean basal area of stems	$m^2\ ha^{-1}$	SOC 20–40 cm	SOC concentration in 20–40 cm	$mg\ g^{-1}$
Tree vol	Mean tree volume	$m^3\ ha^{-1}$	SOC pool	Total SOC pool in 0–100 cm	$Mg\ ha^{-1}$
AGC	Mean above ground carbon pool	$Mg\ ha^{-1}$	STN 0–10 cm	STN concentration in 0–10 cm	$mg\ g^{-1}$
			STN 10–20 cm	STN concentration in 10–20 cm	$mg\ g^{-1}$
(b) Organic layer variables			STN 20–40 cm	STN concentration in 20–40 cm	$mg\ g^{-1}$
Abbreviation	Explanation	Unit	STN pool	Total STN pool in 0–100 cm	$Mg\ ha^{-1}$
Org. matter	Weight of org. matter	$Mg\ ha^{-1}$	P_{av} 0–10 cm	Resin exchangeable P concentration in 0–10 cm	$mg\ kg^{-1}$
OL pH	pH (in H_2O) of org. layer		P_{av} 10–20 cm	Resin exchangeable P concentration in 10–20 cm	$mg\ kg^{-1}$
OL C	C concentration in org. layer	$mg\ g^{-1}$	P_{av} 20–40 cm	Resin exchangeable P concentration in 20–40 cm	$mg\ kg^{-1}$
OL C pool	C pool in org. layer	$Mg\ ha^{-1}$	P_{av} pool	Resin exchangeable P pool in 0–100 cm	$kg\ ha^{-1}$
OL N	N concentration in org. layer	$mg\ g^{-1}$	C/N 0–10 cm	C/N ratio in 0–10 cm	$g\ g^{-1}$
OL N pool	N pool in org. layer	$kg\ ha^{-1}$	C/N 10–20 cm	C/N ratio in 10–20 cm	$g\ g^{-1}$
OL P pool	P pool in org. layer	$kg\ ha^{-1}$	C/N 20–40 cm	C/N ratio in 20–40 cm	$g\ g^{-1}$
OL Ca pool	Ca pool in org. layer	$kg\ ha^{-1}$	C/P 10–20 cm	C/P ratio in 10–20 cm	$g\ g^{-1}$
OL Mg pool	Mg pool in org. layer	$kg\ ha^{-1}$	C/P 0–10 cm	C/P ratio in 0–10 cm	$g\ g^{-1}$
OL K pool	K pool in org. layer	$kg\ ha^{-1}$	C/P 20–40 cm	C/P ratio in 20–40 cm	$g\ g^{-1}$
OL C/N	C/N ratio in org. layer	$g\ g^{-1}$	N/P 0–10 cm	N/P ratio in in 0–10 cm	$g\ g^{-1}$
OL C/P	C/P ratio in org. layer	$g\ g^{-1}$	N/P 10–20 cm	N/P ratio in 10–20 cm	$g\ g^{-1}$
OL N/P	N/P ratio in org. layer	$g\ g^{-1}$	N/P 20–40 cm	N/P ratio in 20–40 cm	$g\ g^{-1}$
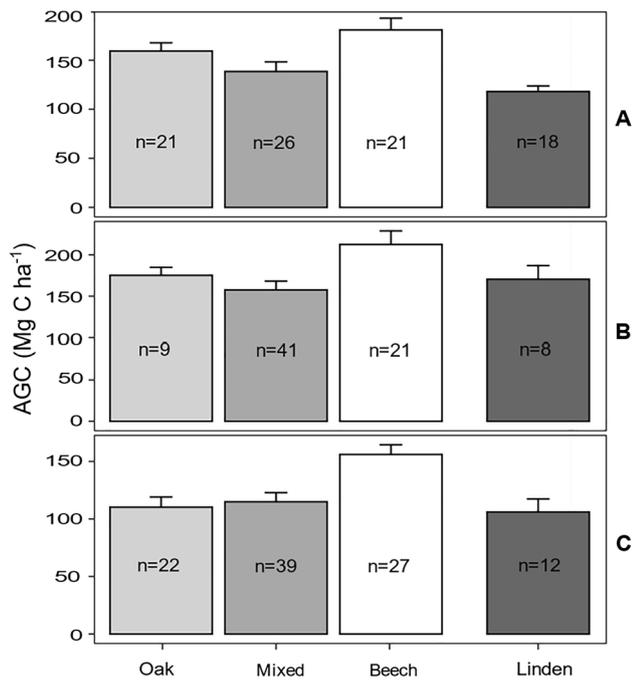
Fig. 7 Store of aboveground carbon (AGC; in Mg C ha⁻¹) in the oak, mixed and beech forest plots (means and SE) of each transect A–C. Plots dominated by linden (basal area of *T. tomentosa* > 66.6%) are also shown. Beech forests: all plots with basal area of *F. sylvatica* > 66.6%, oak forests: all plots with basal area of *Quercus* species > 66.6%, mixed forests: all other forests (except for stands with *T. tomentosa* > 66.6%)

Fig. 8 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 the 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
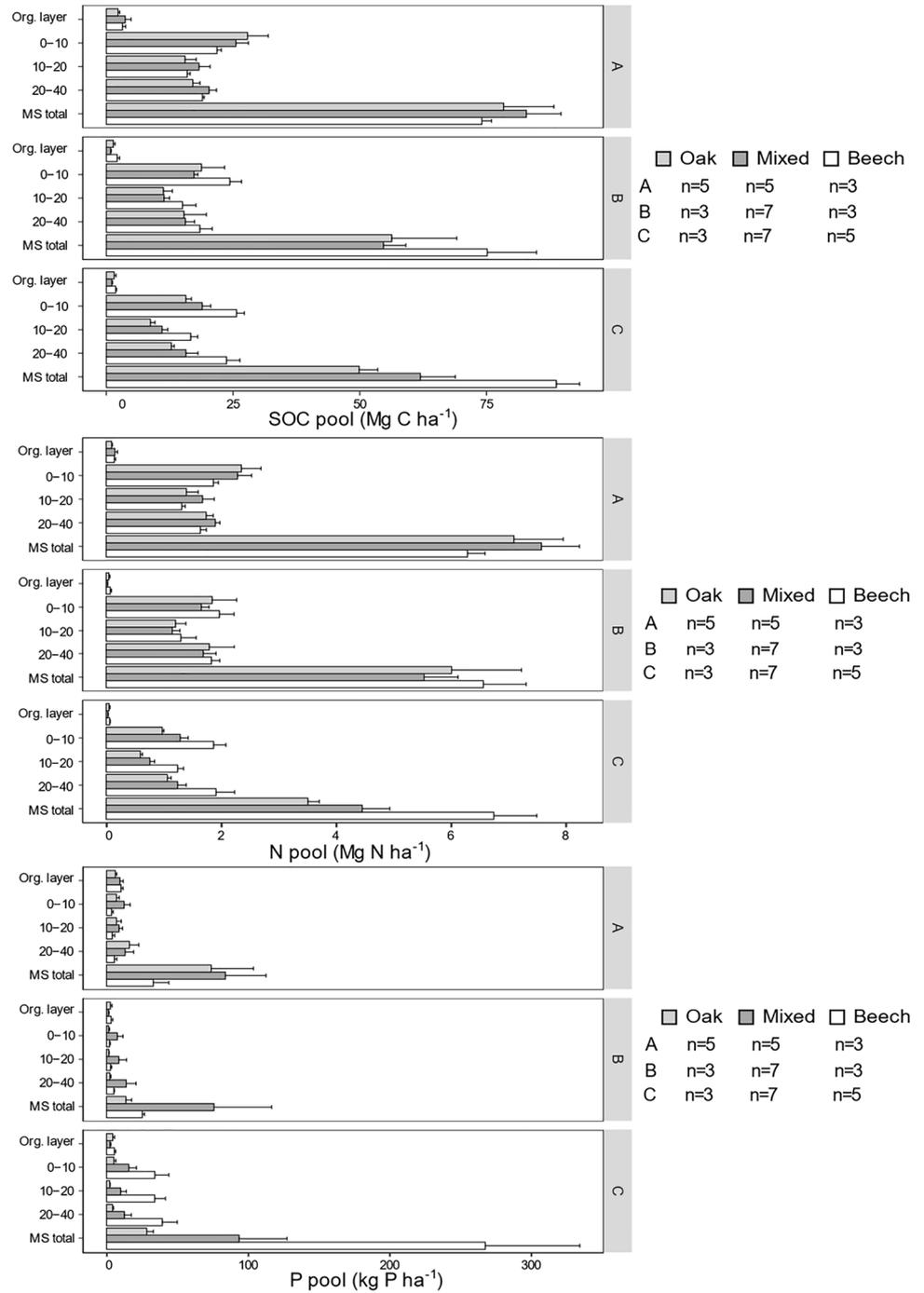
Fig. 9 Means (and SE) of the pool of BaCl$_2$-exchangeable basic cations in the mineral soil of the beech, mixed (beech-oak) and oak stands of the three transects A–C (n = number of plots). Profile totals (MS total) for Ca$^{+2}_{ex}$, Mg$^{+2}_{ex}$ and K$^{+}_{ex}$ are given for a depth of − 40 cm. No samples were taken in the linden forests
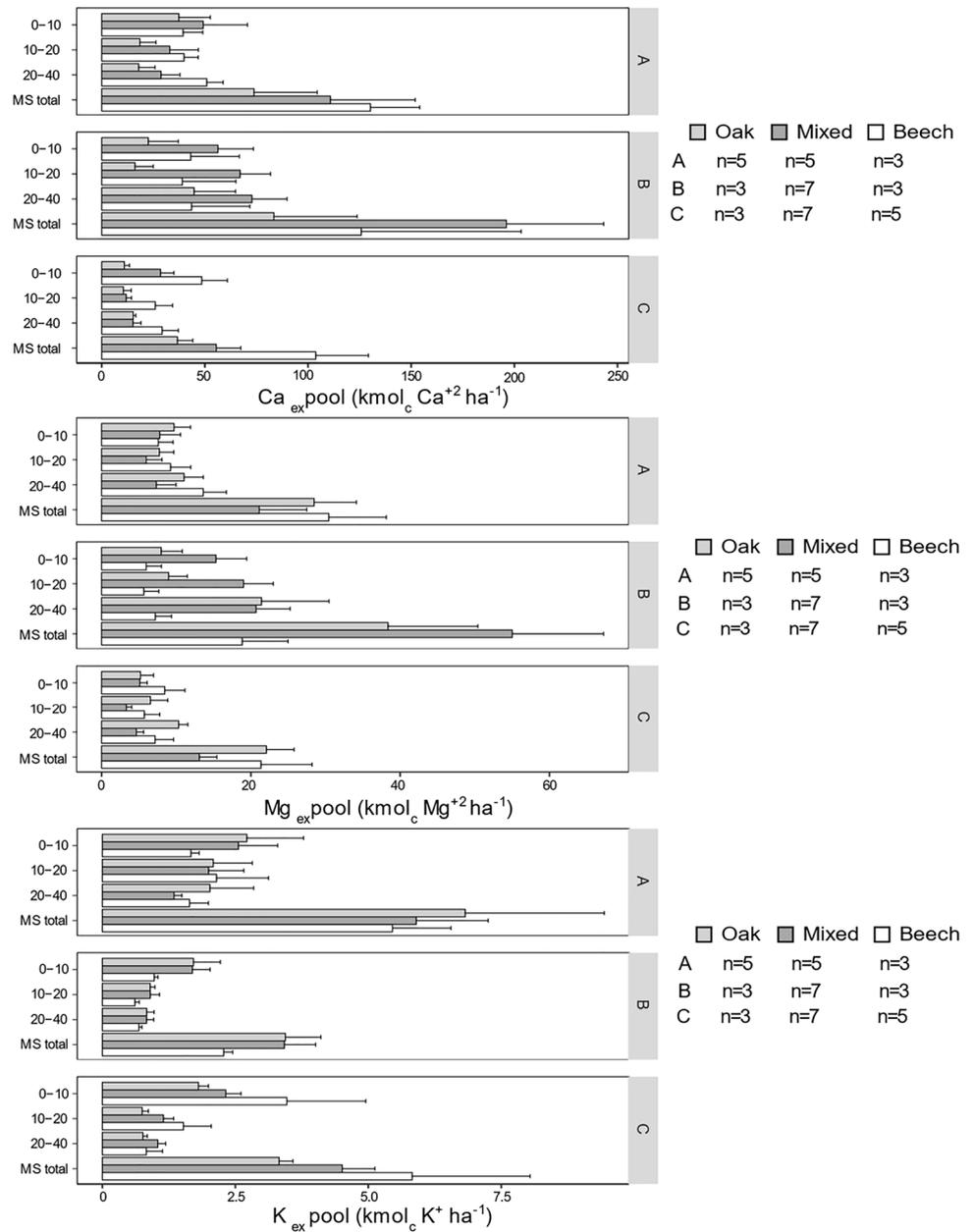
Fig. 10 Detrended correspondence analysis ordination (DCA) calculated with the species` relative basal area, conducted for all species and for the three transects A–C. The plots are marked with different colours for the three transects (*n*=number of plots). The main tree species are in bold, minor tree species in normal font

Declarations

Competing interests The authors declare no competing interests.

References

Ashton MS, Tyrrell ML, Spalding D, Gentry B (2012) Managing forest carbon in a changing climate. Springer, Dordrecht. https://doi.org/10.1007/978-94-007-2232-3

Barriopedro D, Fischer EM, Luterbacher J, Trigo RM, García-Herrera R (2011) The hot summer of 2010: redrawing the temperature record map of Europe. Science 332(6026):220–224. https://doi.org/10.1126/science.1201224

Berg B, McClaugherty C (2014) Decomposition, humus formation, carbon sequestration. In *Plant Litter*. Springer, Berlin. pp. 189–199. https://doi.org/10.1007/978-3-642-38821-7_9

Binkley D, Giardina C (1998) Why do tree species affect soils? The Warp and Woof of tree-soil interactions. Biogeochemistry 42(1–2):89–106. https://doi.org/10.1007/978-94-017-2691-7_5

Binkley D, Valentine D (1991) Fifty-year biogeochemical effects of green ash, white pine, and Norway spruce in a replicated experiment. For Ecol Manag 40(1–2):13–25. https://doi.org/10.1016/0378-1127(91)90088-D

Bohn U, Neuhäusl R, Gollub G, Hettwer C, Neuhäuslová Z, Schlüter H, & Weber H (2000) Karte der natürlichen Vegetation Europas. Maßstab 1:2,500,000. Teil 1–3 [Map of the Natural Vegetation of Europe. Scale 1: 2.5 million. Part 1–3]. Landwirtschaftsverlag, Münster

Bolte A, Ammer C, Löf M, Madsen P, Nabuurs GJ, Schall P, Spathelf P, Rock J (2009) Adaptive forest management in central Europe: climate change impacts, strategies and integrative concept. Scand J for Res 24:473–482. https://doi.org/10.1080/02827580903418224

Borrass L, Kleinschmit D, Winkel G (2017) The "German model" of integrative multifunctional forest management—analysing the emergence and political evolution of a forest management concept. Forest Policy and Economics 77:16–23. https://doi.org/10.1016/j.forpol.2016.06.028

Bosshard HH (1984) Holzkunde: Aspekte der Holzbearbeitung und Holzverwertung. Birkhäuser, Basel. https://doi.org/10.1007/978-3-0348-5378-1

Bouriaud O, Don A, Janssens IA, Marin G, Schulze ED (2019) Effects of forest management on biomass stocks in romanian beech forests. Forest Ecosystems 6(1). https://doi.org/10.1186/s40663-019-0180-4

Bréda N, Huc R, Granier A, Dreyer E (2006) Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. Ann for Sci 63(6):625–644. https://doi.org/10.1051/forest:2006042

Brevik EC (2012) Soils and climate change: gas fluxes and soil processes. Soil Horizons 53(4):12–23. https://doi.org/10.2136/sh12-04-0012

Brinkmann N, Eugster W, Zweifel R, Buchmann N, Kahmen A (2016) Temperate tree species show identical response in tree water deficit but different sensitivities in sap flow to summer soil drying. Tree Physiology 36(12):1508–1519. https://doi.org/10.1093/treephys/tpw062

Burschel P, Kürsten E, Larson BC (1993) Die Rolle von Wald und Forstwirtschaft im Kohlenstoffhaushalt - Eine Betrachtung für die Bundesrepublik Deutschland. In Forstliche Forschungsberichte München - Schriftenreihe der Forstwissenschaftlichen Fakultät der Universität München und der forstlichen Versuchs- und Forschungsanstalt. Frank, München

Caloiero T, Veltri S, Caloiero P, Frustaci F (2018) Drought analysis in Europe and in the Mediterranean basin using the standardized precipitation index. Water 10(8):1043. https://doi.org/10.3390/w10081043

Cavin L, Mountford EP, Peterken GF, Jump AS (2013) Extreme drought alters competitive dominance within and between tree species in a mixed forest stand. Functional Ecology 27(6):1424–1435. https://doi.org/10.1111/1365-2435.12126

Coldea G, Indreica A, Oprea A (2015) Les associations vegetales de Roumanie. Tome 3. Les associations forestieres et arbustives. Presa Universitara Clujeana, Cluj

Czúcz B, Gálhidy L, Mátyás C (2011) Present and forecasted xeric climatic limits of beech and sessile oak distribution at low altitudes in Central Europe. Ann for Sci 68(1):99–108. https://doi.org/10.1007/s13595-011-0011-4

Di Filippo A, Biondi F, Čufar K, De Luis M, Grabner M, Maugeri M, Presutti Saba E, Schirone B, Piovesan G (2007) Bioclimatology of beech (Fagus sylvatica L.) in the Eastern Alps: spatial and altitudinal climatic signals identified through a tree-ring network. J Biogeogr 34(11):1873–1892. https://doi.org/10.1111/j.1365-2699.2007.01747.x

Dinic A, Misic V, Savic D (1999) Silver Linden (Tilia tomentosa M o e n c h) in the Community of Sessile Oak and Hornbeam (Rusco-Querco-Carpinetum B . J o v . 1979 tilietosum tomentosae subass. nova) on the "Fruška Gora" Mountain. National Park Fruška Gora, 63–78

Dolos K, Mette T, Wellstein C (2016) Silvicultural climatic turning point for European beech and sessile oak in Western Europe derived from national forest inventories. Forest Ecology and Management 373:128–137. https://doi.org/10.1016/j.foreco.2016.04.018

Doniță N (1992) Vegetația României [Vegetation of Romania]. Tehnică Agricolă Publishing House, București

INRAE Springer

Ellenberg H (1963) Vegetation Mitteleuropas mit den Alpen [Vegetation of Central Europe with the Alps], 1st edn. Ulmer, Stuttgart

Fang J, Lechowicz MJ (2006) Climatic limits for the present distribution of beech (Fagus L.) species in the world. Journal of Biogeography 33(10):1804–1819. https://doi.org/10.1111/j.1365-2699.2006.01533.x

Fischer HS, Michler B, Fischer A (2019) High resolution predictive modelling of potential natural vegetation under recent site conditions and future climate scenarios: case study Bavaria. Tuexenia 39:9–40. https://doi.org/10.14471/2018.39.001

Fleck S, Eickenscheidt N, Ahrends B, Evers J, Grüneberg E, Ziche D, Höhle J, Schmitz A, Weis W, Schmidt-Walter P, Andreae H, Wellbrock N (2019) Nitrogen Status and Dynamics in German Forest Soils. In: Wellbrock N, Bolte A (eds) Status and Dynamics of Forests in Germany: Results of the National Forest Monitoring, vol 237. Springer, Cham, pp 123–166. https://doi.org/10.1007/978-3-030-15734-0_5

Garamszegi B, Kázmér M, Kolozs L, Kern Z (2020) Changing climatic sensitivity and effects of drought frequency on the radial growth of Fagus sylvatica at the xeric frontiers of central Europe. Idojaras 124(2):227–251. https://doi.org/10.28974/idojaras.2020.2.5

Geßler A, Keitel C, Kreuzwieser J, Matyssek R, Seiler W, Rennenberg H (2007) Potential risks for European beech (Fagus sylvatica L.) in a changing climate. Trees - Structure and Function 21:1–11. https://doi.org/10.1007/s00468-006-0107-x

Giurgiu V, Decei I, Drăghiciu D (2004) Metode şi tabele dendrometrice. In *Editura Ceres*. Bucureşti, p 575

Grüneberg E, Schöning I, Riek W, Ziche D, Evers J (2019) Carbon stocks and carbon stock changes in German forest soils. Status and Dynamics of Forests in Germany Ecological Studies. (Analysis and Synthesis), vol 237. Springer, Cham, pp 167–198. https://doi.org/10.1007/978-3-030-15734-0_6

Guckland A, Jacob M, Flessa H, Thomas FM, Leuschne C (2009) Acidity, nutrient stocks, and organic-matter content in soils of a temperate deciduous forest with different abundance of European beech (Fagus sylvatica L.). J Plant Nutr Soil Sci 172(4):500–511. https://doi.org/10.1002/jpln.200800072

Gurmesa GA, Schmidt IK, Gundersen P, Vesterdal L (2013) Soil carbon accumulation and nitrogen retention traits of four tree species grown in common gardens. Forest Ecology and Management 309:47–57. https://doi.org/10.1016/j.foreco.2013.02.015

Hampe A, Petit RJ (2005) Conserving biodiversity under climate change: the rear edge matters. Ecology Letters 8(5):461–467. https://doi.org/10.1111/j.1461-0248.2005.00739.x

Härdtle W, Niemeyer T, Assmann T, Aulinger A, Fichtner A, Lang A, Leuschner C, Neuwirth B, Pfister L, Quante M, Ries C, Schuldt A, von Oheimb G (2013) Climatic responses of tree-ring width and δ13C signatures of sessile oak (Quercus petraea Liebl.) on soils with contrasting water supply. Plant Ecology 214(9):1147–1156. https://doi.org/10.1007/s11258-013-0239-1

Harvey JE, Smiljanić M, Scharnweber T, Buras A, Cedro A, Cruz-García R, Drobyshev I, Janecka K, Jansons Ā, Kaczka R, Klisz M, Läänelaid A, Matisons R, Muffler L, Sohar K, Spyt B, Stolz J, van der Maaten E, van der Maaten-Theunissen M, … Wilmking M (2020) Tree growth influenced by warming winter climate and summer moisture availability in northern temperate forests. Global Change Biol 26:2505–2518. https://doi.org/10.1111/gcb.14966

Heinrichs S, Walentowski H, Bergmeier E, Mellert KH, Indreica A, Kuzyakov Y, Leuschner C, Petriţan AM, Teodosiu M (2016) Forest vegetation in western Romania in relation to climate variables: does community composition reflect modelled tree species distribution? Annals of Forest Research 59(2):219–236

Hendershot W, Lalande H, Duquette M (2007) Ion exchange and exchangeable cations. In: Carter RE, Gregorich EG (eds) Soil Sampling and Methods of Analysis, 2nd edn. CRC Press, Boca Raton, pp 197–207. https://doi.org/10.1201/9781420005271.ch18

Hill MO, Gauch HG (1980) Detrended correspondence analysis: an improved ordination technique. Vegetatio 42:47–58. https://doi.org/10.1007/BF00048870

Hohnwald S, Indreica A, Walentowski H, Leuschner C (2020) Microclimatic tipping points at the beech–oak ecotone in the Western Romanian Carpathians. Forests 11(9):919. https://doi.org/10.3390/f11090919

Hopkins FM, Torn MS, Trumbore SE (2012) Warming accelerates decomposition of decades-old carbon in forest soils. PNAS 109(26):1753–1761. https://doi.org/10.1073/pnas.1120603109

Horvat I, Glavač V, Ellenberg H (1974) Vegetation Südosteuropas Band 4 von Geobotanica selecta. G. Fischer, Stuttgart. https://doi.org/10.1007/bf02854718

Indreica A, Teodosiu M, Petritan AM, Öder V, Kasper J, Bergmeier E, Leuschner C, Gailing O, Hohnwald S, & Wildhagen H (2019) Nemoral deciduous forests under climatic extremes—phytosociological studies along climatic gradients in SW Romania. In: Proceedings of the 8th Edition of the Biennial International Symposium "Forest and Sustainable Development", Brasov, Romania, 25–27 October 2018, 139–148

Indreica A, Turtureanu PD, Szabó A, Irimia I (2017) Romanian Forest Database: a phytosociological archive of woody vegetation. Phytocoenologia 47(4):389–393. https://doi.org/10.1127/phyto/2017/0201

IPCC (2013) Climate change 2013: the physical science basis. Contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge, United Kingdom and New York, NY. https://doi.org/10.1017/CBO9781107415324.004

Jäger EJ, Welk E (2003) Pflanzengeographische Gliederung Europas. In: Bohn U et al. (eds) Karte der natürlichen Vegetation Europas. Münster: Landwirtschaftsverlag, Münster, pp 79–86

Jandl R, Lindner M, Vesterdal L, Bauwens B, Baritz R, Hagedorn F, Johnson DW, Minkkinen K, Byrne KA (2007) How strongly can forest management influence soil carbon sequestration? Geoderma 137(3–4):253–268. https://doi.org/10.1016/j.geoderma.2006.09.003

Jump AS, Hunt JM, Peñuelas J (2006) Rapid climate change-related growth decline at the southern range edge of Fagus sylvatica. Global Change Biol 12(11):2163–2174. https://doi.org/10.1111/j.1365-2486.2006.01250.x

Karger DN, Conrad O, Böhner J, Kawohl T, Kreft H, Soria-Auza RW, Zimmermann NE, Linder HP, Kessler M (2017) Climatologies at high resolution for the earth's land surface areas. Scientific Data 4:1–20. https://doi.org/10.1038/sdata.2017.122

Kasper J, Weigel R, Walentowski H, Gröning A, Petritan AM, Leuschner C (2021) Replication Data for: Climate warming-induced replacement of mesic beech by thermophilic oak forests will reduce the carbon storage potential in aboveground biomass and soil. . Göttingen Research Online/Data. V1. https://doi.org/10.25625/J3ZOJC

Köcher P, Gebauer T, Horna V, Leuschner C (2009) Statut hydrique des feuilles et flux xylèmique dans le tronc en relation avec la sécheresse du sol pour cinq espèces d'arbres feuillus tempérés à stratégies de consommation d'eau différentes. Annals of Forest Science 66(1):101–101. https://doi.org/10.1051/forest/2008076

König E, Baumann B (1990) The influence of roe deer browsing on the natural regeneration of mixed conifer stands. Allgemeine Forst-Und Jagdzeitung 161(9):170–176

Kunz J, Löffler G, Bauhus J (2018) Minor European broadleaved tree species are more drought-tolerant than Fagus sylvatica but not more tolerant than Quercus petraea. Forest Ecol Manag 414:15–27. https://doi.org/10.1016/j.foreco.2018.02.016

Lal R (2005) Forest soils and carbon sequestration. Forest Ecol Manag 220(1–3):242–258. https://doi.org/10.1016/j.foreco.2005.08.015

Lendzion J, Leuschner C (2008) Growth of European beech (Fagus sylvatica L.) saplings is limited by elevated atmospheric vapour pressure deficits. Forest Ecol Manag 256(4):648–655. https://doi.org/10.1016/j.foreco.2008.05.008

Lenoir J, Graae BJ, Aarrestad PA, AlsosI G, Armbruster WS, Austrheim G, Bergendorff C, Birks HJB, Bråthen KA, Brunet J, Bruun HH, Dahlberg CJ, Decocq G, Diekmann M, Dynesius M, Ejrnæs R, Grytnes JA, Hylander K, Klanderud K, … Svenning JC (2013) Local temperatures inferred from plant communities suggest strong spatial buffering of climate warming across Northern Europe. Global Change Biol 19(5):1470–1481.https://doi.org/10.1111/gcb.12129

Leuschner C (2020) Drought response of European beech (Fagus sylvatica L.) - a Review. Perspectives in Plant Ecology, Evolution and Systematics 47:125576

Leuschner C, Ellenberg H (2017) Ecology of central European forests: vegetation ecology of central Europe, 6th Version. Springer Nature, Cham. https://doi.org/10.1007/978-3-319-43042-3

Leuschner C, Wedde P, Lübbe T (2019) The relation between pressure–volume curve traits and stomatal regulation of water potential in five temperate broadleaf tree species. Annals of Forest Science 76:60. https://doi.org/10.1007/s13595-019-0838-7

Leyer I, Wesche K (2007) Multivariate Statistik in der Ökologie. In Multivariate Statistik in der Ökologie. Springer, Berlin. https://doi.org/10.1007/978-3-540-37706-1

Maclean IMD, Hopkins JJ, Bennie J, Lawson CR, Wilson RJ (2015) Microclimates buffer the responses of plant communities to climate change. Global Ecology and Biogeography 24(11):1340–1350. https://doi.org/10.1111/geb.12359

Maruşca T (2017) Elemente de Gradientica¸si Ecologie Montana (In Romanian). Editura Universita¸tii Transilvania din Bra¸sov. Edi¸tia a II-a, ICDP: Braşov

McGill W, Rutherford P, Figueiredo C, Arocena J (2007) Total Nitrogen. In: Carter RE, Gregorich EG (eds) Soil Sampling and Methods of Analysis, 2nd edn. CRC Press, Boca Raton, pp 239–251. https://doi.org/10.1201/9781420005271.ch22

Meier IC, Leuschner C (2008) Leaf size and leaf area index in Fagus sylvatica forests: competing effects of precipitation, temperature, and nitrogen availability. Ecosystems 11(5):655–669. https://doi.org/10.1007/s10021-008-9135-2

Melillo JM, Frey SD, DeAngelis KM, Werner WJ, Bernard MJ, Bowles FP, Pold G, Knorr MA, Grandy AS (2017) Long-term pattern and magnitude of soil carbon feedback to the climate system in a warming world. Science 358(6359):101–105. https://doi.org/10.1126/science.aan2874

Mellert KH, Ewald J, Hornstein D, Dorado-Liñán I, Jantsch M, Taeger S, Zang C, Menzel A, Kölling C (2016) Climatic marginality: a new metric for the susceptibility of tree species to warming exemplified by Fagus sylvatica (L.) and Ellenberg's quotient. Eur J for Res 135(1):137–152. https://doi.org/10.1007/s10342-015-0924-9

Mellert KH, Lenoir J, Winter S, Kölling C, Čarni A, Dorado-Liñán I, Gégout JC, Göttlein A, Hornstein D, Jantsch M, Juvan N, Kolb E, López-Senespleda E, Menzel A, Stojanović D, Täger S, Tsiripidis I, Wohlgemuth T, Ewald J (2018) Soil water storage appears to compensate for climatic aridity at the xeric margin of European tree species distribution. Eur J for Res 137(1):79–92. https://doi.org/10.1007/s10342-017-1092-x

Mette T, Dolos K, Meinardus C, Bräuning A, Reineking B, Blaschke M, Pretzsch H, Beierkuhnlein C, Gohlke A, Wellstein C (2013) Climatic turning point for beech and oak under climate change in Central Europe. Ecosphere 4(12):1–19. https://doi.org/10.1890/ES13-00115.1

Meusel H, Jager EJ (1992) Vergleichende Chorologie der Zentraleuropäischen Flora, Band III. G. Fischer Verlag, Jena. https://doi.org/10.1002/fedr.19941050520

Moir J, Tiessen H (2007) Characterization of available P by sequential extraction. In: Carter RE, Gregorich EG (eds) Soil Sampling and Methods of Analysis, 2nd edn. CRC Press, Boca Raton, pp 293–307. https://doi.org/10.1201/9781420005271.ch25

Muffler L, Weigel R, Hacket-Pain AJ, Klisz M, van der Maaten E, Wilmking M, Kreyling J, van der Maaten-Theunissen M (2020) Lowest drought sensitivity and decreasing growth synchrony towards the dry distribution margin of European beech. J Biogeogr 47:1910–1921. https://doi.org/10.1111/jbi.13884

Müller J, Bussler H, Bense U, Brustel H, Flechtner G, Fowles A, Kahlen M, Möller G, Mühle H, Schmidl J, Zabransky P (2005) Saproxylic beetles indicating structural qualities and habitat tradition. Urwaldrelikt-Arten - Xylobionte Käfer als Indikatoren für Strukturqualität und Habitattradition. Waldoekologie Online 2:106–113

Nicolescu VN (2018) The Practice of Silviculture. Aldus, Braşov

Novák P, Willner W, Zukal D, Kollár J, Roleček J, Świerkosz K, Ewald J, Wohlgemuth T, Csiky J, Onyshchenko V, Chytrý M (2020) Oak-hornbeam forests of central Europe. Preslia 92(1):1–34. https://doi.org/10.23855/preslia.2020.001

Öder V, Petritan AM, Schellenberg J, Bergmeier E, Walentowski H (2021) Patterns and drivers of deadwood quantity and variation in mid-latitude deciduous forests. Forest Ecol Manag 487:118977. https://doi.org/10.1016/j.foreco.2021.118977

Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, & Wagner H (2019) vegan: Community Ecology Package. R package version 2.5–6. https://CRAN.R-project.org/package=vegan. Accessed 12 June 2020

Penuelas J, Boada M (2003) A global change-induced biome shift in the Montseny mountains (NE Spain). Global Change Biology 9(2):131–140. https://doi.org/10.1046/j.1365-2486.2003.00566.x

Petritan AM, Petritan IC, Hevia A, Walentowski H, Bouriaud O, Sánchez-Salguero R (2021) Climate warming predispose sessile oak forests to drought-induced tree mortality regardless of management legacies. Forest Ecol Manag 491:119097. https://doi.org/10.1016/j.foreco.2021.119097

Pickett STA (1989) Space-for-time substitution as an alternative to long-term studies. Long-Term Studies in Ecology. Springer, New York, pp 110–135. https://doi.org/10.1007/978-1-4615-7358-6_5

Pretzsch H (2005) Stand density and growth of Norway spruce (Picea abies (L.) Karst.) and European beech (Fagus sylvatica L.): evidence from long-term experimental plots. Eur J Forest Res 124:193–205. https://doi.org/10.1007/s10342-005-0068-4

R Core Team (2018) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Radoglou K, Dobrowolska D, Spyroglou G, Nicolescu VN (2009) A review on the ecology and silviculture of limes: (Tilia cordata Mill., Tilia platyphyllos Scop, and Tilia tomentosa Moench.) in Europe. Bodenkultur 3:9–20

Revelle W (2015) psych: procedures for personality and psychological research. Northwestern University, Evanston, Illinois, USA. https://CRAN.R-project.org/package=psychVersion=1.9.12. Accessed 12 June 2020

Schär C, Vidale PL, Lüthi D, Frei C, Häberli C, Liniger MA, Appenzeller C (2004) The role of increasing temperature variability in European summer heatwaves. Nature 427(6972):332–336. https://doi.org/10.1038/nature02300

Scharnweber T, Manthey M, Criegee C, Bauwe A, Schröder C, Wilmking M (2011) Drought matters - declining precipitation influences growth of Fagus sylvatica L. and Quercus robur L. in

INRAE   Springer

north-eastern Germany. Forest Ecol Manag 262(6):947–961. https://doi.org/10.1016/j.foreco.2011.05.026

Scherrer D, Bader MKF, Körner C (2011) Drought-sensitivity ranking of deciduous tree species based on thermal imaging of forest canopies. Agricultural and Forest Meteorology 151(12):1632–1640. https://doi.org/10.1016/j.agrformet.2011.06.019

Schönwiese CD, Janoschitz R (2008) Klima-Trendatlas Deutschland 1901–2000. In Ausgabe 4 von Berichte des Instituts für Atmosphäre und Umwelt der Universität Frankfurt/Main, Main Institut für Meteorologie und Geophysik Frankfurt. Inst. für Atmosphäre und Umwelt der Univ. Frankfurt, Main, p 63

Schuldt B, Buras A, Arend M, Vitasse Y, Beierkuhnlein C, Damm A, Gharun M, Grams TEE, Hauck M, Hajek P, Hartmann H, Hiltbrunner E, Hoch G, Holloway-Phillips M, Körner C, Larysch E, Lübbe T, Nelson DB, Rammig A, … Kahmen A (2020) A first assessment of the impact of the extreme 2018 summer drought on Central European forests. Basic Appl Ecol 45:86–103. https://doi.org/10.1016/j.baae.2020.04.003

Schulze ED, Bouriaud O, Wäldchen J, Eisenhauer N, Walentowski H, Seele C, Heinze E, Pruschitzki U, Dănilă G, Marin G, Hessenmöller D, Bouriaud L, Teodosiu M (2014) Ungulate browsing causes species loss in deciduous forests independent of community dynamics and silvicultural management in central and Southeastern Europe. Annals of Forest Research 57(2). https://doi.org/10.15287/afr.2014.273

Skjemstad J, Baldock J (2007) Total and organic carbon. In: Carter RE, Gregorich EG (eds) Soil Sampling and Methods of Analysis, 2nd edn. CRC Press, Boca Raton, pp 225–239. https://doi.org/10.1201/9781420005271.ch21

South A (2011) rworldmap: A new R package for mapping global data. R Journal 3(1):35–43. https://doi.org/10.32614/rj-2011-006

Spathelf P, Stanturf J, Kleine M, Jandl R, Chiatante D, Bolte A (2018) Adaptive measures: integrating adaptive forest management and forest landscape restoration. Ann For Sci 75(55). https://doi.org/10.1007/s13595-018-0736-4

Tashi S, Singh B, Keitel C, Adams M (2016) Soil carbon and nitrogen stocks in forests along an altitudinal gradient in the eastern Himalayas and a meta-analysis of global data. Global Change Biology 22(6):2255–2268. https://doi.org/10.1111/gcb.13234

Thomas PA (2000) Trees: Their Natural History. Cambridge University Press, Cambridge. https://doi.org/10.1017/CBO9780511790522

Trendelenburg R, Mayer-Wegelin H (1955) Das Holz als Rohstoff, 2nd edn. Hanser Verlag, München

van Genuchten MT, Leij FJ, Yates S, Williams J (1991) The RETC code for quantifying hydraulic functions of unsaturated soils. Environmental Protection Agency EPA/600/2-91/065, Washington, D.C.

Vidal C, Alberdi I, Hernández L, Redmond J (2016) National forest inventories: Assessment of wood availability and use. In National forest inventories: assessment of wood availability and use. Springer, Cham. https://doi.org/10.1007/978-3-319-44015-6

Walentowski H, Bergmeier E, Evers J, Hetsch W, Indreica A, Kroiher F, Reif A, Simon A, Teodosiu M (2015) Vegetation und Standorte in Waldlandschaften Rumäniens – Plants and Habitats of Wooded Landscapes in Romania. Verlag Dr Kessel, Remagen-Oberwinter

Walentowski H, Bergmeier E, Gossner M, Reif A, Schulze E, Bußler H, Strätz C, Adelmann W (2014) Fagus sylvatica forests and their faunal diversity: a regional and European perspective. Annals of Forest Research 57(2):215–231. https://doi.org/10.15287/afr.2014.172

Walentowski H, Bußler H, Bergmeier E, Blaschke M, Finkeldey R, Gossner MM, Litt T, Müller-Kroehling S, Philippi G, VV, P, Reif A, Schulze ED, Strätz C, Wirth V (2010) Sind die deutschen Waldnaturschutzgebiete adäquat für die Erhaltung der buchenwaldtypischen Flora und Fauna? Eine kritische Bewertung basierend auf der Herkunft der Waldarten des mitteleuropäischen Tief- und Hügellandes. Forstarchiv 71:95–117. https://doi.org/10.2376/0300-4112-81-195

Walentowski H, Falk W, Mette T, Kunz J, Bräuning A, Meinardus C, Zang C, Sutcliffe LME, Leuschner C (2017) Assessing future suitability of tree species under climate change by multiple methods: a case study in southern Germany. Annals of Forest Research 60(1):101–126

Walthert L, Ganthaler A, Mayr S, Saurer M, Waldner P, Walser M, Zweifel R, von Arx G (2020) From the comfort zone to crown dieback: sequence of physiological stress thresholds in mature European beech trees across progressive drought. Science of the Total Environment 753(2021):141792. https://doi.org/10.1016/j.scitotenv.2020.141792

Wellbrock N, Eickenscheidt N, Grüneberg E, Bögelein R (2019) Environmental Settings and Their Changes in the Last Decades. In: Wellbrock N, Bolte A (eds) Status and Dynamics of Forests in Germany: Results of the National Forest Monitoring, vol 237. Springer. Cham, Switzerland, pp 29–54. https://doi.org/10.1007/978-3-030-15734-0_2

Wickham H (2009) *ggplot2*. Springer, New York. https://doi.org/10.1007/978-0-387-98141-3

Willner W, Di Pietro R, Bergmeier E (2009) Phytogeographical evidence for post-glacial dispersal limitation of European beech forest species. Ecography 32(6):1011–1018. https://doi.org/10.1111/j.1600-0587.2009.05957.x

Winter S, Begehold H, Herrmann M, Lüderitz M, Möller G, Rzanny CM, Flade M (2015) Praxishandbuch Naturschutz imBuchenwald: Naturschutzziele und Bewirtschaftungsempfehlungen für reife Buchenwälder Nordostdeutschlands. Ministerium für Ländliche Entwicklung, Umwelt und Landwirtschaft, Brandenburg

Zaehle S (2013) Terrestrial nitrogen-carbon cycle interactions at the global scale. Philosophical Transactions of the Royal Society B: Biological Sciences 368(1621). https://doi.org/10.1098/rstb.2013.0125

Zebisch M, Grothmann T, Schroeter D, Hasse C, Fritsch U, Cramer W (2005) Climate change in Germany. Vulnerability and adaptation of climate sensitive sectors. Federal Environmental Agency (Umweltbundesamt), Dessau

Authors and Affiliations

Jan Kasper[1] · Robert Weigel[1] · Helge Walentowski[2] · Anja Gröning[1] · Any Mary Petritan[3] · Christoph Leuschner[1]

Robert Weigel
robert.weigel@uni-goettingen.de

Helge Walentowski
helge.walentowski@hawk.de

Anja Gröning
anja.groening@stud.uni-goettingen.de

Any Mary Petritan
apetritan@gmail.com

Christoph Leuschner
cleusch@gwdg.de

[1] Plant Ecology and Ecosystems Research, Georg-August-University of Goettingen, Untere Karspüle 2, 37073 Göttingen, Germany

[2] Faculty of Resource Management, HAWK University of Applied Sciences and Arts, Büsgenweg 1a, 37077 Göttingen, Germany

[3] National Institute for Research and Development in Forestry "Marin Dracea", Eroilor 128, 077190 Voluntari, Romania