



Tree species richness influence productivity and anatomical characteristics in mixed fir-pine-beech forests

Ferhat Kara¹ · Seray Özden Keleş¹

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Abstract

Tree species richness (SR) and stand structural diversity (SSD) have general positive influences on stand productivity, while several studies highlight the remaining uncertainty in our knowledge of the relationships among productivity, species richness and structural diversity. Moreover, our knowledge about how SR influences anatomical cell characteristics is still limited. This study examined if stand productivity was influenced by SR and SSD by comparing the productivity of three forest types; (i) pure Trojan fir (*Abies nordmanniana* subsp. *equi-trojani*) forest, (ii) mixed Trojan fir-Scots pine (*Pinus sylvestris* L.) forest, and mixed Trojan fir-Scots pine-Oriental beech (*Fagus orientalis* L.) forest. Moreover, the study also monitored if SR and SSD affected the anatomical characteristics of fir trees in these forest types. Linear mixed-effect models were utilized to observe the relationships among species richness, stand characteristics and productivity. Stand density index, SR, and an interaction (SR × SSD) had significant effects on stand productivity. This was likely due to the complementary resource use among tree species in the mixed forests where more stratified canopies due to varying levels of shade tolerance and tree growth rates were present. Significant relationships between species richness and anatomical cell characteristics of fir were also explored. The findings of this study will enhance our understanding of species diversity controls in stands comprised of fir, pine and beech.

Keywords *Abies nordmanniana* subsp. *equi-trojani* · Cell characteristics · *Fagus orientalis* · Mixed forest · *Pinus sylvestris*

Introduction

Tree species richness and stand structural diversity usually influence carbon storage (Mensah et al. 2020), tree nutrition (Richards et al. 2010a, b), biological diversity (Pádua and Chiaravalotti 2012), ecosystem functioning (Huang et al. 2018), forest water fluxes (Forrester 2015), and stand productivity (Zhang et al. 2012). Moreover, they can mitigate the negative effects of global warming by enhancing and stabilizing the productivity of mixed forests due to the complementary resource use (del Río et al. 2017). Accordingly, previous studies stated that the impacts of climate

change can be reduced through modifying species composition, stand structure and stand density (Kara and Lhotka 2020a; Bottero et al. 2021). However, although the strength of the association between species richness, stand structure and productivity is widely acknowledged to be context- and environment-specific, the underlying processes of this association are still not entirely understood (Ratcliffe et al. 2017; Ammer 2019).

Quantitative approaches linking tree species richness and structural diversity with stand productivity are particularly important because this quantitative knowledge will enhance our understanding of species diversity control. Recently, there has been a growing interest in how tree species diversity influences stand productivity in different forests ecosystems (López-Marcos et al. 2021), since existing studies have discovered inconsistent relationships among these variables (Whittaker and Heegaard 2003; Kessler et al. 2014; Forrester and Bauhus 2016). It is prominently claimed that tree species richness positively enhances forest productivity (Danescu et al. 2016; Liang et al. 2016; Vitali et al. 2018), and this has been usually associated with more efficient

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✉ Ferhat Kara
fkara@kastamonu.edu.tr
Seray Özden Keleş
sozden@kastamonu.edu.tr

¹ Faculty of Forestry, Kastamonu University,
37100 Kastamonu, Turkey

utilization of resources in mixed stands (Yachi and Loreau 2007; Russo et al. 2019). Conversely, some studies found that tree species diversity may also have negative effects on stand productivity (Edgar and Burk 2001; Wang et al. 2016). Long and Shaw (2010) found non-significant relationships between forest productivity and compositional diversity in ponderosa pine (*Pinus ponderosa* C. Lawson) stands in the western United States. Given the findings of previous research, our knowledge regarding the richness-productivity relationships seems to be still limited. Additional research to quantify and well-understand these relationships is still needed for different forest ecosystems.

Anatomical cell characteristics of trees may also provide additional information about the relations among stand characteristics, environmental factors, growth and development of trees (Gaertner 1964; Forrester 2014; De Micco et al. 2019). Depending on the availability of main resources, trees could reveal structural adaptations of wood (Panshin and de Zeeuw 1980). Wood is composed of several distinct types of wood cells (i.e., tracheids, fibres, vessels, rays) which are responsible for serving the demands of a living tree (Daniel 2009). Tracheid cells ensure both mechanical support and water conduction in gymnosperms, while fibres are responsible for the mechanical support in angiosperms (Tonn and Greb 2017). The vessels conduct water in angiosperms, while rays store starch and lipid in both gymnosperms and angiosperms (Barnett and Jeronimidis 2003). In trees, the variability of wood cells is closely related to the environmental, stand structural and climatic conditions, that is wood cells have a strong capacity for adjusting their size and numbers in a coordinated way under stressful conditions (Hietz et al. 2017). In particular, the size of wood cells has great ecological importance in trees for their survival and productivity and conducting efficiency (Brodribb 2009; Pittermann et al. 2006a, b). To our knowledge, the relationships between anatomical cell characteristics of trees and tree species richness have not been well documented.

Trojan fir (*Abies nordmanniana* subsp. *equi-trojani*), Scots pine (*Pinus sylvestris* L.), and Oriental beech (*Fagus orientalis* L.) are three main native tree species in northern Turkey covering approximately five-million-hectare area which is about 23% of the total forested land in the country (Kara 2018a; General Directorate of Forestry 2020). Mixed forests composed of these species represent important ecosystems regarding economic, ecological and social functions (Odabaşı et al. 2004; Aktürk et al. 2020; Kara and Lhotka 2020b). These tree species exhibit different levels of shade tolerance and growth rates (Varol et al. 2022). Uncertainty remains about the effects of species richness and structural diversity on stand productivity and trees' anatomical characteristics in stands composed of Trojan fir, Scots pine and Oriental beech. The knowledge of the linkages among tree species richness, structural diversity and stand productivity

would give forest managers the ability to implement treatments that enhance stand productivity through silvicultural implications. Therefore, in this study, the main objective was to examine the effects of species richness and stand structural diversity on stand productivity in pure fir (F_{PURE}), mixed fir-pine (FP_{MIX}) and mixed fir-pine-beech (FPB_{MIX}) forests. Moreover, we also aimed to monitor if tree species richness influences anatomical characteristics of fir trees in F_{PURE} , FP_{MIX} and FPB_{MIX} stands.

Methodology

Study site

This study was conducted in Daday district, Kastamonu city, northern Turkey (Fig. 1). The study area is located within the Euro-Siberian phytogeographic region and is in the natural range of Trojan fir, Scots pine and Oriental beech (hereafter, fir, pine and beech, respectively) (Kara 2022). The study area is characterized by a typical continental climate with cold winters and rainy summers. Based on the weather data attained from the General Directorate of Meteorology for the period of 1985–2020, the mean total annual precipitation is 550 mm, while maximum and minimum monthly

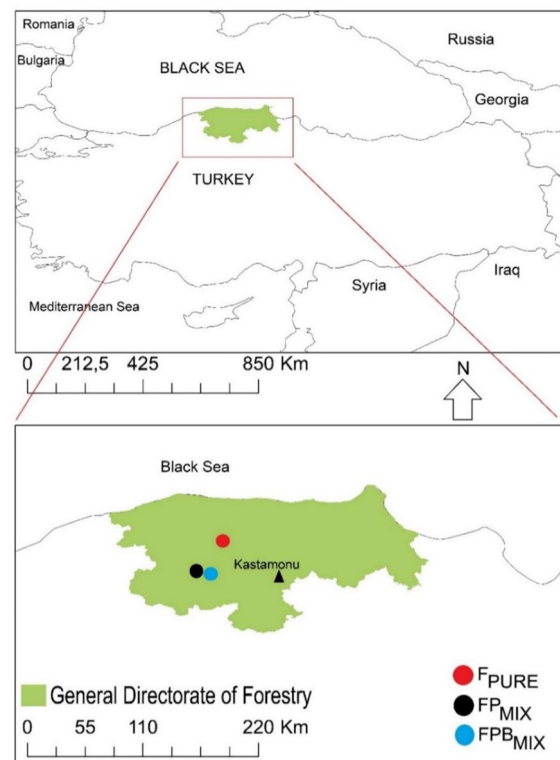


Fig. 1 Location of study forests. F_{PURE} , FP_{MIX} and FPB_{MIX} refer to pure fir, mixed fir-pine and mixed fir-pine-beech stands, respectively

precipitation occur in May (98.1 mm) and July (15.9 mm), respectively, in Daday district. The mean monthly temperature is 9.4 °C, and the lowest and highest mean temperatures are measured in January (−1.3 °C) and August (20.1 °C), respectively. The topography of the area ranges from gently sloping to steep slopes, and elevation varies from 800 to 1400 m above sea level. Black pine (*Pinus nigra* Arnold) and oaks (*Quercus* spp.) are other main tree species of the region, while *Rubus*, *Cornus*, *Juniperus excelsa*, *Pyracantha coccinea*, *Cistus* are some of the understory plants (Köseoğlu and Kara 2019). In the study region pure pine, fir and beech forests as well as mixed forests of these species prevail.

Three forest types were selected within Kastamonu Regional Directorate of Forestry, and named F_{PURE} (41° 36' 43" N, 33° 28' 25" E), FP_{MIX} (41° 22' 31" N, 33° 14' 04" E) and FPB_{MIX} (41° 36' 453" N, 33° 28' 50" E) for pure fir, mixed fir-pine and mixed fir-pine-beech stands, respectively (Fig. 1). The acreage of study forests ranged from 18 to 40 ha. Several factors including climatic parameters, local environmental conditions, forests structure and density are considered confounding factors that can influence diversity-productivity relationships (Vilà et al. 2005; Bravo-Oviedo et al. 2021). Similar climatic conditions, topography and elevation of our study forests are crucial to mitigate the sampling effects, and to separate the effects of these factors from influence of species richness (Forrester and Bauhus 2016). It should be noted that the mixed forests (i.e., FP_{MIX} and FPB_{MIX}) are in close proximity (− 1 km), while the distance between the pure forest and the mixed ones is about 30 km (Fig. 1). The mean total annual precipitation is about 700 mm for F_{PURE}, while it was approximately 810 mm where the mixed forests are located given the weather data for the period of 1985–2020. The average altitude of the forest types is 1180, 1320 and 1410 m for F_{PURE}, FP_{MIX} and FPB_{MIX}, respectively. The topography of the F_{PURE} and FPB_{MIX} are nearly flat, while it was gently sloping in FP_{MIX}. The most prevalent soil of the forest types is brown forest

soil being moderately deep ranging from 50 to 90 cm. The selected forest types presented uneven-aged stand structure.

For each forest type (i.e., F_{PURE}, FP_{MIX}, FPB_{MIX}), three stands were selected. The stands have been mainly managed for timber production for decades using a single-tree selection method with volume control-guiding diameter limit (VGDL) regulation (Guldin and Baker 1998). A cutting cycle of ten years and a target diameter of 55 cm in diameter at breast height (DBH) are commonly utilized in these stands. It should be noted that no silvicultural treatments were conducted in the study stands for more than ten years, including the study period (i.e., from 2011 to 2021).

Sampling and measurements

The data were collected from 400 m² circular plots installed within the study stands (total 106 plots). The number of plots in forest types (i.e., F_{PURE}, FP_{MIX} and FPB_{MIX}) was 40, 36 and 30, respectively, while the number of plots within the stands ranged from 10 to 15 plots depending on the acreage of the stands. The plots were randomly located across the stands. In the present study, the inventories were conducted in the fall of 2021, and trees with a diameter of 8 cm or larger at DBH were included. In each plot, DBHs of trees were measured, and tree species were recorded. Following DBH measurements, quadratic mean diameter (Dq) was calculated using the formula below for each study plot (Eq. 1) (Table 1).

$$Dq = \sqrt{\sum DBHi^2/n} \tag{1}$$

where DBHi is the diameter at breast height of the tree, and n number of trees per plot. Stand basal area (m² ha^{−1}) and the number of trees (ha) for each plot were also calculated (Table 1). Next, stand density index (SDI) of each study plot was calculated using Reineke’s formula (Eq. 2) (Reineke 1933) (Table 1).

Table 1 Descriptive statistics for the variables of pure fir (F_{PURE}), mixed fir-pine (FP_{MIX}) and mixed fir-pine-beech (FPB_{MIX}) stands

Variables	F _{PURE}		FP _{MIX}		FPB _{MIX}	
	Mean	SE	Mean	SE	Mean	SE
Dq (cm)	28.5 (19.6–38.4) ^a	1.11	30.1 (22.7–38.5) ^a	1.51	33.1 (26.6–38.1) ^a	0.84
Basal area	24.3 (10.6–36.8) ^b	1.02	36.1 (21.8–56.2) ^a	1.64	36.6 (22.4–48.5) ^a	1.19
SDI	178 (87.4–268) ^b	6.74	294.2 (183–403) ^a	11.6	266.4 (168–334.4) ^a	8.05
Tree count (ha)	342.6 (225–500) ^b	6.81	443 (250–1025) ^a	18.2	425 (300.2–575.1) ^a	6.31
Volume (m ³)	278.7 (116–437) ^b	7.51	396.1 (170–648) ^a	20.3	421.3 (250–613.5) ^a	8.71
SSD	0.36 (0.18–0.54) ^a	0.01	0.52 (0.19–0.73) ^c	0.03	0.37 (0.20–0.58) ^b	0.02

Different letter superscripts indicate significant difference between forest types (*p* < 0.05)

Dq, SDI, and SSD refer to quadratic mean diameter, stand density index, stand structural diversity, respectively. Numbers in parentheses give the range. SE refers to standard deviation

$$\text{SDI} = \text{number of trees (ha)} + \frac{(25)^{-1.605}}{Dq} \quad (2)$$

As a measure of the stand structural complexity (SSD) of each plot, horizontal differentiation across individual trees within each plot, i.e. coefficient of variation of tree diameters, was calculated as the standard deviation of tree diameters to their arithmetic mean as outlined by Mensah et al. (2020) (Table 1). Tree species richness (SR) at the plot level was defined as the absolute number of distinct tree species within each study plot as suggested by Zeller et al. (2018).

Tree height measurements were taken using a TruPulse Laser Rangefinder (Laser Tech Inc.). Tree volumes were estimated using the volume equations developed for the selected forest types in previous studies (Durkaya and Durkaya 2006; Karabürk 2011). Using the volume data from 2011, a 10-year volume increment (i.e., between 2011 and 2021) was calculated for each plot. Next, productivity was estimated as the mean annual increment of stem volume of a plot in $\text{m}^3 \text{ha}^{-1} \text{yr}^{-1}$ as recommended (Mensah et al. 2020).

Anatomical measurements

The anatomical cell characteristics-species richness relationships were observed using fir trees since fir was the species that existed in all forest types. It should be noted that, soon following the inventories (i.e., in the fall of 2021), the study stands (i.e., F_{PURE} , FP_{MIX} , FPB_{MIX}) were subject to selection cuttings. Following the harvestings, in each forest type, twenty fir stumps were selected. We paid particular attention to the fact that ten of these trees, which were used for anatomical cell measurements, were the same age (i.e., 60) to avoid age effects. The ages of these trees were determined by counting the annual rings on their stumps. The DBHs of the selected stumps ranged from 30 to 40 cm. Next, one wood disc per each stump was obtained for tree ring measurements and anatomical analyses. Therefore, twenty discs were collected for each stand, and a total of 60 discs were analyzed. The discs were taken during the fall season since the latewood proportion of wood is formed in later part of vegetation season. To measure tree-ring widths of fir trees, the surface of 60 wood discs was sanded with sandpaper. Then, the tree ring widths of each wood disc were measured for each study stand. For anatomical cell measurements, we used 10 discs of each stand (F_{PURE} , FP_{MIX} , FPB_{MIX}) which were at same age. In the anatomical investigations, the first 10 tree growth rings (near the pith) were excluded since the first rings generally show great variations in properties compared with later tree growth rings. To measure the tracheid and ray cell characteristics, the small wood pieces were thus taken from the twentieth growth rings of each disc (i.e., 10 samples for each forest type) to provide that each sample was from the same seasons of wood formation.

To measure the tracheid and ray cell characteristics. The selected ten discs were first cut into small wood pieces (almost 1×10 mm in size) for anatomical investigations. The anatomical analyses were conducted on each disc separately (i.e., small wood pieces were taken from the twentieth growth rings of each disc from 10 different discs for F_{PURE} type, the same processes were conducted on FP_{MIX} and FPB_{MIX} types). The small wood pieces were softened in the boiled water and then placed in equal parts of water, glycerol, and ethanol (Yaltırık 1971). Softened pieces were cut into thin strips (around 1×10 mm in size) in the cross and tangential sections of the thickness of 20–25 μm using a sliding microtome. Thin pieces were then stained with safranin to prepare permanent slides and investigate the anatomical properties of wood cells (Bond et al. 2008). The cell anatomical characteristics measured in cross sections were tracheid diameter, tracheid lumen width and tracheid wall thickness. In the tangential section, ray height and ray width were analyzed. Digital photographs were captured using a Leica DM750 photomicroscope (Leica Microsystems Ltd., Switzerland). The size and number of wood cells were identified using the Leica LAS EZ Image Analysis Software. The cell anatomical measurements were conducted based on the IAWA lists of microscopic features for softwoods identification (IAWA 2004).

Analyses

The effects of species richness and structural diversity on productivity were examined using a mixed-effect multiple regression model that was defined by the following formula (Eq. 3).

$$Rv = \beta_0 + Re + X^T + E \quad (3)$$

where Rv is the response variable, while β_0 is the intercept, Re is the random effect, X^T is the transposed matrix of the fixed effects, and E is the error term. Productivity was used as the response variable (i.e., dependent variable) in the model. Apart from SR (i.e., forest type) and SSD, we considered Dq , SDI, average tree age of plots, average height of plots, and potential interactions as fixed effects, as outlined in previous studies (Zeller et al. 2018). The stand was considered as the experimental unit (i.e., replicate), and plots were treated as random effect nested within the stands. In this analysis, we started the model fitting with all parameters described above. Next, variables with p-values greater than $\alpha=0.05$ were sequentially removed from the model, and the model was refit following the removal of each insignificant variable. This iterative process was re-run until only the variables with p-values smaller than $\alpha=0.05$ were included in the model. Normality and homogeneity of variance of data were tested with residual analysis, and no departures

from these model assumptions were found. Multicollinearity among the selected parameters was examined with the variance inflation factor; VIF greater than 10 indicates high collinearity among variables (Dormann et al. 2013). It should be noted that no VIF value greater than 1.5 was detected in the models. Moreover, the Pearson correlation matrix was calculated for the measured variables. Tree ring widths and anatomical properties (tracheid length, tracheid width, tracheid lumen width, tracheid wall thickness, ray height and ray width) were analyzed using the analysis of variance (ANOVA) (α -level=0.05). The Tukey post-hoc test was also used to test differences in anatomical properties among three sites for significance. During statistical analyses, “lme”, “aov” and “cor.test” functions of R-Statistical software (R Development Core Team 2021) were utilized.

Results

Figure 2 depicts the diameter structures of the forest types. The forest types exhibit uneven-aged stand structure; however, they do not utterly possess a reverse J-shaped diameter distribution, which is the typical structure of uneven-aged forests (Fig. 2b). Across the forest types, small- and medium-sized trees (i.e., from 10 to 40 cm) were mostly fir, while pine was primarily in DBH classes of 40–50 cm (Fig. 2b and c). Beech was present in most DBH classes in FPB_{MIX} (Fig. 2c). Fir seedlings in F_{PURE} and FP_{MIX}, and fir and beech seedlings in FPB_{MIX} were usually present in the understory, while none or a few pine seedlings were observed in FP_{MIX} and FPB_{MIX}.

Productivity

The average productivity of the forests types was 2.47 (SE=0.06), 4.17 (SE=0.17) and 4.95 (SE=0.11) m³ ha⁻¹ yr⁻¹ for F_{PURE}, FP_{MIX} and FPB_{MIX}, respectively. The differences of productivity among the forest types were statistically significant ($p < 0.05$). Among the variables used in the analysis of linear mixed effect models, SDI, SR and an interaction (SR x SSD) had statistically significant influences on stand productivity across the forest types ($p < 0.05$) (Table 2). The final structure of the model is given in Eq. 4. An increase in SDI resulted in a rise in stand productivity across the forest types ($p < 0.01$). In addition, our model indicated that stands with more tree species had greater stand productivity ($p < 0.001$) (Table 2). Moreover, no statistically significant effects of SSD, Dq, average tree age and tree height of plots on stand productivity were found in the analysis ($p > 0.05$).

$$\text{Productivity} = \beta_0 + \text{SDI} + \text{SR} + \text{SR} : \text{CV}_D + \text{Re} + \text{E} \quad (4)$$

where β_0 is the intercept while Re is the random effect, and E is the error term.

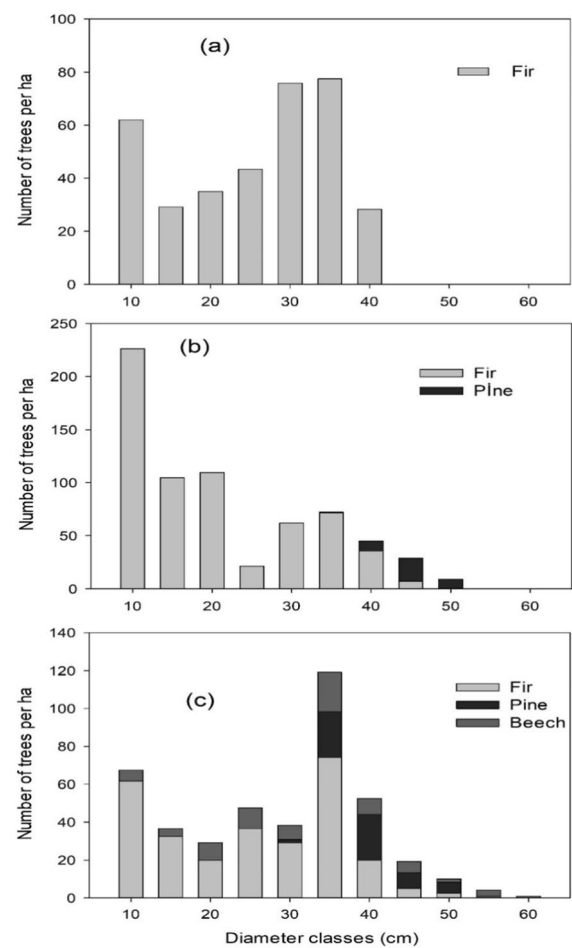


Fig. 2 Diameter distribution of **a** pure fir (F_{PURE}), **b** mixed fir-pine (FP_{MIX}) and **c** mixed fir-pine-beech (FPB_{MIX}) forests

Table 2 Influences of stand density index (SDI), species richness (SR), and stand structural diversity (SSD) on stand productivity (m³ ha⁻¹ yr⁻¹) across forest types

Variables	Value	SE	<i>p</i> -value	VIF
Intercept	2.4118	0.3573	<0.0001	–
SDI	0.0062	0.0031	0.0444	1.23
SR: FP _{MIX} (vs F _{PURE})	3.1792	0.4331	0.0003	1.29
SR: FPB _{MIX} (vs F _{PURE})	4.9283	0.7869	0.0008	1.29
SR x SSD	-1.3934	0.2557	<0.0001	1.43

SE refers to the standard error. VIF refers to variance inflation factor. AIC and BIC values were 195.69 and 219.19 for the productivity models, respectively

Most of the measured variables of the forest types were correlated ranging between 0.23 and 0.71 (Table 3). The strongest correlation was between the SDI and number of trees (ha) across the study plots. The increasing number of trees per hectare increased SDI. Moreover, SSD does not correlate with SDI and SR across the plots (Table 3).

Table 3 Pearson correlation matrix for measured variables

Variables	Number of trees	SDI	SR	SSD
Dq	-0.24*	0.49***	0.47***	-0.31*
Number of trees	–	0.71***	0.23*	0.33*
SDI	–	–	0.55***	0.08 ns
SR	–	–	–	0.06 ns

ns, *, **, *** are not significant, $p > 0.05$, $p < 0.05$, $p < 0.01$, and $p < 0.001$, respectively

Dq, SDI, SR, and SSD refer to the quadratic mean diameter (cm), stand density index, species richness, and stand structural diversity, respectively

Anatomical characteristics

The mean tree ring widths and anatomical cell characteristics were analyzed in each forest type (F_{PURE} , FP_{MIX} , FPB_{MIX}) (Figs. 3 and 4). The mean tree ring widths differed significantly between the three forest types ($p < 0.001$) (Table 4). It was significantly greater in FPB_{MIX} than in FP_{MIX} and F_{PURE} , but the difference between FP_{MIX} and F_{PURE} plots was not statistically significant ($p > 0.05$).

The mean tracheid diameters significantly varied across three forest types ($p < 0.001$) (Table 4). It was significantly greater in FPB_{MIX} than in FP_{MIX} and F_{PURE} (Table 4). The mean tracheid lumen widths were also significantly affected by the forest types ($p < 0.01$). It was found to be significantly higher in FPB_{MIX} than in FP_{MIX} and F_{PURE} . In each forest type, mean tracheid wall thickness of F_{PURE} was significantly different compared to mixed forests ($p < 0.001$). However, surprisingly mean tracheid wall thickness values were almost 1.5–2 times higher in F_{PURE} than in FPB_{MIX} and FP_{MIX} . The mean ray height and ray widths values did not show significant differences between the three forest types ($p > 0.05$) (Table 4).

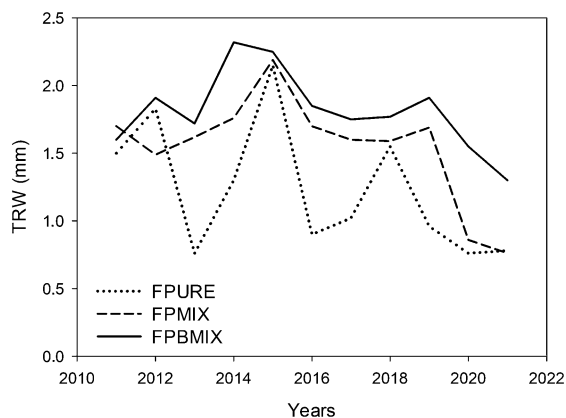


Fig. 3 Mean tree ring widths of pure fir (F_{PURE}), mixed fir-pine (FP_{MIX}) and mixed fir-pine-beech (FPB_{MIX}) forests in the period of 2011–2021 years

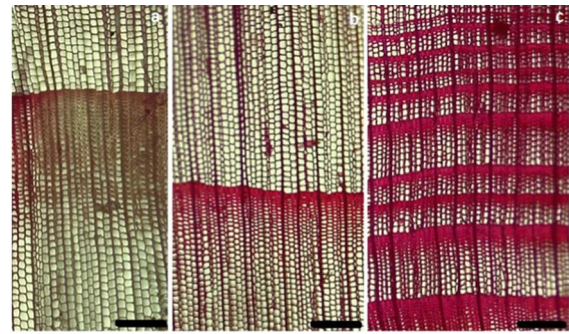


Fig. 4 Cross sections in **a** FPB_{MIX} , **b** FP_{MIX} , and **c** F_{PURE} . Bar = 150 μm

Discussion

Productivity

This study aimed to examine the effects of species richness and stand structure on productivity in pure fir, mixed fir-pine and mixed fir-pine-beech forests, as well as to monitor if tree species richness influences anatomical characteristics of fir trees in these forests. Stand structure and species richness affected stand productivity, and anatomical cell characteristics of fir was influenced by species richness. The selected stands of this study are managed using single-tree selection silviculture under high stand densities. Fir and beech are very shade-tolerant tree species, while pine is considered a shade-intolerant species (Pardos et al. 2007; Topacoglu et al. 2017; Kara 2018b). This is the main reason why fir seedlings in F_{PURE} and FP_{MIX} , and fir and beech seedlings in FPB_{MIX} were present in the understory, while none or a few pine seedlings were observed in FP_{MIX} . Previous research stated that the small-scale disturbances created by single-tree selection method in mixed fir-pine forests are not adequate to establish and recruit pine seedlings (Kara and Lhotka 2020b). Moreover, forest managers mostly prefer firs when marking trees of overstory during harvesting in mixed stands in the country. Firs are considered more competitive than pine and beech when high stand density is maintained through selection silviculture, thus retention of pine and beech is usually aimed when managers mark trees in the mixed stands (Odabaşı et al. 2004; Savacı et al. 2021). As a result, the contribution of pine and beech in basal area was mostly in large DBH classes in the mixed stands. Under current silvicultural implications, the disappearance of pine in the mixed forests may not be surprising over the long term.

The growth patterns of tree species within a mixture as well as their interactions lead to the diversity-productivity relationships (Forrester and Bausch 2016). One of the main reasons for the positive influence of tree species richness on stand productivity is considered to be the complementary

Table 4 The mean values of tree ring widths and anatomical variables of fir trees in three forest types (F_{PURE} , F_{MIX} , $F_{\text{PB}_{\text{MIX}}}$)

Variables	F_{PURE}	F_{MIX}	$F_{\text{PB}_{\text{MIX}}}$	<i>p</i> -value
Tree ring width	1.20 ± 0.23 ^a	1.56 ± 0.08 ^a	1.80 ± 0.13 ^b	<i>p</i> < 0.001
Tracheid diameter	158 ± 6.78 ^a	179.8 ± 6.20 ^b	202.7 ± 5.74 ^c	<i>p</i> < 0.001
Tracheid lumen width	4.47 ± 0.22 ^a	5.12 ± 0.17 ^b	5.21 ± 0.19 ^c	<i>p</i> < 0.01
Tracheid wall thickness	3.24 ± 0.14 ^c	1.5 ± 0.14 ^a	1.99 ± 0.06 ^b	<i>p</i> < 0.001
Ray height	314.6 ± 20.8 ^a	353.9 ± 28.3 ^a	390.9 ± 37.5 ^a	<i>p</i> > 0.05
Ray widths	28.7 ± 1.60 ^a	29 ± 1.54 ^a	28.9 ± 2.46 ^a	<i>p</i> > 0.05

Values indicate the mean ± standard error (SE); *n* = 20 for each study site for the parameters. Different letters in rows indicate significant differences between means (*p* < 0.05) following Tukey's HSD test

Tree ring width (mm), tracheid diameter (μm), tracheid lumen width (μm), tracheid wall thickness (μm), uniseriate ray height (μm), uniseriate ray width (μm)

resource use among tree species in mixed forests (Zhang et al. 2012; Liang et al. 2016; Pretzsch et al. 2017). Mixed forests comprised of species with varying shade tolerance mainly develop stratified canopies and root stratification (Pretzsch et al. 2017), as a result, the complementary resource use among tree species leads to greater stand-level productivity (Kelty 2006; Gamfeldt et al. 2013; Zeller et al. 2018). The litter fall nutritional contents and decomposition rates are usually greater in mixed forests, and these commonly lead to faster rates of nutrient cycling, which increases nutrient availability and uptake (Richards et al. 2010a, b).

Another attribute that drive richness-productivity relationships is water. The species that can reach deeper and moister soil layers favor the species with a shallower root system by redistributing the water to shallower and drier soil during dry seasons in mixed forests (Neumann and Cardon 2012; Prieto et al. 2012). Fir and beech are considered as anisohydric species (Bowers and Williams 2016; Leuschner et al. 2022) while pines are mostly isohydric (Salmon et al. 2015). When anisohydric and isohydric species are mixed, water competition may be lessened, and consequently, one of the species may be able to access and absorb more water (Pretzsch et al. 2013).

The positive effects of species richness and productivity can also be attributed to light conditions in the stand. In comparison to pure stands of less shade-tolerant species, mixtures including fast-growing shade-intolerant species and more shade-tolerant species are expected to have better light absorption (Forrester et al. 2012). In addition, species with varying shade-tolerance in mixed forests may be able to occupy a larger canopy volume due to inter-specific variations in the vertical distribution of leaf area and in crown morphologies, which may increase light absorption (Pretzsch 2014). Moreover, Morin et al. (2011) found that the higher diversity in shade tolerance in mixed forests generally results in forests responding faster to small-scale disturbances, which is also the case in the studied stands. They further stated that competition among species for

light alone can cause a positive effect of species richness on stand productivity in mixed forests composed of species with varying light requirements.

Previous studies revealed that stand structural complexity could positively influence stand productivity (Bohn and Huth 2017; Silva Pedro et al. 2017). In contrast, Bourdier et al. (2016) found that higher diversity in shade tolerance in mixed forests may result in a decrease in stand productivity. The inconsistency among studies regarding structural complexity-productivity relationships is likely due to the fact that pure stands of some species can develop as complex structure as their mixed stands (Zhang et al. 2015). The effect of structural complexity on stand production was insignificant in the present study, but, our data revealed a significant interaction of species richness and the complexity on the productivity. Relevantly, Zeller et al. (2018) examined the effects of stand structural complexity on stand productivity, and obtained an interaction of species richness and the complexity on the productivity, substantiating our findings.

Previous research pointed out that stand density can negatively or positively affect stand productivity (Uhl et al. 2015; Forrester and Bauhus 2016). The inconsistent findings on density-productivity relationships in previous studies may be due to differences in location and climatic variables such as temperature and precipitation (Zeller et al. 2018). The present study found a positive influence of stand density on stand productivity. Pretzsch and Biber (2016) monitored the effect of species mixing on maximum density in mixed forests of Europe, and revealed that stand density increased stand productivity by finding higher maximum density in mixed stands than pure stands. This can be associated with greater resource use efficiency and higher carrying capacity in mixed forests compared to pure forests (Kelty 2006; Pretzsch and Biber 2016). Relevantly, former studies stated that the density-productivity relationships will probably rely on the resources impacted by species interactions and how the density shift affects those resources (Boyden et al. 2005; Forrester et al. 2013).

Tree rings and anatomical characteristics

Tree ring width is one of the important growth parameters in trees since it may present crucial information related to the response of tree to environmental conditions. Trees generally produce wider rings with higher access to water sources so they can grow faster; while trees exhibit narrower rings with limited access to water sources (O'Donnell et al. 2015). Wider tree rings thus could show the environmental conditions that are ideal for tree growth and development. In this study, the tree ring width of fir trees was higher in FPB_{MIX} than in F_{PURE}. In this study, tree ring widths of fir on average 1.5 times wider in mixed (FPB_{MIX}) compared with pure (F_{PURE}) stands. This could be related to the survival strategy of the fir trees since fir developed more greatly competition-induced mortality in mixed stands when compared to the other two tree species (Scots pine and Oriental beech). We can therefore suggest that fir trees were more productive in FPB_{MIX} stands than in pure stands. These results are in agreement partly with those of Zeller et al. (2017) who found tree ring widths of Scots pine were wider in mixed stands compared to pure Scots pine stands.

Tracheids are one of the important wood cells in gymnosperms which has functions of both mechanical support and water transportation (Murmanis 1970; Larson 2001). The size of the tracheid is thus an important parameter for conducting efficiency in gymnosperms (Sperry et al. 2006). The wider size of tracheid diameters could allow better hydraulic conductance or efficiency (Pittermann et al. 2006a, b). Here, it can be suggested that fir trees which grew in mixed stands (pine and beech) may produce better hydraulic efficiency and thus exhibit better growth performance in their growth than which were grown in pure stands. Overall, we can suggest that fir trees produced more regular competitive interactions in their anatomical structure in mixed stands than pure stands.

Management implications

Although their many advantages over pure forests, natural regeneration in mixed forests composed of tree species, which exhibit different levels of shade tolerance (i.e., fir-pine-beech mixture), is considered more difficult. Yet, this study points out the importance of maintenance of tree mixture in natural Trojan fir-Scots pine-Oriental beech forests. On the other hand, there has been a growing concern by forest managers over the decreasing proportion of Scots pine trees in these mixed forests in northern Turkey. This study along with the previous research indicates that small-scale disturbances created by single-tree selection method does not create favorable conditions for the establishment and recruitment of Scots pine under canopy in these forests. It will be crucial to make use of the different silvicultural

options available for managing mixed stands, as well as to create a reliable balance between lowering stand density and preserving complementarity among species. If the harvest is of appropriate density and timely, small scale disturbances may still be an alternative to ensure the mixture. To maintain tree mixture in mixed stands composed of tolerant and intolerant tree species, group selection method can be used. The groups can be created in favor of the shade-intolerant species, and the tolerant species is maintained using single tree selection within the rest of the stand (i.e., outside groups). Moreover, if complete vegetation removal in groups is not desired, group shelterwood with a canopy closure of 40% can be alternatively utilized to maintain Scots pine in mixed fir-pine-beech forests.

Conclusions

In particular, mixed natural forests provide more forest ecosystem goods and services compared to pure forests. Therefore, creating or maintaining tree mixtures in stands, and enhancing structural complexity have become two common measures for sustainable forest management in the last two decades. The sustainability and maintenance of these forests have gained much interest among forest managers. This study demonstrates the importance of tree mixture for the productivity and anatomical characteristics in fir-pine-beech forests. This research focused on productivity, anatomical characteristics and tree species richness rather than overall ecosystem productivity. However, discovering the correlations among species richness, anatomical characteristics and stand productivity would help us better understand the entire forest ecosystem. Knowing these relationships, multiple ecosystem goods and services could be more efficiently supplied. Initial data in this research would enhance our understanding of species diversity control within stands of fir, pine and beech.

Given the inconsistencies in previous researches regarding stand richness-structure-productivity relationships, our knowledge about how complementarity effects with tree ontogeny and stand age vary over time, as well as potential feedbacks from higher production to resource consumption seems to be still limited. Therefore, long-term extensive research into stand richness-structure-productivity relationships along various stress gradients is required. Future monitoring is also recommended to examine and compare the productivity as well as anatomical characteristics in pure and mixed stands of Scots pine and Oriental beech.

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Declarations

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

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