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The effect of bedrock and species mixture on wood density and radial wood increment in pubescent oak and black pine

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Abstract

Wood density and radial wood increment were examined in trees of pubescent oak (*Quercus pubescens* Willd.) and black pine (*Pinus nigra* Arnold., subsp. *nigra*) in relation to stand mixture and underlying bedrock. Trees of both species from pure and mixed stands were sampled across two types of bedrock, limestone and flysch. Trees from each species were similar in age. Wood density was estimated in standing trees using resistance drilling and increment cores were taken from a smaller subsample of trees of both species. Tree-ring, earlywood and latewood widths were measured and compared to radial profiles of wood density. The influence of stand mixture, diameter at breast height and bedrock on wood density was examined using a Bayesian general linear model. Wood density was significantly higher in pubescent oak than in black pine. Stand mixture was found to affect wood density positively, although the magnitude of the effect was relatively small when compared to other influencing factors also included in the current study. The effect of diameter on wood density was positive on both bedrocks in pubescent oak and negative or neutral in black pine. The size of the effect varied by bedrock and species. On flysch bedrock, the influence of diameter on wood density was stronger than it was on limestone. These indirect bedrock effects on wood density are probably a result of different soil fertility rather than the bedrock itself. There was a notable difference in radial wood increment in both species across the two bedrocks, whereas the differences in densities were smaller. Higher wood densities found on flysch in the subsample of pubescent oaks are likely an effect of higher proportions of latewood, while the opposite trend was observed in black pine. Higher wood density was found on limestone in black pine despite higher latewood percentages on flysch. In the context of forest management, the species composition of the naturally occurring mixtures in the sub-Mediterranean region should be adjusted slightly to favor pubescent oak, since it is a climax species and will bind more carbon for longer than black pine due to higher wood densities. Future forest management should also promote the overall development of pubescent oak trees

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in sub-Mediterranean stands. The results are especially important in the European context, because the share of sub-Mediterranean stands is expected to rise with global warming.

Keywords: Karst, wood structure, resistograph, resistance drilling, *Quercus pubescens*, *Pinus nigra*, limestone, flysch

1. Introduction

Global climate change and altered disturbance regimes negatively affect tree performance (Jentsch et al., 2011). Forests as long-lived ecosystems are to some degree resilient and can adapt to changing environmental conditions; however, any rapid changes or increased frequency and severity of natural disturbances may exceed the natural adaptive capacity of tree species (Keenan, 2015). Consequently, tree species distributional ranges and the composition of forests will probably change. This could lead to local extinctions and the loss of important functions and services, including reduced forest carbon stocks and sequestration capacity (Anderegg et al., 2015). To adapt forest ecosystems to anticipated environmental changes well in time appropriate forest management actions should thus be considered to lessen the risk and magnitude of tree dieback and mortality (Jump et al., 2017).

Future projections of tree-species compositions in European forests show significant changes until the end of the 21st century with a decline in species richness in the Mediterranean and Central European lowlands, while Scandinavian and Central European high-elevation forests are projected increasing diversity (Buras and Menzel, 2019). On the one hand, the abundance of currently economically most important tree species of Central and Northern Europe is either expected to decrease, as in the case of *Pinus sylvestris* and *Picea abies*, or would remain unchanged, as with *Fagus sylvatica* and *Quercus robur*. On the other hand, there are several currently dominant tree species in the Mediterranean that are projected partly to fill the gaps, such as *Quercus ilex, Pinus pinaster, Pinus halepensis, Pinus nigra, Castanea sativa and Quercus pubescens* (Buras and Menzel, 2019). While the ecological relevance of these species has been recognized in the Mediterranean regions, their expected increasing importance as a replacement of locally declining tree species in Central Europe has generated considerable interest in their wood properties in recent years, as can be observed for *Q. pubescens* and *P. nigra* (Todaro et al., 2015; Dias et al., 2018; Tintner and Smidt, 2018; Humar et al., 2020). In Slovenia, too, long-term monitoring of tree growth, wood properties and carbon-water fluxes at the ecosystem level has been continuously carried out in the drought-sensitive sub-Mediterranean region to better understand the effect of climate on future tree performance and woody biomass (Ferlan et al., 2011; Vodnik et al., 2019, e.g.).

Proper knowledge of wood structure and properties is a prerequisite for its rational use. One of the most important wood properties is wood density, since it directly affects both overall timber quality and carbon storage. It is also strongly correlated with other wood mechanical properties, such as strength and stiffness (Dinwoodie, 1981). Although measuring wood density in standing trees is traditionally both time and resource demanding, technological advances have resulted in the development of a relatively accurate and fast measurement technique for this purpose by using resistance drilling (Rinn et al., 1996; Gao et al., 2017). Wood density is closely related to tree-ring width and its structure, more precisely to the structural differences between earlywood and latewood. Unlike in diffuse-porous species (e.g. European beech, *Fagus sylvatica* L.), in which wood structure is fairly homogeneous, these differences are much more pronounced in ring-porous species (e.g. oak) and conifers (e.g. pine) (Dinwoodie, 1981). A higher proportion of thick-walled and narrow latewood cells positively contributes to wood density (Dinwoodie, 1981). In addition to the non-linear relationship of earlywood / latewood proportion with tree-ring width, the structure of these two tissues is not homogenous and may change in response to various internal and external stimuli (Rao et al., 1997). Consequently, the relationships between wood density and influencing environmental factors are not yet entirely clear. A review by Zobel and van Buijtenen (1989) reported no clear relationships between the effect of site, soil, soil moisture or climate on wood properties. They can all have an impact, depending on the species and other factors.

Several studies have examined what affects wood density in softwoods, however, there was relatively little research done on the species included in the current study. Wood density in softwoods was generally reported to be affected by genetics (Lasserre et al., 2009), initial planting spacing (Rais et al., 2014; Lasserre et al., 2005; Šimić et al., 2017), early respacing and thinning (Macdonald and Hubert, 2002; Cameron, 2002; Eriksson et al., 2006; Cameron et al., 2015; Pape, 1999), tree crown properties (Lindström, 1996; Krajnc et al., 2019) and tree age (Kimberley et al., 2017). In pine species generally, wood density was reported to be affected by mixtures (Zeller et al., 2017), thinning (Aslezaeim, 2016; Peltola et al., 2007), tree social position within an individual stand (Deng et al., 2014; Tsoumis and Panagiotidis, 1980) and unaffected by tree size and stand density (Zeller et al., 2017). Compared to the wood density in pine species, very little research has been done on how tree and stand properties effect wood density of oak trees. A study conducted on *Quercus petraea* (Liebl.) showed little to no influence of forest management and environment on oak wood density (Guilley et al., 2004), while wood density decreases with tree age (Guilley et al., 1999).

One of the most studied factors in relation to forest growth in general over the last decade has been the influence of mixture, e.g. stands with several different species. Mixed stands have been found to have several advantages over monocultures. It has been reported that mixed stands have higher sums of crown projection areas than monocultures, since there are more crowns overlapping in mixed stands. This probably results in increased light interception, higher stand density and therefore higher stand productivity. Mixed stands have also been reported to be more resilitient to disturbances (Pretzsch, 2014). Even though canopies in mixed stands are denser with higher crown overlap as reported by Pretzsch (2014), stem quality remains unaffected by mixtures (Benneter et al., 2018). Mixed stands in Europe are generally more productive than pure stands, assuming that the species in the mixture occupy different ecological niches. If the species niches are similar, however, mixed stands are less productive (Pretzsch, 2009). There have been conflicting reports on the influence of mixtures on wood properties. The three grade-determining properties (wood density, stiffness and strength) were reported to increase or decrease in mixtures, depending on species. Timber knottiness is likely to increase in mixtures (Pretzsch and Rais, 2016). Rais et al. (2020) reported that, compared to monocultures, dynamic modulus of elasticity of European beech trees was negatively affected when grown in mixtures. The species *Pinus sylvestris* and *Quercus petraea* when growing in mixed stands positively affected the growth of beech trees while negatively affecting wood quality overall (Rais et al., 2020). The influence of mixtures on stand productivity varies with stand and environmental factors, it is not always positive/negative by default (Mina et al., 2018).

However, almost no studies reviewing the effect of mixtures on forest growth have been done in sub-Mediterranean and Mediterranean forest stands. *Pinus* sp. and *Quercus* sp. relatively often form mixed stands in forest ecosystems all over the globe (Cain and Shelton, 2000; Inclán et al., 2007; Naudiyal and Schmerbeck, 2016). Pubescent oak (*Quercus pubescens* Willd.) is one of the most important deciduous broadleaved sub-Mediterranean tree species. It is well adapted to grow on poor, shallow and dry soils, preferably on limestone, with a rooting system that can penetrate deep into rocky soils (Kotar and Brus, 1999). It can be found over a great altitudional range, between 100 and 1500 m a.s.l. *Q. pubescens* requires warm temperatures but is also relatively resistant to winter cold (Bordács et al., 2019). Despite its low economic relevance so far (mostly used as a firewood) pubescent oak is ecologically important for the Slovenian sub-Mediterranean since it prevents degradation of vulnerable, shallow and erosion-prone soil (Brus, 2004). Black pine (*Pinus nigra* Arnold.) is a fast growing and light-demanding conifer species with multiple subspecies and a dispersed and discontinuous areal ranging from North Africa in the SW to Crimea in the NE (Isajev et al., 2004). This tree species is adapted to a wide range of bioclimatic conditions; it is resistant to drought and wind, its areal considerably varies in terms of altitude (350-2200 m above sea level; a.s.l.) and it can grow on various types of bedrock, including limestone, dolomites or serpentine, flourishing also on dry and shallow soils (Kotar and

Brus, 1999; Isajev et al., 2004).

The main aim of the current study was to quantify the size and direction of the stand mixture effect on wood density in pubescent oak and black pine, while the secondary aim was to assess the potential differences in wood density between the two examined bedrocks, limestone and flysch. Wood density was measured at breast height using resistance drilling in mixed and pure forest stands on two different bedrocks. To examine the impact of variations in wood structure on wood density, detailed anatomical analyses of tree rings were performed on a subsample of 12 pubescent oak and black pine trees. The results will contribute to more informed decision-making on the future management of similar stands.

2. Material and methods

2.1. Study area

The study was performed on Podgorski Kras (N45°32′56.3″ E13°54′36.1″, 430 m a.s.l.), a karst region in south-west Slovenia. The site belongs to the sub-Mediterranean phytogeographic region and was abandoned about 30 years ago. It has since been encroached by naturally occuring various woody plant species with pubescent oak (*Quercus pubescens*) and black pine (*Pinus nigra*, subsp. *nigra*, also known as Austrian black pine) being among the dominant tree species growing in either pure or mixed stands. Black pine was used extensively in the past to afforest the Karst region in the south-western Slovenia to improve soil conditions on degraded sites. It is now being replaced by the natural succession of native tree species, including pubescent oak (Gajšek et al., 2015). The sub-Mediterranean climate is characterized by harsh winter conditions and frequent dry periods in summer. The mean annual air temperature in the period 1992–2019 was 11.9 °C with the lowest mean monthly temperature recorded in January (2.9 °C) and the highest in July (21.5 °C), as calculated from the nearby climate station (at Kozina) belonging to the Slovenian Environmental Agency (ARSO). Precipitation is relatively abundant, on average 1310 mm per year, with rainfall peaks in late spring and autumn. The research plots were located on the edge of a plateau, where the bedrock changes from limestone to flysch. While limestone is very common in karst regions, flysch appears less frequently. The soil on limestone was rendzic leptosol, with uneven depth ($< 0.5m$) and poor water retention capacity. The soil on flysch was classified as eutric cambisol, with high water retention capacity and deeper soil depth ($> 0.6m$) (Vodnik et al., 2019).

2.2. Sampling and material

Six large rectangular transect plots were formed in the vicinity of the already established experiments in the Podgorje region. The two species of interest were pubescent oak and black pine and the plots were stratified by mixture type, where each stand was classified as either pure or mixed stand. No other species were present in mixed stands. The plot width was the same for all plots (8 meters), while the plot length was determined by the terrain. Selected plots were placed within a radius of 150 meters, close to the edge of the plateau where the bedrock changes. The plots were placed at least 20 meters from the edge of the plateau to avoid any edge effects. The plateau and its edge are further illustrated in Vodnik et al. (2019). Half of the plots were on a limestone bedrock and half on a flysch bedrock. The plots were as homogeneous as possible in all stand characteristics. In each plot, the diameters at breast height (DBH) of all trees were measured, as were tree heights. Each tree was assigned into one of the five crown social classes using the Kraft classification system (Assmann, 1970). None of the stands have been actively managed. Some plot characteristics are shown in Table 1.

Table 1: Individual plot properties, showing plot area, number of trees (per ha) and basal area (per ha).

Bedrock	Mixture	Species	Plot	Area	N	BA
limestone	pure	pubescent oak	3	214	936	21
	pure	black pine	2	276	833	27
	mixed	mixed	1	388	1057	31
flysch	pure	pubescent oak	4	350	458	20
	pure	black pine	5	354	566	44
	mixed	mixed	6	337	920	33

Note: area in m^2, number of trees N/ha, basal area in m^2/ha.

All trees on plots were drilled at breast height using a resistance drilling device Resistograph SC-650 (Rinntech, Heidelberg, Germany) with a 50 mm long drilling needle, which can be used for accurate estimation of wood density in the radial direction (Rinn et al., 1996; Bouffier et al., 2008; Gao et al., 2017) and is a relatively fast method of estimating wood density in standing trees when compared to other density estimation methods. Wood density at breast height is a reasonably good representation of wood density of the whole tree in both softwoods and hardwoods (Zobel and van Buijtenen, 1989). The obtained density profiles were oriented perpendicular to the prevailing wind direction to avoid any influence of reaction wood. The profiles were drilled through the approximate center of the tree and were bark-to-bark, since the drilling was stopped once the device's drilling needle emerged on the opposite side of the tree. The resistance drilling measurements were imported into the R statistical environment using the R package *densitr* (Krajnc, 2020), which enables further manipulation of the measurements in R. The measurements were first trimmed to exclude the bark portion of each density profile and to avoid the influence of starting and ending portion of the measurement, after which the measurements were detrended automatically using a linear regression fit provided by the R package *densitr*. As the radial profile sometimes crosses knots or other non-homogeneous sections inside the tree stem, median values of resistance drilling density were used to summarize wood density profiles as they are less affected by outliers than mean values. The density values presented in the current study are tree median values of resistance drilling density, converted into basic wood density using a calibration factor. The calibration factor for each species was determined using 25 stem discs of each species, which were drilled using the Resistograph SC-650 immediately after felling the trees. The volume of each stem disc was measured, after which the discs were dried in an oven. The calibration factor was then determined by comparing the median wood density of each stem disc and the basic wood density using green volume and dry weight of each disc. The conversion factor for pubescent oak trees was 1.42 and for black pine 1.41, which were used to convert resistance drilling density into basic wood density.

To determine the relationships between wood anatomy and wood density, a subsample of 12 trees of each species from the immediate vicinity of the selected plots was also cored using increment borers and drilled using the Resistograph resistance drilling device. The 5 mm wide cores were extracted from trees at breast height in pure stands, six on limestone and six on flysch. Each core of pubescent oak was cut into pieces about 5–6 cm long, so that they could be placed on objective glasses for further analysis. Permanent cross-sections of 25 µm in thickness were prepared on a WSL-Lab sledge-microtome (WSL, Zürich, Switzerland) with disposable blades. The sections were stained with a safranin (Merck, Darmstadt, Germany) (0.04%) and astra blue (Sigma-Aldrich, Steinheim, Germany) (0.15%) water mixture (van der Werf et al., 2007), mounted in Euparal (Waldeck, Münster, Germany) and analyzed under an Olympus BX51 (Tokyo, Japan) light microscope and the Nikon NIS-Elements Basic Research v.2.3 image analysis system (Tokyo, Japan). The cores of black pine were dried, sanded and digitally recorded using the Atrics system (Levanič, 2007), after which the tree-ring, earlywood and latewood width were measured using the software CooRecorder (Cybis Elektronik & Data AB, Saltsjöbaden, Sweden). These parameters were measured to analyze and compare radial wood increment across the two different bedrocks. In order to analyze the width data, robust mean chronologies were calculated using the R package *dplR* (Bunn, 2008) and a subsample of the widths from each bedrock was modeled by fitting a generalized additive model (GAM) using restricted maximum likelihood for the selection of smoothing parameters. This was done by using the R package *mgcv* (Wood, 2004).

2.3. Statistical analysis

Statistical analysis was conducted in an open source statistical environment R (R Core Team, 2020) by using a Bayesian general linear model. This approach allows a more informative inference by incorporating uncertainty into the model itself (Kruschke, 2014). The model was implemented in Stan (Carpenter et al., 2017), with the help of the R package *rethinking* (McElreath, 2020a). The priors used were weakly informative, the model was specified as follows:

$$
\begin{aligned}
&\rho_b \sim Normal(\mu_i, \sigma)\\
&\mu_i = \alpha + \gamma_{species[i]} + \delta_{bedrock[i]} + \eta_{mixture[i]} + \theta_{social\ class[i]}\\
&+ \zeta_{(species[i]*bedrock[i])} + (\beta_{dbh[i]} + \beta_{species[i]} + \beta_{bedrock[i]}) * DBH\\
&\alpha \sim Normal(400, 50)\\
&\gamma_j, \delta_k, \eta_l, \theta_m \sim Normal(0, 50) \text{ for } j, k, l = 1..2 \text{ and } m = 1..5\\
&\beta_{dbh[i]}, \beta_{species[i]}, \beta_{bedrock[i]} \sim Normal(0, 10)\\
&\sigma \sim Exponential(100)
\end{aligned}
$$

Tree median basic wood density was the modeled variable, while the explanatory variables were species, bedrock, mixture type, crown social class and diameter at breast height. The effect of diameter on wood density was assumed to vary between species and bedrock. The effect of bedrock on wood density was also assumed to vary between species. Other interactions were also tested, and the model presented here is the best-fit model, both from a causal and predictive perspective. Tree height was highly correlated with tree diameter (Pearson's $\rho = 0.8, p < 0.001$) and was therefore excluded from further analysis. All models were manually checked for convergence and effective numbers of samples as described by McElreath (2020b).

3. Results

3.1. Tree-level properties

A total of 150 trees was measured across both species. More information is presented in Table 2. The differences in wood density both between species and between the two examined bedrocks appear to be noteworthy. Trees from mixed stands on flysch were found to have higher mean densities than trees from pure stands, although this difference was relatively small ($\sim 4\%$). This trend was reversed on limestone, with pure stands having slightly higher wood densities. There was also more variability in wood density of oak on flysch ($\sim 15\%$) than on limestone ($\sim 8\%$). The average values of diameter and tree height also appear to vary between bedrocks, the variation appears larger than when comparing the averages across the two species. Trees from pure stands on flysch had a higher diameter in both species. Differences in diameters between the species were less pronounced on limestone ($\sim 4cm$) than on flysch ($> 5cm$). Larger tree heights were observed on flysch overall, with pine trees being 2 meters taller than oak trees on average.

Table 2: Tree-level properties: displaying mean values of diameter at breast height (DBH), tree height (h) and basic wood density (ρ_b). Coefficient of variation in brackets.

Bedrock	Species	Stand mixture	N	DBH	h	ρ_b
limestone	black pine	mixed	17	20.9 (31)	9.0 (12)	420 (8)
		pure	21	20.1 (25)	9.7 (11)	430 (8)
	pubescent oak	mixed	24	16.5 (28)	7.3 (34)	650 (7)
		pure	22	16.6 (21)	7.2 (24)	660 (9)
flysch	black pine	mixed	16	21.0 (32)	10.1 (19)	520 (10)
		pure	20	30.7 (24)	13.0 (19)	490 (5)
	pubescent oak	mixed	14	19.4 (32)	9.8 (28)	700 (18)
		pure	16	22.2 (40)	11.7 (20)	630 (13)

Note: DBH in cm, h in m, ρ in kg/m^3.

3.2. The effect of species, bedrock, mixture and diameter on wood density

The relationships between the measured/observed variables and basic wood density were examined using a general linear model, as described in Section 2.3. The posterior distributions of model parameters are presented in Table 3. Species, mixture, bedrock, diameter and crown social class all had an effect on wood density. These relationships are further illustrated in Figures 1-3.

Table 3: Posterior distribution of the general linear model parameters: mean values, standard deviation and a percentile interval.

			Percentile interval	
	Mean	SD	5.5 %	94.5 %
Intercept	450.2	42.0	383.1	517.3
σ	20.3	0.4	19.8	20.9
Species				
black pine	-14.4	39.1	-77.1	47.2
pubescent oak	64.0	38.2	3.4	124.8
Bedrock				
limestone	21.3	38.8	-40.4	84.6
$limestone_{pine}$	-34.1	38.1	-95.1	26.7
$limestone_{oak}$	55.8	37.7	-4.4	115.7
flysch	27.8	38.9	-34.4	90.1
$flysch_{pine}$	19.6	38.4	-40.7	81.7
$flysch_{oak}$	8.5	37.6	-51.7	68.7
Stand mixture				
mixed	35.5	32.0	-15.8	86.9
pure	15.5	32.0	-36.0	66.4
Diameter				
dbh	0.7	7.1	-10.6	11.9
dbh_{pine}	-1.8	6.0	-11.3	8.0
dbh_{oak}	2.4	6.0	-7.1	12.2
$dbh_{limestone}$	-0.2	6.2	-10.2	9.5
dbh_{flysch}	1.0	6.2	-9.0	10.6
Crown social class				
predominant	70.4	23.5	32.9	108.1
dominant	11.5	22.1	-24.4	46.8
co-dominant	2.8	21.7	-31.8	37.5
dominated	-7.9	21.9	-42.9	26.9
overtopped	-26.4	22.1	-62.3	8.7

The distributions of differences in individual model parameters for species, bedrock and mixture are presented in Figures 1A-C. Given the data and the formulated model, there was a notable difference in density between the two examined species. Pubescent oak was found to exceed the density of black pine by 78 kg/m^3 on average after excluding the effects of bedrock, mixture and diameter. Bedrock by itself had a negligible effect on wood density (mean parameter difference of 6 kg/m^3), however, the effect of bedrock was confirmed to vary between species, as illustrated in Figures 2A-B. Black pine trees had higher wood densities on flysch (mean parameter difference of 60 kg/m^3), while pubescent oak trees had higher wood density on limestone (mean parameter difference of 41 kg/m^3). The effect of stand mixture on wood density was positive (average difference 20 kg/m^3) when compared to trees from pure stands, although the magnitude of the effect was smaller than the difference between species.

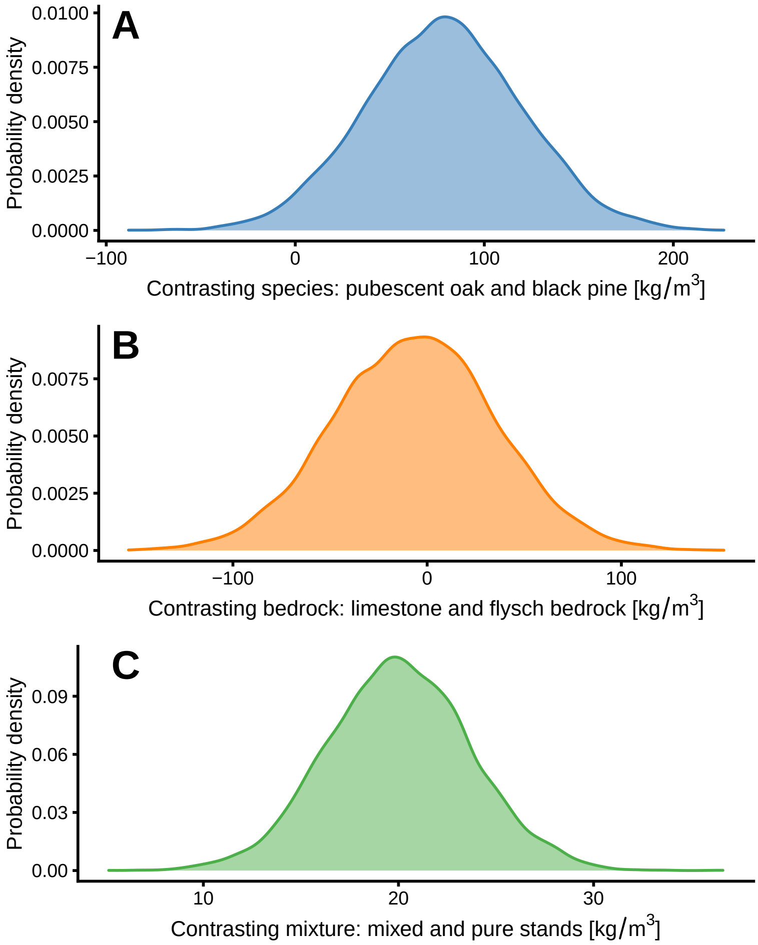

Figure 1: Distributions of differences in posterior distributions of individual model parameters for the effects of species, bedrock and stand mixture.

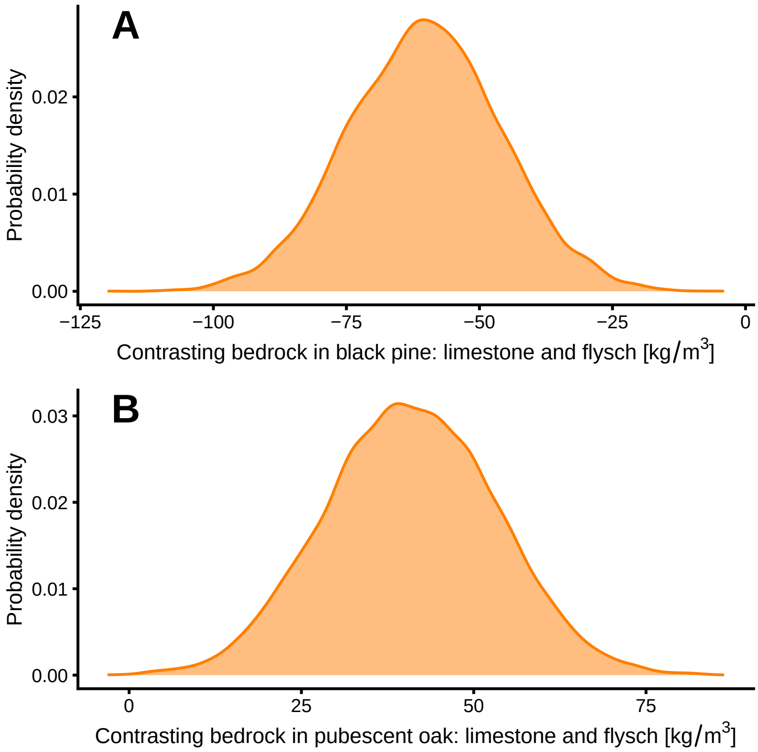

Figure 2: Distributions of differences in posterior distributions of individual model parameters for the effects of bedrock interacted with species.

The effect of diameter on wood density varied between species and bedrock. The effect of diameter on wood density across bedrock and species is shown in Figure 3. Diameter had a positive effect on wood density on both bedrocks in pubescent oak, neutral in black pine on flysch and negative on limestone. The effect is more pronounced in pubescent oak than in black pine, while the magnitude of the effect also varied by bedrock. An increase in DBH of 1 cm will on average affect the wood density by 1 to 6 kg/m^3 in pubescent oak, while having little effect on flysch or a decrease of up to -3 kg/m^3 on limestone.

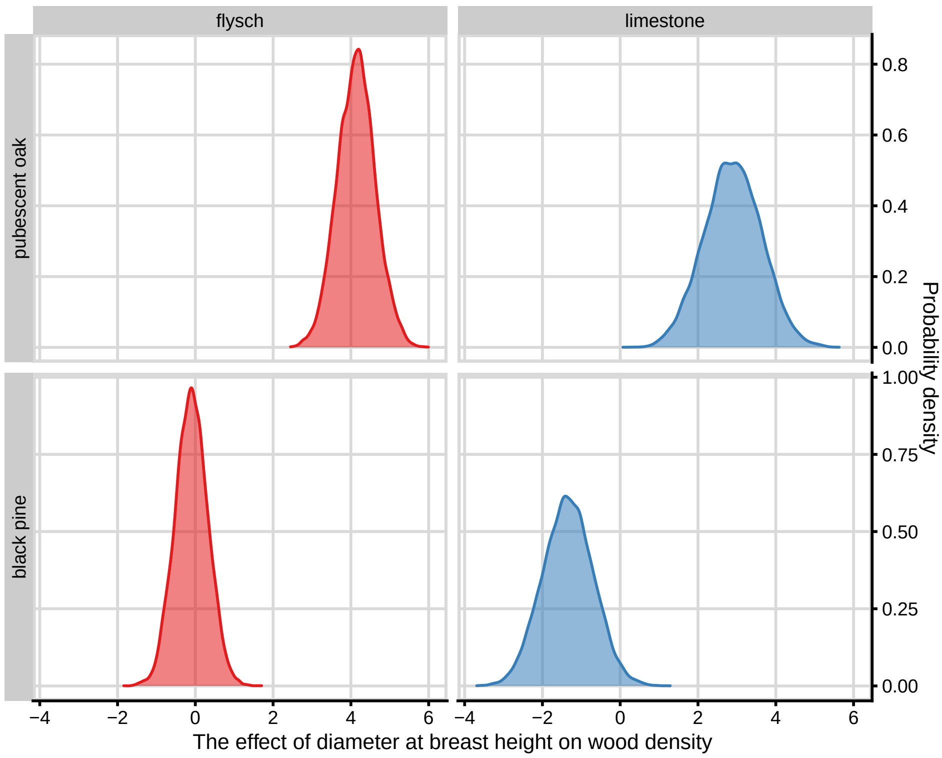

Figure 3: Posterior distributions of the effect of diameter on density by bedrock and species.

Notable differences were also found between different social classes, with the differences between the most dominant trees and completely suppressed trees matching the magnitude of other included variables.

3.3. The effect of bedrock on radial wood increment

In order to examine the relationship between wood density and wood structure more closely, wood density was measured in the examined trees using resistance drilling and compared with the tree-ring, earlywood and latewood widths (Figure 4). Of the 12 sampled trees of each species used for detailed anatomical analysis, half of the trees were growing on limestone, while the other half were growing on flysch. The average tree age of pubescent oak (and standard deviation) was 58.3 (±9.8) years on limestone and 56 (±8.8) years on flysch. Black pine trees were younger, 35.3 (±8.8) years on limestone and 32.8 (±2.9) years on flysch. Because the tree age was similar across the two bedrocks within the same species, age was unlikely to be an influencing factor on either growth or density in the current study. Similarly, climate itself had no influence on growth or wood density, since it was the same across both sampled bedrocks. Tree-ring width chronologies are shown in Figures 4 and 5.

In pubescent oak on flysch, the average tree-ring width (and standard deviation) was 2.02

(0.89) millimeters, while on limestone those values were lower 1.28 (0.83) millimeters. After the first 30 years of growth, the differences appear to stabilize and remain stable up to the present (see Figure 4).

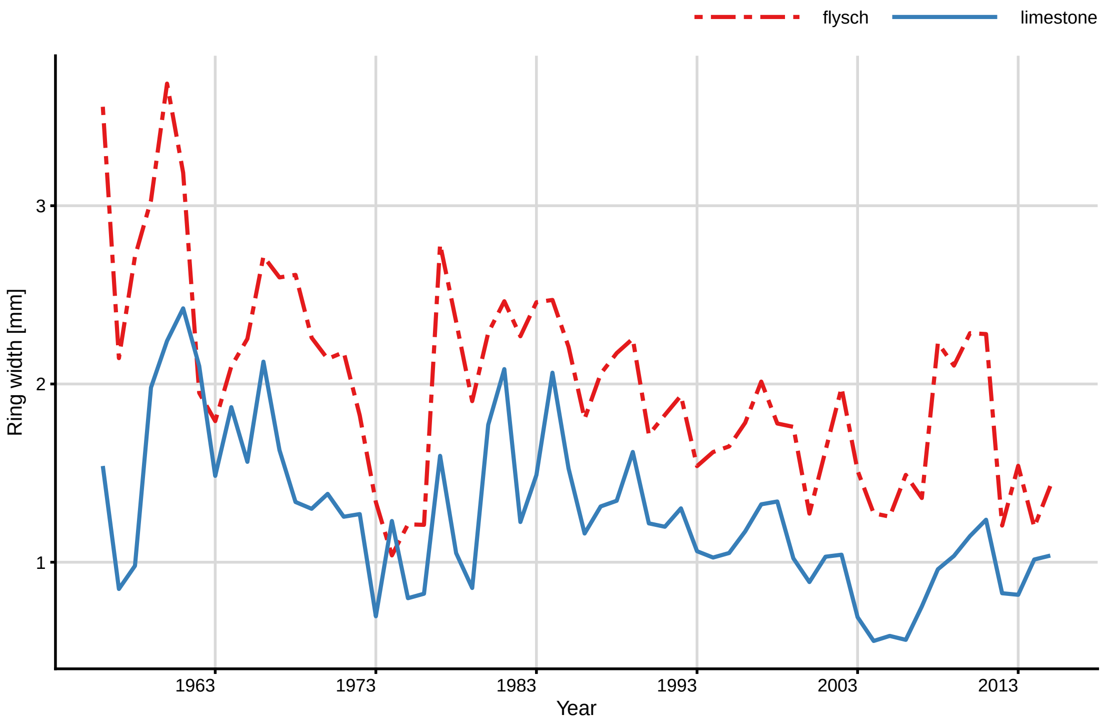

Figure 4: Robust mean chronology for each bedrock, pubescent oak (N = 12, 6 on each bedrock).

A similar trend can also be observed in black pine (see Figure 5). In black pines on flysch, the average tree-ring width (and standard deviation) was 3.27 (1.12) millimeters, while on limestone those values were lower and were 2.56 (1.13) millimeters.

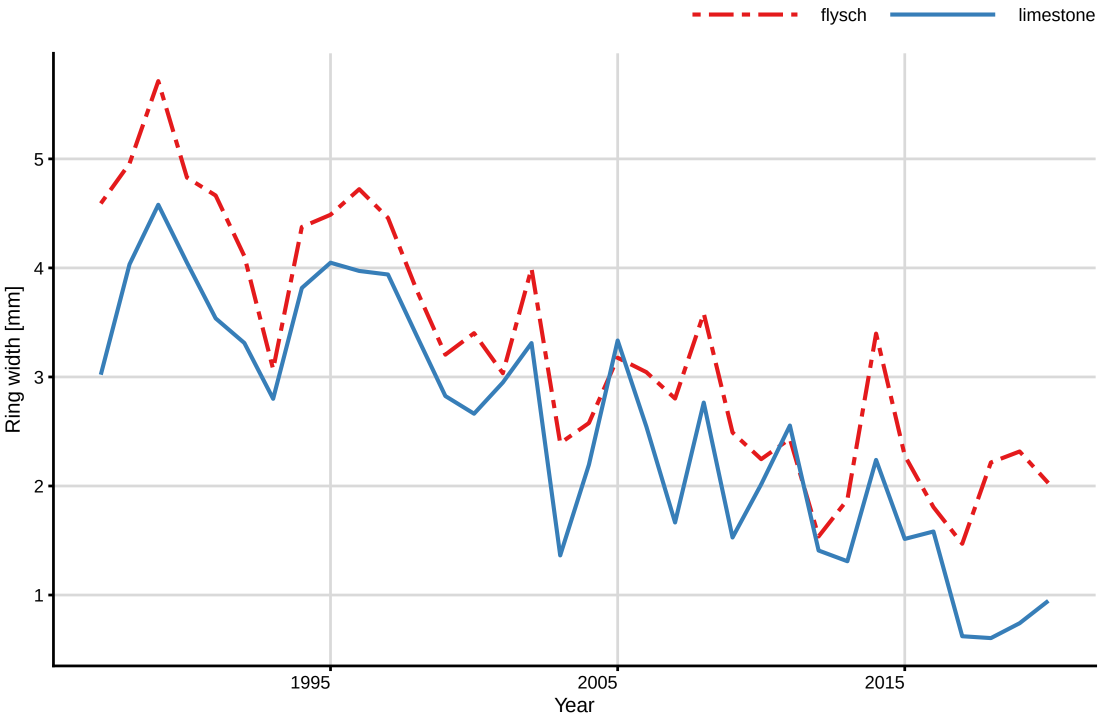

Figure 5: Robust mean chronology for each bedrock, black pine (N = 12, 6 on each bedrock).

3.4. The effect of radial wood increment on wood density

The density data for the subsample of 12 oak trees is shown in Figure 6A, together with a GAM smoothing model for each bedrock. The proportion of latewood and earlywood width for the same trees are displayed in Figure 6B-C. Wood densities were generally higher on flysch (average difference of around 25 kg/m^3), as was the proportion of latewood and absolute earlywood width (0.57 mm on flysch, 0.41 on limestone). The overall mean latewood proportion on flysch was 0.66, on limestone 0.57.

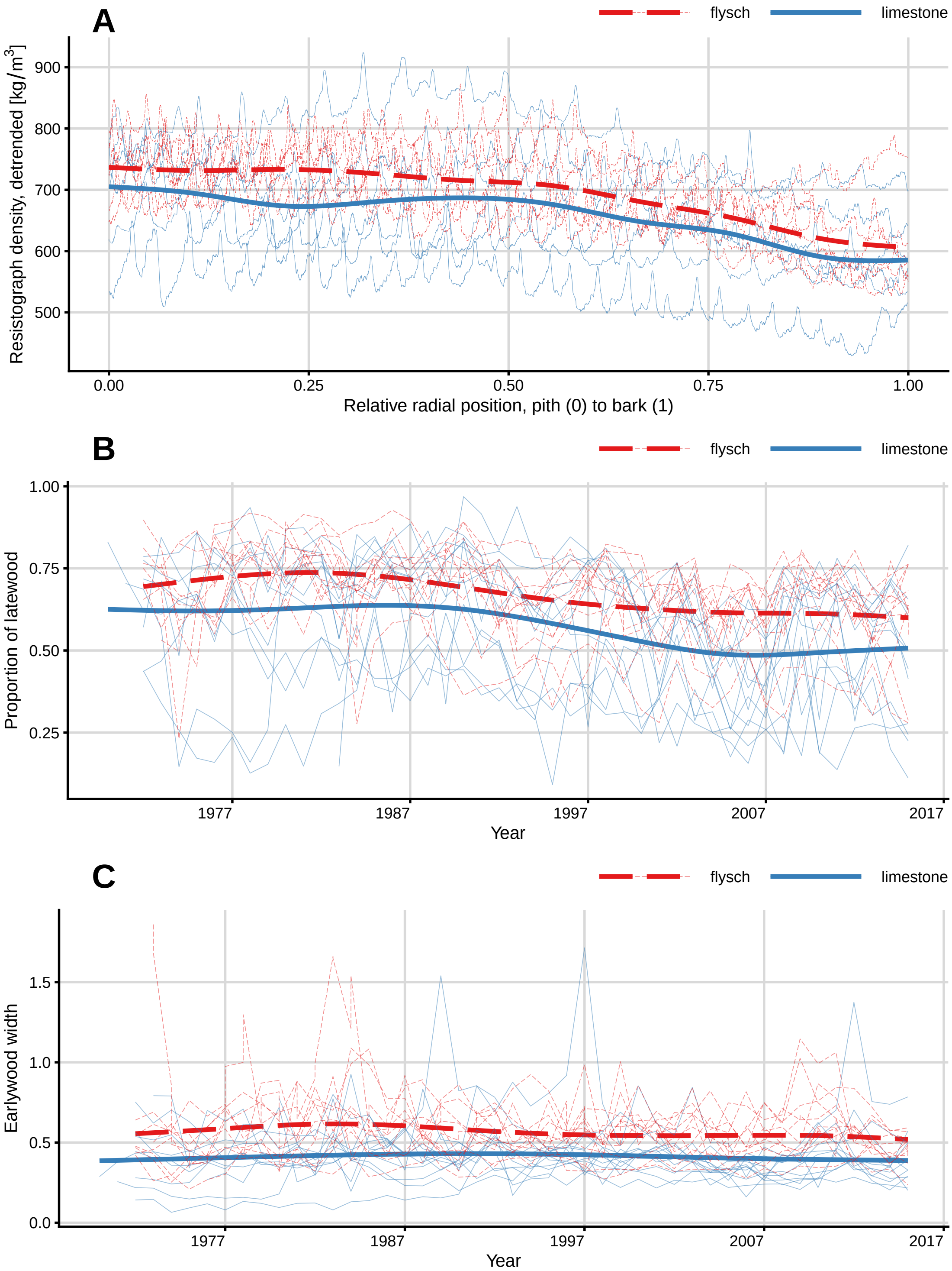

Figure 6: Wood density of pubescent oak by relative radial position, proportion of latewood and earlywood width with a GAM smoothing model for each bedrock (bold line).

The density data for the subsample of 12 pine trees is shown in Figure 7A, together with a

GAM smoothing model for each bedrock. The proportion of latewood and earlywood width for the same trees are displayed in Figure 7B-C. Wood densities were generally higher on limestone (average difference of around 30 kg/m^3). Absolute earlywood width was higher on flysch (1.35 mm, 2.56 on limestone), as was the overall mean latewood proportion (0.41 on flysch, 0.35 on limestone).

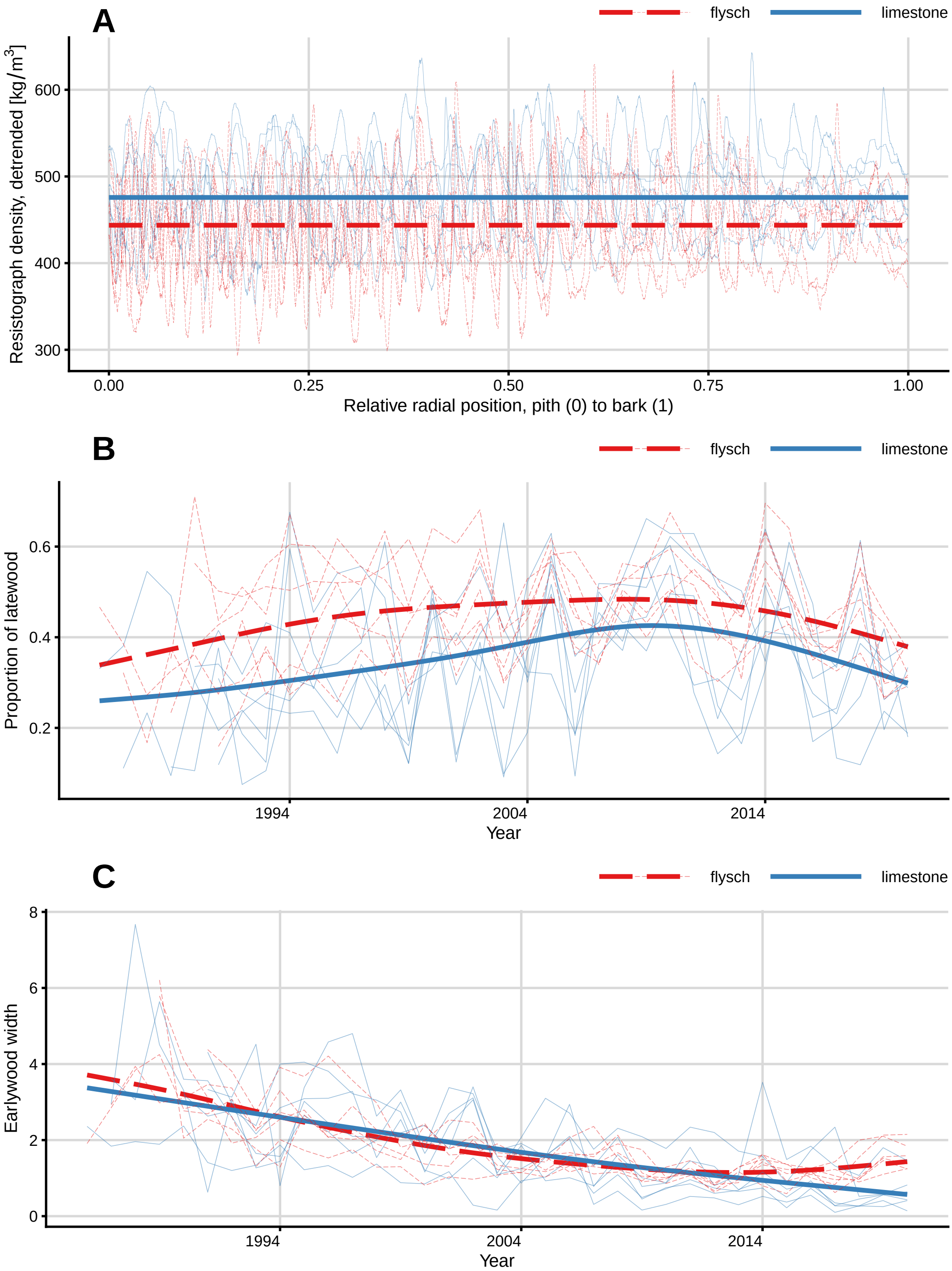

Figure 7: Wood density of black pine by relative radial position, proportion of latewood and earlywood width with a GAM smoothing model for each bedrock (bold line).

In addition, deviations from normal conifer wood structure composed of earlywood and latewood was observed. It was characterized by intra-annual density fluctuations (IADFs); i.e. the occurrence of latewood-like cells within earlywood or earlywood-like cells within latewood (de Luis et al., 2007). The frequency of IADFs at breast height varied with cambial age; they were most frequent in the first 20 years - see Figure 8. The frequency differed also between the bedrock. Of the 376 and 349 analysed tree rings, 49% (±21%) and 26% (±11%) showed IADFs on limestone and flysch, respectively.

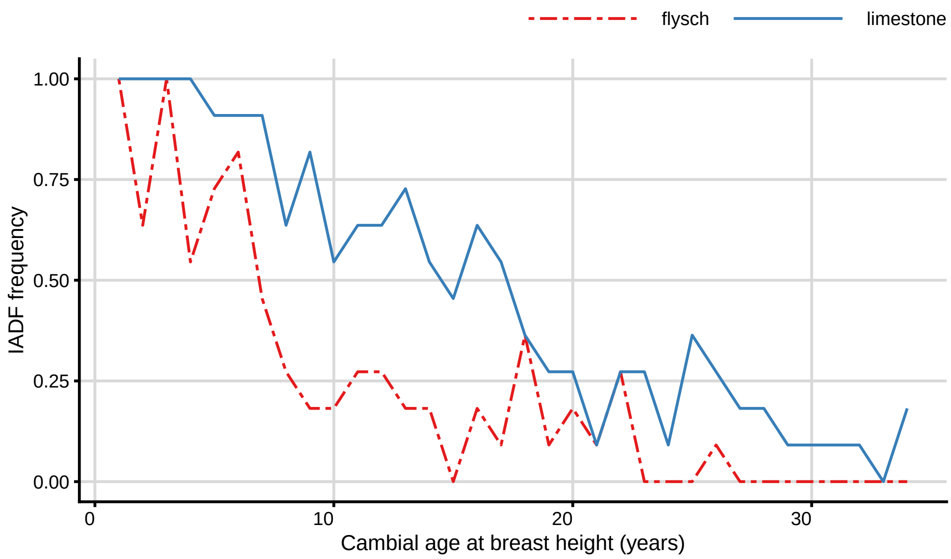

Figure 8: The frequency of intra-annual density fluctuation (IADFs) by cambial age and bedrock in black pine.

4. Discussion

4.1. The effect of studied variables on wood density

The difference in basic wood density at breast height between the two species (around 80 kg/m^3) was in line with previously reported differences in values for both species (Dias et al., 2018; Humar et al., 2020). The average oven-dry density of pubescent oak is 648 kg/m3 (Humar et al., 2020), which is comparable to the density of *Q. robur* (650 kg/m^3) or *Q. rubra* (660 kg/m^3) (Wagenführ, 1996). The average density of *P. nigra* wood is 588 kg/m^3 (Dias et al., 2018). The absolute values of wood density of black pine wood reported in the current study were lower than previously established values, which was most likely due to the relatively young trees in our case (30+ years) and therefore a high proportion of juvenile wood was likely included in the radial density measurements. Juvenile wood is characterized by a lower density because of lower proportion of latewood cells having thinner walls compared to mature wood (Panshin and de Zeeuw, 1980).

Black pine trees had higher wood density on flysch, while pubescent oak trees had higher wood density on limestone. The main cause of differences in wood density between the two examined bedrocks was most likely not the bedrock itself, but was rather a consequence of the differences between the bedrocks in soil depth and/or soil fertility in connection with water retention capability. The difference in wood density between species was also relatively large even within the same bedrock, which could be attributed to differences in diameter and soil pockets with different depths on karst, affecting micro-site fertility (Ferlan et al., 2011).

Mixed stands were found to have higher wood density than pure stands, even after accounting for the effect of competition by including crown social class in the statistical model. Although the mixed plots had higher stem densities, this was likely rendered unimportant by including the crown social classes. The observed differences in wood density due to mixture found in the current study were relatively small when compared to the magnitude of other influencing factors studied.

Crown social class had a direct effect on wood density, with predominant trees having the highest densities and suppressed trees having the lowest densities. These findings are line with what was found by Tsoumis and Panagiotidis (1980) in black pine and somewhat contrary to what was recently reported in three other softwood species (Krajnc et al., 2019), indicating the importance of species-specific approach to similar studies. Higher competition pressure generally results in narrower radial wood increment, which can affect wood density in conifers or ring porous hardwood species (Zobel and van Buijtenen, 1989), such as those included in the current study. However, lower diameters are not always directly correlated with lower densities, as discussed in the next paragraph. In contrast, species with diffuse-porous wood (*e.g.* European beech) are likely to be unaffected, since ring width does not significantly affect their wood density. The differences in density between different social classes were not negligible and social class or other competition indices should be included in similar studies where possible.

The effect of diameter on wood density was confirmed to vary between both species and bedrock. Although diameter is normally not the best representation of growth rate, due to the many influencing factors (*e.g.* age), trees from the current study were all of a similar age within each species and therefore diameters reflect the differences in growth rate. Zobel and van Buijtenen (1989) aggregated 40 studies studying pine species; the majority found no relationship between growth rate and specific gravity across a variety of pine species. In contrast, a positive relationship between the two variables was reported by the same authors for the majority of examined ring-porous hardwoods, which included several oak species. This was confirmed in the current study in both species, as the effect of diameter was positive on both bedrocks in pubescent oak while being neutral or negative in black pine.

Since the difference in wood density between the two species was partly dependent on diameter, the difference between species will likely increase at different rates across the two study sites and therefore extra caution is needed when comparing wood density values of trees with different diameters across different species. These findings confirm what was suggested by Pretzsch et al. (2018) and Mina et al. (2018), that conversion of growth measurements into carbon sequestration is not straight forward and needs to include more influencing factors in calculations than previously thought. Future research should include more plots containing a wider range of stem densities across different mixture proportions to examine further the relationship between mixtures, wood density, ring width and species.

4.2. The relationship between wood structure and wood density

Bedrock appeared to have a direct effect on radial wood increment, since the current study found notable and consistent differences between the two examined bedrocks in both species. As discussed above, this is more likely due to the difference in soil productivity than to the different bedrock. Although various soil characteristics directly affect radial wood increment (Zobel and van Buijtenen, 1989), some soil characteristics are likely to have a more pronounced effect on wood properties (Macdonald and Hubert, 2002). For example, the ratio of soil carbon to nitrogen could have a direct effect on wood density, as reported by Kimberley et al. (2017). Past research has reported a difference in the carbon-to-nitrogen ratio (Gričar et al., 2019) between soils on limestone and soils on flysch, whereby these differences are likely to be a consequence of the different water retention capacity of the soils (Jackson et al., 2002). Since flysch, with higher water retention capability, seems more productive for tree growth than limestone, trees growing on it will likely have a more pronounced response to (un)favorable growing conditions.

Oak ring widths followed a similar pattern of difference as wood densities; however, the difference in ring widths was almost a factor of two, while the difference in densities was smaller ($\sim 5\%$). The wood density of the examined oaks showed a declining trend overall, as did the latewood proportion. Earlywood width remained more or less constant throughout the lifetime of the examined trees, whereas tree-ring and latewood widths were positively correlated. This is consistent with previous research (Dinwoodie, 1981), in which the wood density of ring-porous oak trees was positively affected by increasing latewood proportions. Latewood density in oaks was reported to be higher (ca. 800 kg/m^3) than that of earlywood (ca. 560 kg/m^3), as evidenced by data for *Q. petraea* (Guilley et al., 1999).

The opposite pattern of differences was found between ring widths and wood density in black pine. While ring widths were consistently higher on flysch, wood density was lower. Ring widths were significantly closer to each other across the two bedrocks than in pubescent oak, while the difference in wood density was similar. Wood density was also more consistent over time and was not declining like in oak trees. The proportion of latewood is currently declining, as is absolute earlywood width. Since pine trees were younger than oak trees, those trends were likely a direct reflection of the transition from juvenile wood into mature wood and would likely be higher in older trees. As already previously mentioned typical of juvenile wood is lower density because of lower proportion of latewood cells having thinner walls compared to mature wood (Panshin and de Zeeuw, 1980).

IADFs were frequently observed in tree rings of pine trees, with a higher frequency on limestone. It has been reported that severe conditions during the growing season, such as shortage of water, may trigger the formation of IADFs (de Luis et al., 2007; Piermattei et al., 2020). The site on limestone is more sensitive to water stress due to lower water retention capability as indicated from narrower wood increments in both species and a more pronounced response to unfavorable growing conditions was observed in pine through appearance of IADFs. The presence of IADFs in all pines in our study on limestone and in 82% trees on flysch in 2003, when extreme drought and heat wave occurred in Europe, further support these assumptions. Similarly to Novak et al. (2013) in *Pinus halepensis*, we also found that IADFs frequency varied with cambial age and bedrock. They were most frequent during the first two decades of growth. The presence of IADFs in some of the tree rings in combination with juvenile wood would explain a lack of negative relationship between tree-ring width and wood density as typically found in wood of conifers, in which wider tree-rings contain a higher proportion of low-density earlywood (Dinwoodie, 1981). Thus, in Mediterranean conifers IADFs need to be considered to affect wood properties, which may consequently differ from those in 'normal' wood.

The wood-anatomical analyses of both species are in line with previous studies that reported that the structure of earlywood and latewood is not uniform and that any changes in the structure also affect wood density (Rao et al., 1997). In general, the relationship between tree-ring width and earlywood/latewood proportions is quite complex, depending on site-, age-, and species-specifics. For a better insight into the impact of variations in wood structure within-tree rings on wood density, detailed anatomical analysis of transverse sections, in combination with other methods, seems to be an appropriate approach.

4.3. Implications of the current study in a broader context

Due to global warming, the increasing proportion of abandoned pastures in the karst region of Slovenia over the last few decades and natural succession, these two species are expected to spread in the sub-Mediterranean phytogeographic region. Although both species are currently relatively unimportant economically, this will likely change in the future. Hanewinkel et al. (2013)

predicted an increase in Mediterranean oak forest type coverage across Europe by the year 2100, due to global warming. These changes will impact the global forest sector in terms of timber supply, demand and production, which could result in substantial economic losses in some parts of Europe (Kirilenko and Sedjo, 2007; Hanewinkel et al., 2013). Existing forest stands in the sub-Mediterranean and Mediterranean regions are therefore an ideal sampling ground to measure and monitor how different factors affect wood development and tree growth overall, which will provide valuable data for the future. Similarly, the mechanical properties of the two species should also be examined to study the effects of bedrock and mixture types. As black pine has multiple subspecies with specific areals throughout Europe, findings of the current study should not be generalized to other subspecies and would need to be verified in those subspecies, which could have different physical and mechanical properties due to the difference in environmental conditions during growth. Whether mixed forests are the better option in terms of carbon storage, remains to be tested. Numerous studies on forest responses and vulnerability to recent climate change have already increased our understanding of these relationships and provided improved capacity to predict and assess ecosystem responses (Keenan, 2015). However, more targeted research is needed. The current study confirmed that multiple factors, such as different relationships of radial wood increment to wood density across different soil fertilities, need to be taken into account when calculating the correct carbon sequestration capacity for activities associated with Land-Use, Land-Use Change and Forestry (LULUCF) under the United Nations Framework Convention on Climate Change (Burke et al., 2012).

5. Conclusions

The current study confirmed that of bedrock has an effect on wood density of pubescent oak or black pine. It also confirmed that the relationship between wood density and radial wood increment is both species- and bedrock-dependent. These indirect bedrock effects are most likely a result of different soil fertility rather than the bedrock itself. The current study has confirmed higher wood density in trees from mixed stands across both species, even after accounting for different levels of competition between stands by including crown social class into the model. Although there was a notable difference in the radial wood increment of trees across the two bedrocks and both species, the differences in densities were smaller. This confirms past findings, that the relationship between radial wood increment and wood density is relatively complex and depends on multiple factors. The results of the current study indicate that future forest management should promote the overall development of pubescent oak trees when optimizing forest management of sub-Mediterranean stands for increasing carbon storage. The species composition of naturally occurring mixtures, such as those investigated in the current study, should be adjusted slightly to favor pubescent oak, since it is a climax species and will bind carbon for longer. Black pine, on the other hand, is a typical pioneer species with a relatively short lifespan. Future similar studies should include detailed anatomical analyses, since only a combination of methods is capable of revealing the complicated relationships between wood formation and wood density.

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