Article

Past and Future of Temperate Forests State under Climate Change Effects in the Romanian Southern Carpathians

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Abstract: Research Highlights: Carpathian forests hold high ecological and economic value while generating conservation concerns, with some of these forests being among the few remaining temperate virgin forests in Europe. Carpathian forests partially lost their original integrity due to their management. Climate change has also gradually contributed to forest changes due to its modification of the environmental conditions. Background and Objectives: Understanding trees' responses to past climates and forms of management is critical in foreseeing the responses of forests to future conditions. This study aims (1) to determine the sensitivity of Carpathian forests to past climates using dendrochronological records and (2) to describe the effects that climate change and management will have on the attributes of Carpathian forests, with a particular focus on the different response of pure and mixed forests. Materials and Methods: To this end, we first analysed the past climate-induced growth change in a dendrochronological reference series generated for virgin forests in the Romanian Curvature Carpathians and then used the obtained information to calibrate spatially explicit forest Landis-II models for the same region. The model was used to project forest change under four climate change scenarios, from mild to extreme. Results: The dendrochronological analysis revealed a climate-driven increase in forest growth over time. Landis-II model simulations also indicate that the amount of aboveground forest biomass will tend to increase with climate change. Conclusions: There are differences in the response of pure and mixed forests. Therefore, suitable forest management is required when forests change with the climate.

Keywords: temperate forests; climate change effects; Southern Carpathian forest management; forest growth; forest biomass; virgin forests

1. Introduction

Forests have a specific structure and function that determine their capacity to provide multiple ecosystem services, including C (carbon) sequestration [1,2], which has a main role in atmospheric CO_2 (carbon dioxide) balance and, therefore, climate change mitigation strategies and agreements. Environmental conditions, particularly with regard to the soil and climate, play a significant role in forest structure development, forest succession, productivity, etc. Since the climate is continuously changing [3,4], forests also do [5,6]. Even when climate extremes do not have strong effects at the local level, forest changes are forced by direct [6] and indirect [7] climate change effects [8].

However, in terms of structure and composition, forests are often characterized by a high diversity and spatial heterogeneity [9,10]. Carpathian temperate forests, for instance, host both pure and mixed altitudinal forests [11,12], which have very different ecological preferences and properties [11,13,14]. Mixed stands proved to have high resistance and resilience and, often, a high level of productivity, compared to pure stands [15–19]. On the other hand, even-aged monospecific stands instead are less complex functionally and structurally complex [20]. Functional diversity, particularly in mixed forests, provides

redundancy [21,22], resistance [15,16,22] and resilience [16,17] to different disturbances. Having a relatively high forest integrity compared to other temperate regions in the world [10,18,19], the mixed forests in the Carpathians are usually constituted by uneven-aged stands with high structural and functional diversity [9,23,24].

Characterized by their high stability and adaptability to climate change and stress factors [25] and by their high productivity [26], the mixed forest management model of the Carpathians might be a useful reference for other managed forests [23,27] in the region. Forest management, including its effect on forest structure and functioning, can be used to promote long-term forest resilience and resistance [22,28,29], contributing to C sequestration, as part of the atmospheric CO_2 balance and climate change mitigation and adaptation strategies and specific programs [22,30]. However, a careful assessment of the forest's state is required.

Even though mixed stands benefit from functional diversity [31], they are also sensitive to management and changes in environmental conditions [31]. Proven drivers of mixed forest change include temperature rises [16] and drought [17]. Functional diversity guarantees greater stability at the stand and forest levels and can increase stress resilience and productivity under drought events [16], but climate change can trigger modifications in species abundance [16,32,33] and can, therefore, alter the structure and functioning of mixed forests, as well as the services they provide [1]. There is still high uncertainty regarding the local impacts of climate change and their potential changes in temperate forests [30], either pure or mixed, as well as their capacity for stocking biomass under regular management. There is also the need to reconstruct and to reanalyse past changes [8] in the context of climate change effects in order to explore future changes.

The complexity of the ecosystem processes and the need for reliable forecasts of climate change mitigation and adaptation actions make the use of a model approach that integrates plant–soil–climate relationships necessary. Landis-II models have been proven to be robust in simulating ecophysiological processes at the cohort level, including natural disturbances and management at the landscape spatial scale [34]. Landis-II models, coupled with the PnET model [35], cover local climate effects on vegetation development [35,36], and they are suitable tools for climate change forecasting [36]. However, their implementation is complex, because many parameters are intercorrelated, and many data inputs must be measured locally [36]. In addition, their calibration is complex and potentially affected by operator decisions [36]. Error propagation can affect the entire model, and the calibrated model can rarely be exported to other contexts, either geographical or temporal. Therefore, new alternatives for models' implementation are required, and this may be achieved by integrating ecological models with machine learning (ML) tools [37–39] and by utilizing the best data available, such as those from long-term ecological research databases [24], e.g., dendrochronological records.

It is well known that tree ring width is significantly influenced by climate variation [40], and therefore, tree ring cores provide a historical record of the climate variability (dendroclimatology) [41], forest growth and age structure, disturbances, site conditions (dendroecology) [42], etc. Climate reconstruction is commonly achieved through the study of the climate signals found in the tree rings [40–43] of open-grown trees [14,40,44], because they are more exposed to climate events and because isolated trees are less affected by competition and other ecological processes [14,45]. Non-isolated trees, mainly in virgin mixed forests, are the best option for tackling intra- and inter-specific interactions. Carpathian virgin forests, internationally recognized for their conservation value, for research and for the services they provide [22,25,46], together with other old-grown forests in the Curvature Carpathians, give an opportunity to deepen our understanding of the roles of mixed vs. pure forests role and their response to long-term processes [23,40–43], such as climate change [8,44,47], as well as their effects on biodiversity, productivity and C cycling [9,22,29]. Understanding species interactions and responses to past climates and forms of management is critical in foreseeing forest responses to future conditions and in creating optimal strategies for climate change mitigation and adaptation. Within

this context, this study aims (1) to determine the sensitivity of Carpathian forests to past climates using dendrochronological records and (2) to describe the future effects of forest management and climate change on Carpathian Forest biomass, with a particular focus on the different response of pure and mixed forests.

2. Materials and Methods

2.1. Study Area

The research area is located in the Penteleu Mountains within the Penteleu Forest District (Figure 1). It is a very representative area of Eastern Europe temperate forests specific to the Romanian Curvature Carpathians, at altitudes between 400 and 1800 m.a.s.l. The average annual temperature ranges between 4 °C and 6 °C. The minimum and maximum absolute temperatures recorded are −33.5 °C and +38 °C. The frost period ranges from 120 days at 800 m.a.s.l. to 220 days at the highest peaks. The average annual precipitation is 830 mm, mainly concentrated in summertime. The prevailing winds come from the NW, W and NE directions, with a 6–7 m·s^{-1} annual average speed in high-altitude areas and 2.5–3.5 m·s^{-1} in low-altitude areas.
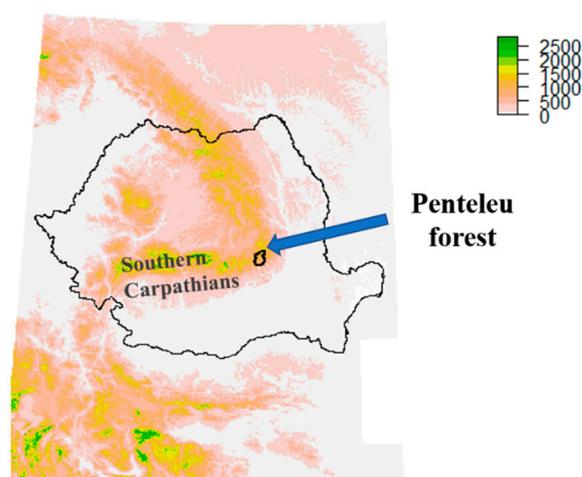

Figure 1. Study area location in Southern Carpathians.

Most of the forest stands included in the research area are temperate montane mixed conifer–broadleaved forests. The main species in terms of timber volume are *Fagus sylvatica* L. (beech—34.6%), *Picea abies* (L.) H. Karst. (Norway spruce—38.1%) and *Abies alba* Mill. (silver fir—22.6%). Other deciduous and softwood species provide less than 4.7% of the overall volume [48]. There is no historical evidence that extreme events (such as windthrows, drought, insect damage, fires, etc.) had a relevant role in the development of the Penteleu forest over time.

Penteleu forest, similar to most of the Romanian Carpathian forests, suffered the effects of profound changes in its management. Being initially private property owned by local landowners and local communities, logging at the beginning of the 20th century was carried out at the pleasure of the owners and in accordance with market demand. However, forest integrity was not heavily affected, regardless of the massive harvests that occurred around a forest railway. Within this period, conifer stands were clear-cut and artificially regenerated afterwards. Mixed stands were subjected to selective cutting, extracting only conifers with a diameter greater than 30 cm, while beech was not extracted for commercial purposes, because it was considered, at that time, a species of low economic value. The Romanian forest nationalization of 1948 was an important step toward obtaining quality timber in maximum quantities, while, at the same time, satisfying the protection functions. Later, in 1975, the forest protection status generated by a change in the forest legislation (especially functional zoning of forests in particular) contributed to forest conservation. Nowadays, protected forests, in which no silvicultural prescriptions or only

special conservation prescriptions are allowed, occupy 39% of the total area [48]. The remaining areas are only eligible for selection cuttings (99.6%) and clear-cut prescriptions in a very small amount (0.4%). As a result, around 60% of the forest is older than 60 years old, with almost 20% of it being more than 100 years old [48], including over 200 hectares of virgin and quasi-virgin forests [49,50]. Within the context of temperate European forests, an important fraction of the Penteleu forest district area is occupied by relatively old forest.

The historical management of the different stands in Penteleu forest was reconstructed for the modelling approach following the ecological conditions and actual stand age structure and composition. In general, given the historical management changes and the information contained in the management plans [48], there is a high level of confidence in the historical management of the vast majority of the stands. An estimative historical management of Penteleu forest can be found in Supplementary Material S1.

The climate variables taken from van Oldenborgh et al.'s [51] multi-model mean climate change CMIP5 scenarios (https://climexp.knmi.nl/start.cgi; accessed on 1 July 2020) and additional climate series [43,52] for the region 25–26 E 45–46 N were statistically downscaled to 50 m resolution following Zorita et al. [53] using WorldClim 1.4 and 2.0 [54]. The downscaled monthly climate variables are the Tmin (monthly average of minimum temperature), Tmax (monthly average of maximum temperatures), PET (average monthly evapotranspiration), Prec (average monthly precipitation) and BAL (average monthly water balance). Spectral analysis of the climate variables is provided in Supplementary Material S2. Monthly radiation was also taken from WorldClim [54]. These climate products with past observations and future climate change forecasts until 2100 were used to analyse climate signal in dendrochronological series and in Landis-II simulations.

2.2. Dendrochronological Series and Climate Signal

In order to understand the principles of forests' structure and functioning, a deep analysis of the past and present structure and functionality of virgin forests was performed in a 1 ha control plot inside the Penteleu forest. This control plot (circular, with a 56.41 m radius) was installed and measured in 2014 in a representative temperate montane conifer–broadleaved mixed–virgin forest stand. The stand is unevenly aged, and the reference plot includes 439 trees from three species (beech—63%, Norway spruce—26% and silver fir—11%) [48]. Being unaffected by human activity, we assumed that this stand is optimal for detecting climate signals on tree growth and species interactions.

Tree spatial distribution, breast height diameter (DBH) and height (h) were measured for all living trees over 8 cm DBH. The aboveground tree volume (v) of each tree was calculated with the following regression equation: $\log v = b_0 + b_1 \cdot \log d + b_2 \cdot \log^2 d + b_3 \cdot \log h + b_4 \cdot \log^2 h$, where b_0, b_1, b_2, b_3 and b_4 are the species' national regression coefficients [55]. The overall stand volume measured was 803 m^3. Tree aboveground biomass was computed using species wood density [55].

To build the reference dendrochronological series of silver fir, beech and Norway spruce, 406 radial core samples of living trees collected from the control plot were analysed and processed. The radial growth was calculated with CooRecorder 7.4 image analysis techniques [47,56]. Measurement checking and cross-dating was performed with COFECHA [42,57], and the growth series standardization was carried out with ASTRANwin [58]. The age structure was intensively analysed in an exploratory analysis to ascertain how stand development might have affected tree growth. DBH, measured through tree ring radial growth, was analysed by linear mixed models and analysis of variance in R software [59].

The statistical analysis of the dendrochronological series was performed with dplR [60], treeclim [61] and waveslim [62] packages in R software [59], and wavelet coherence among species dendrochronological series was explored with biwavelet [63]. The overall and moving correlations between climate variables (i.e., Tmin, Tmax, PET, Prec, BAL) and tree ring growth for the main species were calculated by treeclim dcc response and correlation function analysis [61]. In order to find interactions among species in mixed stands, the

moving correlation matrices were inspected. This was completed with a factorial analysis of the of the species' moving.

In addition, since there was a net change in the slope, the 1 ha plot was divided into 2 sectors during the fieldwork in order to explore and compare the relative species abundance in both sectors as a function of the local conditions. Being representative of 2 ecoregions, the reconstruction of the tree aboveground biomass in the 2 sectors was later used in the calibration of the Landis-II models.

2.3. Climate Change Projections

Landis-II [34,64], coupled with PnET models [35,65,66], was developed to simulate forest succession and the effect of climate [66] and management [67] under different climate change scenarios [66]. We built Landis-II models for the Penteleu forest district, aiming to assess management effects and the climate change impacts on Carpathian forest ecoregions, i.e., forests with homogeneous local conditions.

The model parameterization was performed following Gustafson [53] recommendations, using data extracted from scientific and technical works [12,68–71]. Since the full dataset had missing data issues, inconsistency, etc., the values were not used directly in the Landis-II model, but as input data for Landis-II calibration using the genetic algorithms (GA) [39,72] machine learning (ML) technique, with GA R package [38,39,59]. For calibration purposes, the GA fitness function for a given set of chromosome values used the difference in the biomass estimated for the 1 ha plot sectors (using the dendrochronological series) and the biomass predicted by the Landis-II models for those sectors (introduced in the model as fully independent ecoregions). In this, the supervised species calibration was bypassed, and species parameter values that are valid for the whole study area were set. Only the last period of the dendrochronological series was taken into account in order to minimize the effects of the stand dynamics effects on the calibration process.

After the calibration, the 50 m × 50 m resolution landscape was segmented in ecoregions combining the site type, forest types and relative productivity class in the management plans [48]. Soil properties for the ecoregions' parameterization were also extracted from the management plan [48]. Overall, 22 ecoregions, covering an altitudinal gradient and a wide range of site properties, were established. Every ecoregion was provided for monthly photosynthetically active radiation (PAR) from WorldClim 2.0 radiation [54], downscaled CMIP5 Tmax, Tmin and Prec data (https://climexp.knmi.nl/start.cgi; accessed on 1 July 2020), and atmospheric CO_2 concentrations for the 1500–2100 period [3] under the 2.6, 4.5, 6.0 and 8.5 greenhouse gas (GHG) atmospheric concentration RCP scenarios [3].

The 1685 forest stands in the Penteleu forest district were aggregated into 568 management system types, from which 1369 treatment prescriptions (silvicultural regeneration interventions) were sequentially combined and implemented over time at the stand and management system levels, according to historical changes in forest management, species composition and abundance, silvicultural system and age structure. All of the spatial information was managed in R software [59] spatial libraries [73–76].

The silvicultural systems implemented in Landis-II are as follows: (i) strict protection (mostly mixed uneven-aged forests; all virgin forests, quasi-virgin forests and some pure stands are covered by this management type); (ii) old selection forests (predominantly mixed uneven-aged forests); (iii) selection forests (natural composition, often mixed stands, with an uneven-aged structure); (iv) quasi-selection systems (transformation to selection forests 60–70 years; natural composition with relative even to relative uneven-aged structures); (v) group selection system (even aged with pure and mixed composition); (vi) clear-cut system (mostly even-age pure stands and some mixed stands with non-native species).

The timeframe covered by the Landis-II models comprises four main management types and periods: (i) virgin forests and traditional selection forests (1900–1940); (ii) salvage logging (1941–1973); (iii) selection forests (1973–2020); (iv) increased protection of forests (2021–2100).

Disturbances (e.g., windthrows) were modelled through harvest extension, because (a) management plans show evidence of their low relevance and (b) the salvage logging, which is commonly practiced in disturbed stands, has similar effects to unplanned clearcuttings.

The Landis-II models, calibrated and validated for the entire research area, were computed for past conditions in the 1900–2010 period and for the 2010–2100 period under the RCP 2.6, 4.5, 6.0 and 8.5 climate change scenarios. Biomass and, implicitly, C stock, capitalizing on the energy and mass fluxes within the modelling approach, were the main target variables in this study. The ecoregions' biomass over time and the biomass in the natural distribution areas of pure and mixed forests were fitted and analysed using linear mixed models and an analysis of variance. Three key periods (1901–1910, 2001–2010 and 2091–2100) were targeted and compared. Comparisons between those periods were performed for every ecoregion and climate change scenario using Benjamini–Hochberg FDR correction [77]. The familywise and post hoc comparisons were carried out with nlme [78] and multcomp packages [79] in R software [59].

3. Results

3.1. Forest Sensitivity to Past Climate

Older trees in the 1 ha plot mixed–virgin forest stand are more than 350 years old and the maximum tree DBH is 110 cm. Exploratory analysis of the age structure and recruitment suggest that, despite the truncated diameter-based sampling, the age structure follows a geometric distribution, with a strong predominance of young age classes. This age structure has been quite stable over time, emphasized by the small peaks of recruitment detected over the last 300 years.

The analysis of the climate signal in a mixed–virgin forest stand indicates that tree radial growth depends on climate and interspecific relationships. Tree DBH, reconstructed from radial core samples collected in the Penteleu 1 ha plot, increased approximately linearly over time (Figure 2) at the stand level. The mean growth of the central 90% (0.05–0.95 quantiles) of trees in the plot ranged from 0.9 to 4.2 cm·year^{-1}. At the tree level, radial growth has the general tendency to be constant over time, with a few exceptions. Radial growth changed strongly over time for a reduced number of trees: some trees with intense radial growth in the early stages of development gradually reduced their growth rate when they reached physiological maturity, while other trees with reduced radial growth in the early stages suddenly increased their growth rate in later stages. The dendrochronological dataset analysis showed a non-significant effect of the tree age on the tree ring width (*p*-value > 0.05).
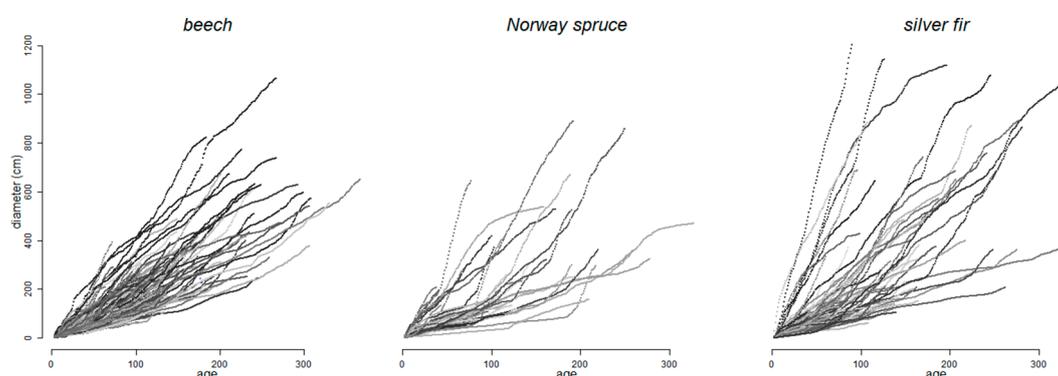

Figure 2. DBH–age relationship in Penteleu 1 ha mixed–virgin forest plot.

All three biwavelets among pairs of species (Figure 3) contain regions with significant wavelet coherence among dendrochronological series of pairs of species. Anti-phase relationships dominate in the beech–silver fir biwavelet, while beech–Norway spruce and silver fir–Norway spruce biwavelets tend to be in phase when there is a lag in the phase.
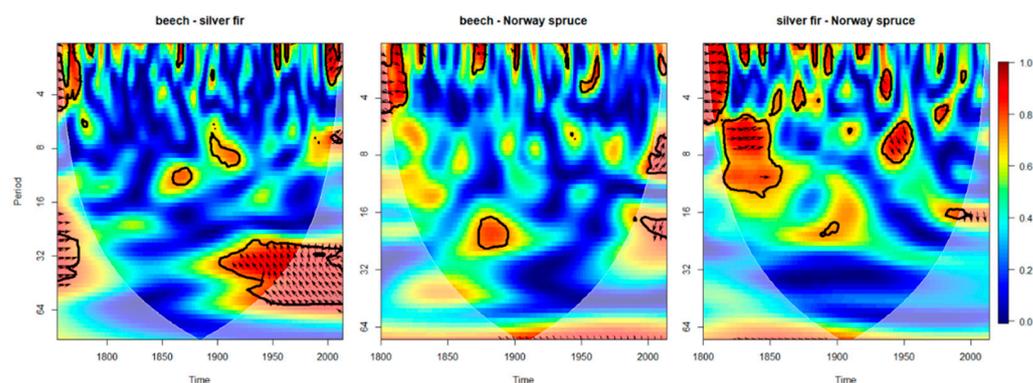
Figure 3. Dendrochronological biwavelet between species, after 100 Monte Carlo randomizations. Arrows direction indicate that both dendrochronological series are in phase (pointing to the **right**) or anti-phase (pointing to the **left**), the black contour indicates ≤0.05 significance, and the transparency, the cone of influence.

Climate has a significant effect on tree ring growth. At the stand level, it was summarised the relationship between some of the main climate variables (i.e., Tmin, Tmax, PET, Prec and BAL) and the radial growth extracted from tree cores through moving correlations (details can be found in Supplementary Material S3), and then assessed the similarities between the responses of the three main species in the study area (silver fir, beech and Norway spruce) to the climate variables (Figure 4). The results showed synergic and antagonistic responses to the climate. Silver fir showed a similar trend to the Norway spruce, with the first not being as significant as the second. Silver fir tended to show negative correlations with climate variables in periods in which beech and Norway spruce growth were favoured. Beginning with the end of the 19th century and until the beginning of the 20th century, a consistently positive growth rate was recorded for beech, correlated with higher-than-average summer temperatures. Beech's correlation with September Prec and BAL varied over time, from a negative correlation to a positive one. Beech growth also had a positive correlation with late spring Prec. Norway spruce, in general, tended to show negative correlations with climate variables in the same periods in which beech was favoured by the climate. Beech moving correlations around 1750 showed significant negative correlations with September Prec and BAL, as in 1840. Additionally, around 1840, positive growth was associated with spring Prec and BAL. Later, around 1900, positive correlations were detected with spring Tmin, Tmax and PET. Around 1965, growth was positively correlated with September Prec and BAL and negatively correlated with July and September Tmin. Silver fir growth correlated negatively with spring Tmin and PET and positively with late-summer Prec and BAL around 1970. During the 19th century, silver fir growth was negatively correlated with May Tmin, Tmax and PET, although it was positively correlated with September and April Tmin and Tmax and also with May Prec and BAL. At the beginning of the 20th century, silver fir growth was negatively correlated with late-summer Tmin, Tmax and Prec and positively correlated with April Prec and BAL. Later, occasional positive significant positive correlations were detected with Tmin, Tmax and PET, while negative correlations were detected with July and August Prec and August BAL. Finally, no correlations were found for the 21st century. Norway spruce growth showed positive significant correlations with September Tmin, Tmax and PET around 1825, though negative correlations were found with April Prec and BAL. Later, until 1990, positive correlations tended to occur with spring and summer Tmin, Tmax and PET, particularly around 1875, 1925 and 1970. Significant positive correlations with April and June Prec were detected in the last decades of the 19th century and at the beginning of the 20th century. Finally, around 1945 and 1985, Norway spruce growth was eventually negatively correlated with late-summer Prec and BAL.
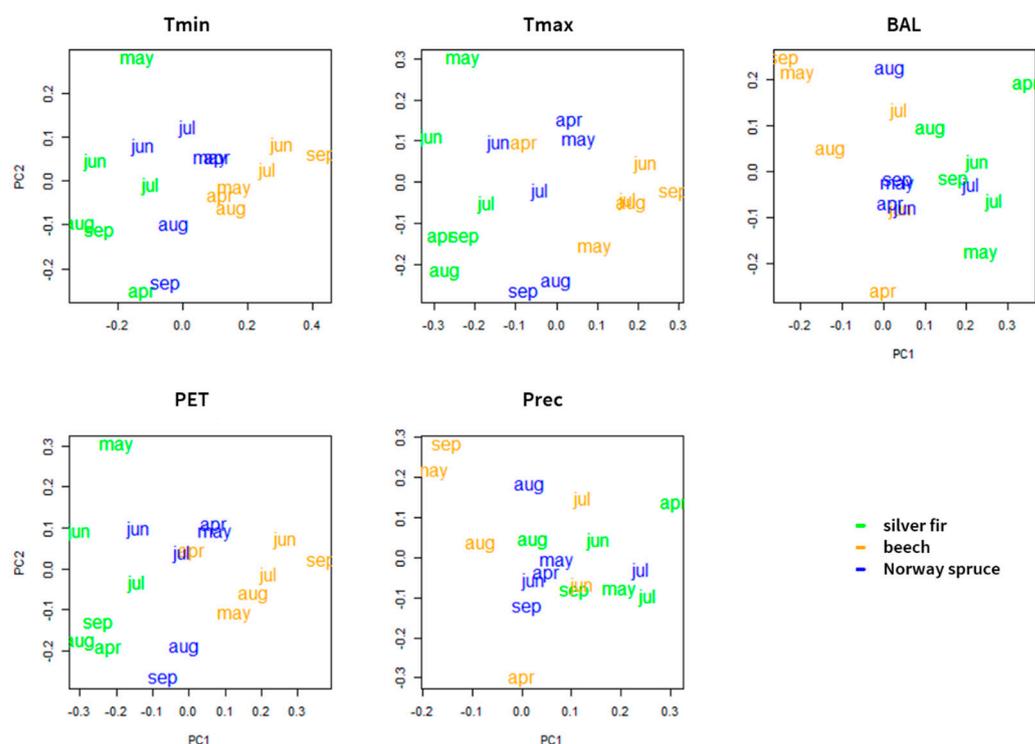
Figure 4. Saturation of the first and second components of the factorial analysis of beech, silver fir and Norway spruce moving correlations between tree ring growth and monthly climate variables (from April to September, respectively: Apr, May, Jun, Jul, Aug, Sep), here sorted by climate variable (i.e., Tmin, Tmax, BAL, PET, Prec).

Thus, the first and second components of the factorial analysis of the moving correlation matrices were built based on the antagonistic behaviour of beech and silver fir. Norway spruce displayed an intermediate behaviour, and consequently, less weight was placed on the construction of the first and second components.

Tree biomass reconstructed from tree cores showed that, at the stand level, around one third of the current biomass in the Penteleu 1 ha plot was produced more than 150 years ago and approximately half was formed in the last 50 years (Figure 5a). Regarding species biomass, before 1850, most of it belonged to beech. After 1900, only half of the biomass found was attributed to beech, with the remaining biomass being provided by conifers, particularly silver fir.

Due to the plot's heterogeneity and microtopography, we compared the biomass accumulation on steep and flat terrain. Before 1850, the accumulated tree biomass was higher in the flattest sector of the plot compared to the steepest one. After 1950, the biomass per hectare in the steepest sector (Figure 5b) was equal to the biomass in the flat sector. As extracted from the dendrochronological series, beech and silver fir are the dominant and codominant species in both sectors, with silver fir being dominant in the steep sector and beech in the flat. Norway spruce, having the lowest contribution in terms of biomass, accumulated more than 1.5 times the biomass per hectare in the flat sector, as compared to the amount of biomass measured in the steep sector.
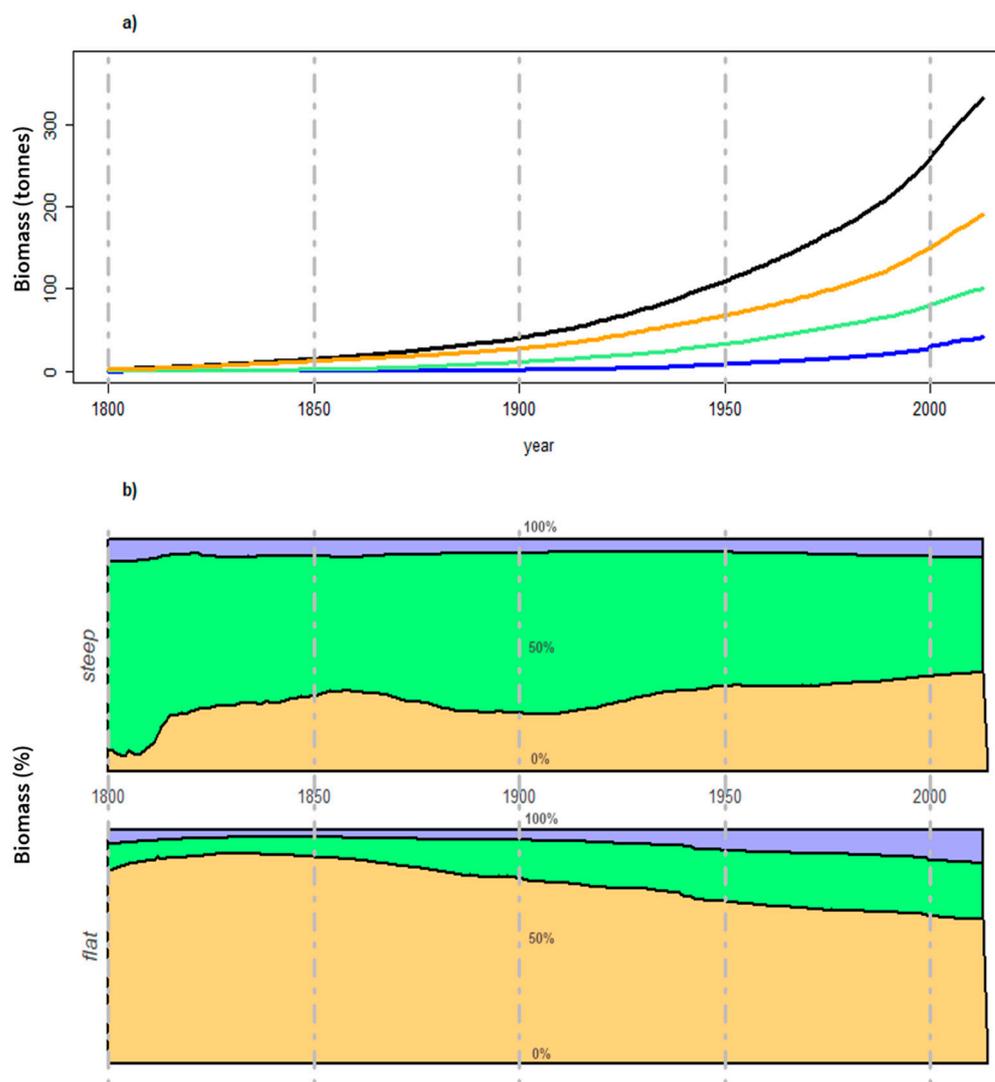
Figure 5. Biomass (tonnes) reconstruction based on tree rings (**a**) at the stand level (continuous) and (**b**) the relative abundance of the main species for the steepest (dotted) and flattest (continuous) sectors in the Penteleu 1 ha plot (black), beech (orange), silver fir (green), Norway spruce (blue).

3.2. Aboveground Living Biomass under Climate Change Scenarios

Landis-II simulations show that the forest biomass changed from 1900 to 2010 in almost all of the ecoregions (Figure 6). Some ecoregions showed a moderate increase in biomass throughout the period. Other ecoregions hardly changed, while the remaining few displayed a reduced amount of biomass. Biomass reductions in the ecoregions were often associated with the harvesting process.

Harvesting caused very strong biomass reductions in some ecoregions, particularly through clearcutting during the 1941–1973 period. However, biomass reductions were also found in other periods, harvest types and management systems, such as selection cuttings in shelterwood systems. The rise in the level of forest protection, together with the aging of the forest, contributed to a reduction in biomass loss and to moderate biomass accumulation in recent decades. In ecoregions with null or very low harvest intensity, the amount of biomass tends to increase.
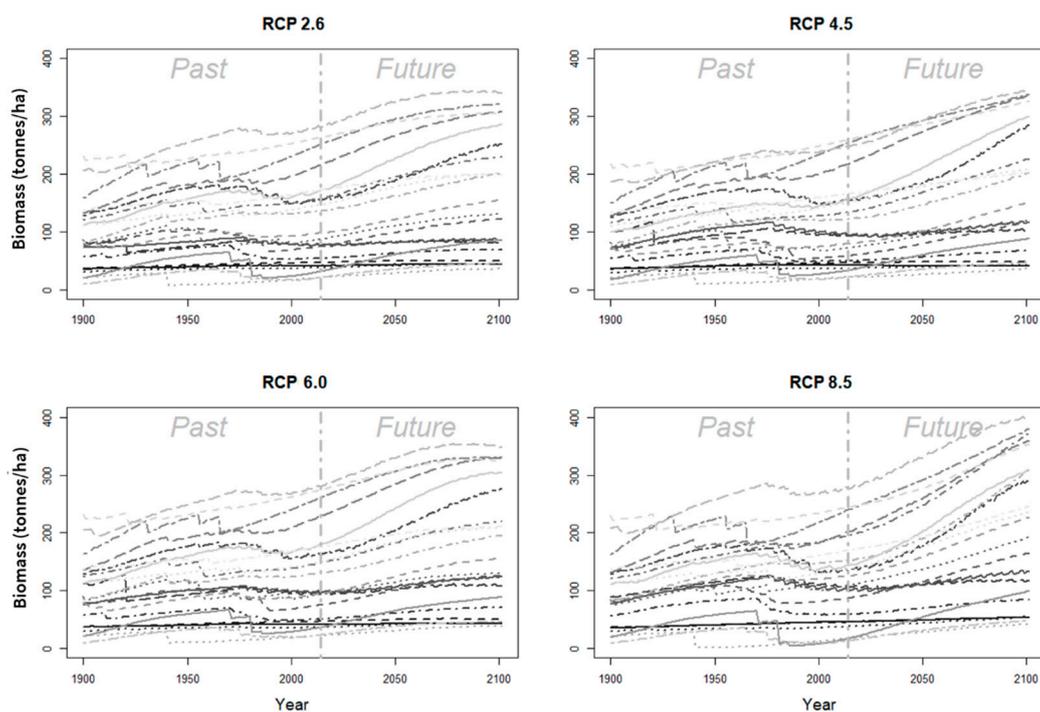
Figure 6. Average quantity of biomass (tonnes/ha) in the 22 ecoregions (different line styles) under the four climate change scenarios: RCP 2.6, RCP 4.5, RCP 6.0 and RCP 8.5.

Management, which, in the past, caused strong reductions in biomass through intense harvest, will contribute to biomass accumulation in the future through protection and low harvest pressure. The Landis-II projections show that, from 2010 to 2100, under a more protective management, the amount of biomass in most of the ecoregions will increase, particularly after 2025.

Apart from harvest effects, the different climate change scenarios (RCP 2.6 to RCP 8.5) had a significant role on forest biomass accumulation after 2010 (p-value ≤ 0.05). This increase in biomass was particularly noticeable in periods where harvesting was less intense. The intensity of the growth differed strongly among the ecoregions. After 2010, the accumulation of biomass is a result of a combination of both local ecoregion conditions, management and climate change scenarios. There is no common response to climate scenarios for all ecoregions, even though intense climate change scenarios, particularly RCP 8.5, tend to increase biomass accumulation. Indeed, some ecoregions have the lowest accumulated biomass under intermediate climate change scenarios (RCP 4.5 and RCP 6.0) and the highest under RCP 8.5. The amount of accumulated biomass barely changed over time in some ecoregions.

The ecoregions, aggregated according to their domination by pure and mixed forests (Figure 7), had different biomass accumulated at the beginning of the study period and over time. In 1900, when salvage logging had not begun, the biomass per hectare in pure stands was higher than in mixed stands. Around 2010, the amount of biomass was still higher in pure forest ecoregions. However, in the last period of the simulations (up to 2100), the biomass per hectare in mixed forests was similar to or even higher than that of pure forests, particularly in RCP 8.5, where the biomass per hectare in mixed forests broadly surpasses that of pure forests.
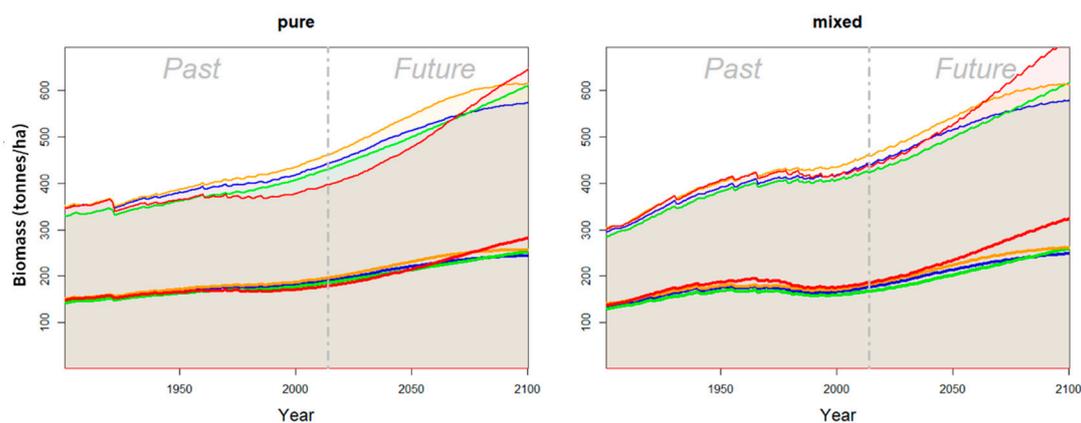
Figure 7. Average quantity of biomass (tonnes/ha—width lines) in pure and mixed forests from 1990 to 2100 and confidence intervals (shaded areas).

4. Discussion

This study shows that, even though virgin forests have a proven stability, both tree radial growth and biomass are affected by climate change and species interactions, thus providing long-term faithful records that are unaffected by management. In addition, it explores the reconstruction of the forest stand aboveground biomass in the past, projection in the future under different climate change scenarios and the C sequestration, as part of the atmospheric CO_2 balance.

Tree DBH reconstructed from Penteleu dendrochronological series was approximately linear, as also found in other similar studies [8,31,80]. Thus, radial growth is not particularly affected by tree age. Radial growth and, thus, the DBH–age relationship, is conditioned by the environmentally limiting conditions [80] and by biological stress. Additionally, the change in the growth rates of individual trees often depends on their interactions with neighbouring trees (e.g., facilitation and competition) and other processes (e.g., mortality) [11,81], meaning that they are likely the cause of the changes found in the measured trees in Penteleu.

We found that small differences in the ecological preferences, local conditions and climate lead to several spatiotemporal patterns in the biomass accumulation over time. In mixed–virgin forest stands, intra- and inter-specific interactions have a strong impact on tree growth, while also having further consequences at the stand level. Such interactions differ in relation to local conditions and species dominance and abundance, which can lead to modifications even at short distances. The results showed that there are differences between growth rates of some trees in early vs. late stages, which (presumably) strongly depend on the physiological activity and dynamics of the in-stand competition and mortality [11,81] of the species. In the Penteleu virgin forest 1 ha plot, the steepest areas are dominated by silver fir, which is less susceptible to warmer and drier conditions than beech [13], while flat areas are occupied by beech, which is also accompanied with a higher abundance of Norway spruce. Having a higher abundance in the flattest area, beech, compared to silver fir and Norway spruce shows better resistance to different stress factors and also has a significant growth in the understory [23,81]. Due to withstand such conditions (including drought), beech growth usually has a low variability [11] compared to coniferous species. These heterogeneous responses to the climate are produced in mixed forests even when the climate conditions are favourable for all three species.

The dendrochronological series analysis proved that silver fir and beech tend to have opposite behaviours in response to climate in mixed stands, while Norway spruce, displaying intermediate behaviour, tends to negatively correlate with the climate when beech correlations are positive. Having different ecological preferences and life traits, the beech–silver fir association in mixed stands is advantageous in terms of their ability to endure drought [13,17,31,33,82] and also because of their efficient light use [83,84]. There

is also evidence that beech–Norway spruce mixed stands perform better than beech pure stands [13,33] due to the complementarity of the two species.

The overall biomass, capitalizing all ecological processes, is homogeneously distributed over the 1 ha plot, highlighting the stability and species complementarity in mixed forests, as other studies have suggested [13,18,19,33]. However, despite their high efficiency in terms of the use of resources, there are concerns on the response of mixed and pure forests to climate change (e.g., Piovesan et al. [32]). It was emphasized that pure beech forests have already been affected by climate-change-induced drought in recent decades [32], as Norway spruce shows high drought resistance when compared to beech [17,82,85]. Additionally, silver fir is expected to be less susceptible to warmer and drier conditions than beech [13].

Since tree ring measurements include the effects of past conditions, such types of long-term data can be used in a modelling approach to analyse past changes and to foresee, anticipate and manage future changes [86,87]. However, the complexity, variability and information gaps contained in biological records [87,88] often require solutions such as ML methods [37,86]. GA [38,39] provided a suitable mechanism to speed up and objectivize the modelling approach and was successfully used in this study for Landis-II model calibration in order to simulate landscape changes and for forest change forecasting under different climate change scenarios, which proved to be robust.

The Landis-II models demonstrate that management had a strong impact on forest structure and functioning over time, in agreement with official records and statistics [48]. Forest resilience to management in terms of relative biomass compared to the pre-harvest level is high at the ecoregion level. Biomass commonly recovers in less than 50 years, although impacts on other forest attributes, e.g., diversity, last much longer [48]. Forest resistance to management is very low, as denoted by both (a) the impact of punctual harvest events at the ecoregion level and (b) sustained biomass stock changes due to the change in the silvicultural system, following stakeholders and policymakers' decisions in the past and expectations after 2025, when even more protective management will be implemented.

Biomass change in the different ecological regions is not only related to management, but also to climate change effects. The most important impacts of climate change in the Carpathians will be caused by rising temperature and CO_2 levels. Precipitation will be similar to the current conditions in some areas and may even slightly increase [4]; therefore, drought events are not expected to have a significant role, other than in a few ecological regions and marginal areas of the Carpathians [4]. Temperate forests will benefit from relative stability and better conditions for growth [2,4], contrary to Mediterranean forests, where droughts and fires will be the main drivers of change [89].

Some areas in the Carpathians will endure harsher conditions [4], and our results indicate that impacts will also differ at the local scale, with some ecoregions being more affected than others.

Uncertainty of climate change impacts and characteristics on forest ecosystems is relatively high [30,90], and our results show that temperate forest resistance to climate change is relatively low; however, forest biomass is predicted to be relatively similar under different climate change scenarios. Despite the findings of Nabuurs [2], projections from our Landis-II model also show that the Penteleu forest's C sequestration capacity is still far from saturation, and the aboveground biomass will continue to grow at least until the end of the current century, even when signs of deceleration appear at the end of the period in some ecoregions.

It is important to note that this C pool-growing trend is also related to a rise in the level of forest protection provided, forest aging and the decreasing harvest pressure throughout the period. Thus, the management of temperate forests has the potential to increase carbon sinks and mitigate climate change [1].

On the other hand, adaptation strategies can focus on sustainable management. The general interest is to promote C sequestration and management should be oriented toward

forest adaptation to climate change, by reducing potential negative climate change impacts, e.g., drought events [2,89], etc.

In this regard, management can be used to promote mixed forests, which reach higher biomass accumulation under intense climate change scenarios, and thus, to maximize C sequestration. Mixed stands and their particularities contribute to forest resistance and resilience at the landscape level, in comparison to pure stands [15–17].

5. Conclusions

The dendrochronological series in mixed stands not only contain climate signal, but species interactions, and they are useful for past events and projections. Beech, Norway spruce and silver fir, whose radial growth was not dependent of tree age, have complementary responses in mixed stands.

PnET-Landis-II models, GA calibrated using dendrochronological records, applied to the Penteleu forest, which hosts virgin and managed stands, brings to light (i) the relevance of virgin forests in vegetation long-term monitoring and as a reference data source for all forests in the Carpathians, (ii) the similarities and differences in the structure and functioning of mixed and pure forest stands and their adaptative management and (iii) the effect of climate on tree growth and climate change impact on forests, in which mitigation and adaptation strategies, programs and actions must be implemented.

Landis-II models provide valuable insights into the medium- to long-term succession for forest management and forest planning. They provide a good approach to climate change impacts, which are becoming increasingly accentuated. Landis-II simulations revealed that aboveground forest biomass changed in almost all ecological regions in the Carpathian Curvature, often associated with harvesting. Forest projections demonstrate that climate change in the Carpathian Curvature will promote forest aboveground biomass and C sequestration. Climate change will modify species and cohort interactions, leading to changes in the forest structure and functioning. Climate change impacts will depend on climate change intensity and local conditions and management. Among forest ecosystems, mixed forests are capable of higher C sequestration and higher biomass accumulation under intense climate change.

In this study, management, which is one of the main factors modifying forest structure and succession, can be used to promote resilient mixed forests, which are expected to accumulate higher biomass quantity under intense climate change, and thus, contributes to climate change mitigation and adaptation.

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