Shifts in Forest Species Composition and Abundance under Climate Change Scenarios in Southern Carpathian Romanian Temperate Forests

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Abstract: The structure and functioning of temperate forests are shifting due to changes in climate. Foreseeing the trajectory of such changes is critical to implementing adequate management practices and defining long-term strategies. This study investigated future shifts in temperate forest species composition and abundance expected to occur due to climate change. It also identified the ecological mechanisms underpinning such changes. Using an altitudinal gradient in the Romanian Carpathian temperate forests encompassing several vegetation types, we explored forest change using the Landis-II landscape model coupled with the PnET ecophysiological process model. We specifically assessed the change in biomass, forest production, species composition and natural disturbance impacts under three climate change scenarios, namely, RCP 2.6, 4.5 and 8.5. The results show that, over the short term (15 years), biomass across all forest types in the altitudinal gradient will increase, and species composition will remain unaltered. In contrast, over the medium and long terms (after 2040), changes in species composition will accelerate, with some species spreading (e.g., *Abies alba* Mill.) and others declining (e.g., *Fagus sylvatica* L.), particularly under the most extreme climate change scenario. Some forest types (e.g., *Picea abies* (L.) karst forests) in the Southern Carpathians will notably increase their standing biomass due to climate change, compared to other types, such as *Quercus* forests. Our findings suggest that climate change will alter the forest composition and species abundance, with some forests being particularly vulnerable to climate change, e.g., *F. sylvatica* forests. As far as productivity and forest composition changes are concerned, management practices should accommodate the new conditions in order to mitigate climate change impacts.

Keywords: LANDIS-II; PnET; climate change; Southern Carpathians; forest biomass; production; species composition; species abundance; Romanian temperate forests

1. Introduction

Human-induced climate change is one of the major processes affecting the global environment nowadays [1]. However, the impacts are so complex and diverse that the net effect of climate change on forest systems is still uncertain. For instance, while the increase in atmospheric CO_2 concentrations often leads to greater productivity [2,3], the aridity caused by warming [4,5] and the intensification of disturbances regimes [6] usually have a negative impact on forests' structure and productivity. Recent studies have suggested that despite the positive climate change-associated effects [7,8], the negative ones often prevail [9,10].

Climate change effects, both positive and negative, will trigger quantitative and qualitative changes in forest composition, structure and functioning and will push for species adaptive responses [1,11]. Plant responses to climate change will be species specific [4], though species with similar vital attributes are expected to have close responses [5,12]. Thus, angiosperms and gymnosperms/conifers have different ecophysiological responses to raised CO_2 concentrations, potentially affecting the regional response of each forest type [12].

Temperate forests occupy 1097 M ha worldwide, retain 118.6 Pg of terrestrial carbon [13] and provide 40% of the world's forest harvest [14], thus playing an important role in the overall carbon balance. Shifts in temperate forests' structure, functioning and distribution, such as those driven by climate change and mitigation measures, will affect their economic value [15] and will have notable consequences on their capacity to sequester carbon and to provide other ecosystem services [10,16–19]. Forest carbon stocks and sequestration primarily depend on forest productivity and disturbance regimes [10,14], both of which are expected to change with climate change [6,18]. A study by Nabuurs et al. [19] described the first signs of carbon sink saturation in European forests. Such weakening in C sink/sequestration capacity may be related to aging forests, decreased summer humidity, etc. A lower C sequestration capacity would also be related to the change in disturbance regimes. The main disturbances in temperate forests include drought, insects, windthrows, pathogens and fire [6]. However, disturbances are often interconnected and can generate significant feedback effects [6]. This is, for instance, the case of bark beetle attacks, which are secondary disturbances that tend to occur after drought, harvest or windthrows.

Other studies have already suggested that some temperate forests will eventually decline due to summer droughts [20] and their habitat distribution will be reduced to montane areas due to altitudinal shifts [21]. Some temperate forests will be more intensely affected than others [6,10,16], with vulnerability being related to species composition [16], health status, disturbances regimes [22] and the phytogeographical context [23]. In this context, the evolution of European temperate forests under climate change is largely uncertain, with studies suggesting that conifers will be severely damaged by climate change [16], while beech (*Fagus sylvatica* L.) forests, already affected by drought in recent decades [20], will be more sensitive to climate change. Given the gaps in the knowledge and the relevance of mixed (broadleaf and conifer) forests [24–26], such discrepancies require further research.

This study aimed to unveil the future effects of climate change and its interactions with natural disturbances and land management on the structure and composition of temperate forests by implementing a forest simulation modeling approach. The Southern Carpathian forests were used as a case study as they harbor a large diversity of forest types and are representative of European temperate forests. The forest simulation model LANDIS-II [27] coupled with the PnET model [28,29], which have been highlighted for their capacity to model complex forest dynamics under multiple interacting drivers (e.g., climate, management, pests, windthrows) [30–33], was used to increase our understanding of the potential impact of natural disturbances on temperate forest composition, structure and its productivity. In particular, this study addressed two main questions: (1) What future changes in forest species composition and abundance are expected to occur due to climate change? (2) What are the ecological mechanisms underpinning forest type and species (variable effects—geographical and species dependent) changes?

We hypothesized that species in the lower part of the altitudinal gradient (e.g., oaks) will grow in abundance and those in the high altitudes, particularly conifers, will be constrained, and that the main mechanisms driving the change are warmer climate and increments in droughts and disturbances, all of them modifying species interactions.

2. Materials and Methods

2.1. Study Area

The study area is located in the Fagaraş Mountains, in the Romanian Southern Carpathians (Figure 1). It occupies around 6400 km^2 and comprises a large geographical gradient that extends 110 km north to south and 73 km east to west, covering the main forested lands in the Argeş, Sibiu and Braşov counties. The altitude ranges from 185 to 2544 m.a.s.l, with plain landscapes (c. 12% average slope, elevation < 500 m) on the southern sector and steep and rough topography (c. 32% average slope, elevation > 1000 m) on the high-altitude northern sector. The climate varies along the altitudinal gradient [23]: the annual mean temperature in the highlands is lower than 4 °C, with a winter mean temperature below −5 °C and a summer temperature around 14 °C. The precipitation approaches 1000 mm, with summer rainfall of around 315 mm. The climate in the plains is warmer and drier, with a 10.5 °C annual mean temperature, mean winter temperatures below 0 °C and summer temperatures over 20 °C. The annual precipitation here is about 700 mm, with summer rainfall of around 260 mm. In general, September and October are the driest months, while May and June are the wettest ones. Soil types in the area include protosols, spodozols, cambisols, argiluvisols and hydromorphic soils with pseudogleic properties [34,35].
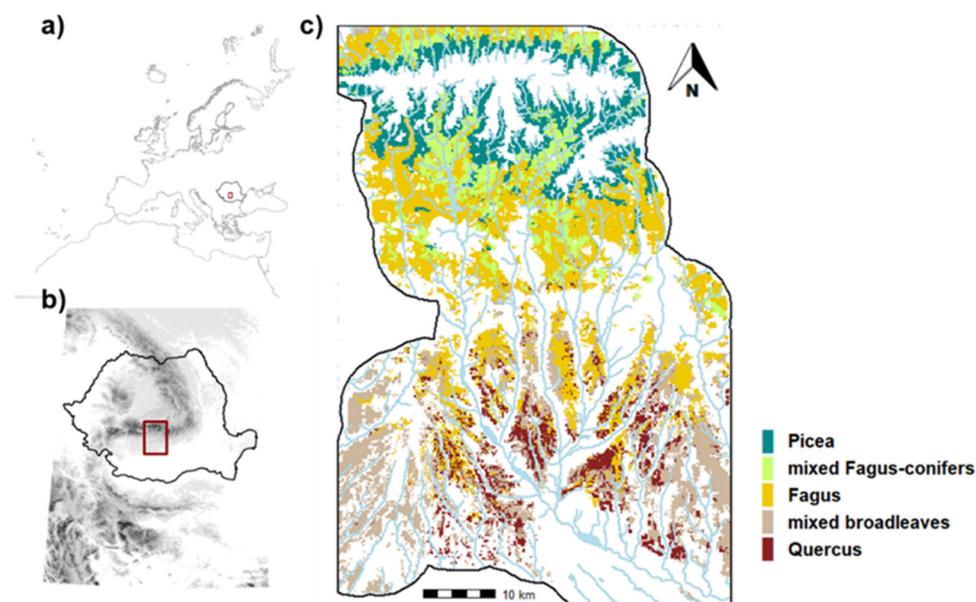
Figure 1. (**a**) Location of the study area within Europe and (**b**) the Carpathians; (**c**) distribution of the five forest types within the study area.

Temperate forests, whose composition changes across the altitudinal belts, cover 52% of the total study area. There are five general forest types: (a) *Picea abies* (L.) karst forests, (b) mixed *Fagus sylvatica* L.–conifer forests, (c) *F. sylvatica* forests, (d) mixed broadleaved forests and (e) *Quercus* forests. *Picea* forests (Norway spruce) occupy the subalpine and montane superior belts. Mixed *Fagus*–conifer forests, mainly *Picea* and *Abies alba* Mill., dominate the intermediate montane belt, with the beech abundance increasing as the altitude decreases. Mixed *Fagus*–conifer forests are substituted by pure *Fagus* forests first and mixed broadleaved forest (*F. sylvatica* and *Carpinus betulus* L.) later, both of them in the inferior montane belt [24,36]. Oaks gradually appear in mixed broadleaved forests in the colline belt and, in low-altitude areas, reach the point where *Quercus* forests dominate the landscape. Within *Quercus* forests, there is an altitudinal transition from *Quercus petraea* (Matt.) Liebl. to *Quercus robur* L., *Quercus cerris* L. and *Quercus frainetto* Ten. in the most southern thermophilus areas [36].

Some of the forested lands are actively managed for timber production, with *F. sylvatica* providing 34% of the overall standing wood volume, *P. abies* 28%, *Quercus* spp. 17%, *A. alba* 5% and other species the remaining 16% [37–46]. Depending on forest species and conditions, different management systems are implemented including tree selection, shelterwood and clearcutting. Clearcutting is practiced only for small areas (lower than 3 ha) in Norway spruce (*P. abies*) and non-natural forest stands [47,48]. The rest of the forested land is either subjected to conservation management to protect forest health (e.g., phytosanitary felling, trees affected by small local windthrows) or is strictly protected with no management actions allowed. The most common natural disturbances in the area include windthrows and insect attacks [49]. Windthrow events mostly affect conifers in the north sector of the study area [50], particularly *Picea* forests, with insect outbreaks (*Hylobius abietis* L., *Ips duplicatus* Sahlberg and *I. typographus* L.) being a common secondary disturbance following windthrows [51] and drought [49,52] in conifer forests.

2.2. Landis-II Model

Landis-II is a collection of spatially explicit forest landscape models [53] that simulate forest change as a function of succession and disturbances [33]. The landscape in Landis-II is defined as a grid of cells (here 200 × 200 m), each of which belongs to an ecoregion (i.e., areas of homogeneous soil and climate) and can contain multiple species cohorts that can be independently killed by disturbances, competition or age-related mortality, as the succession progresses. Landis-II integrates a number of ecological process models through its modular design. Here, we used the PnET succession extension [54] to underpin tree species establishment, growth, mortality and decomposition. This extension embeds elements of the PnET ecophysiology model of [55] and accounts for competition for available light and water. Biomass growth is the result of a number of processes (e.g., photosynthesis, evapotranspiration) controlled by species ecophysiological parameters (e.g., foliar N concentration, photosynthetic rates) given a number of conditions that include precipitation, temperature and atmospheric CO_2 concentration. Climate change and CO_2 enrichment are interwoven as change in environmental parameters over time, making the PnET extension convenient for climate change modeling [30,56,57].

Landis-II interdependent disturbance extensions were used to model the impacts of harvest [31,58], wind [59] and insect outbreaks [60,61]. The harvest module [62] implements prescriptions in different management areas according to a temporal schedule, management systems and stand characteristics, including resource availability, age structure or stand composition. The biological disturbance agent module [63] implements insect impacts based on pest species preferences and resource availability. The wind module [64], which models windthrow events and operates independently of climate, was used to trigger insect outbreaks.

2.3. Landscape Design: Ecoregions and Forest Communities

The initial landscape for Landis-II simulations was built based on the local management plans that were available for the public forests (approximately 60% of the total forest land) [37–46]. Management plans contained the spatial delimitation of forest stands and information of their species composition and cohort ages, with stands ranging from 0.1 to 50 ha, the legal maximum allowed, with a median of 3.25 ha. Stands were classified into 14 ecoregions of homogeneous climate, soil type and tree species abundances (Supplementary Table S1; Supplementary Figure S1). Ecoregions were ascribed to one of the five forest types according to species composition (Figure 1). To constrain the number of communities, i.e., cohorts and species combinations that conform to a forest stand, a total of 223 initial communities, comprising from 1 to 4 species and a range of 1 to 17 age cohorts, were identified in the management plans and assigned, based on their frequency, to the corresponding stand and ecoregion in the simulated landscape. The area of private forest lands, for which information was not available, was delimited based on Corine Land Cover 2012 [65]. To ascribe ecoregions and initial communities in private forests, a random forest algorithm [66]

was trained using information from the management plans and environmental variables (DEM, [67], climate [68], soil properties and classification [34] and distance to infrastructure and populations [69,70]). The overall accuracy of the prediction reached 96.7% over the independent testing dataset.

2.4. LANDIS-II Parameterization

The modeled species included *Abies alba* Mill. (silver fir), *Alnus glutinosa* (L.) Gaertn. (European alder), *Alnus incana* (L.) Moench (grey alder), *C. betulus* (European hornbeam), *F. sylvatica* (European beech), *P. abies* (Norway spruce), *Q. cerris* (Turkey oak), *Q. frainetto* Ten. (Hungarian oak), *Q. petraea* (Matt.) Liebl. (sessile oak) and *Q. robur* L. (pedunculate oak). Species contributing less than 2% to the overall wood volume in the study area were not included in the simulation. Tree species parameters required by the model were measured in the study area [71], compiled from unpublished data or obtained from the local Romanian literature [36,72,73] and other international sources [74,75]. Model parameterization was performed following the recommendations of [29]. The three main background disturbances of the studied area were modeled to increase the accuracy of the simulated landscape and were considered a key element in this study.

The wind disturbance extension required the windthrow return interval and severity, which were modeled/introduced based on national historical records [76]. The average wind speed [68] and the area occupied by conifer forests were used to determine the windthrow local impact on each ecoregion. The mortality of age cohorts was based on Popa [76]. It was assumed that wind event occurrence will not be affected by climate change.

Bark beetle outbreaks were linked to windthrows and were followed by harvesting interventions as per standard practices in the study area. Three main bark beetle species were modeled: *I. typographus* and *I. duplicatus,* which target mature *Picea* stands [49,77], and *H. abietis*, which targets stands with a high density of *A. alba* saplings [78]. Pest species preferences (host species and age cohort) and impacts were defined based on expert knowledge, forest health status monitoring [79–81] and national Romanian research studies [49,51,52,82].

Harvesting prescriptions were defined following the national Romanian regulatory framework [47,48,83,84] which establishes that logging cycles for the main species in the study area are between 100 and 200 years for beech, Norway spruce, sessile oak and silver fir, 70 to 160 years for other oaks and up to 80 years for broadleaved softwood species, depending on the silvicultural system, forest function, site productivity and other specific situations. The simulated landscape was divided into management areas, composed of multiple stands, that included unmanaged, strictly protected forest (<1%), protected forest with special conservation prescription practices (less than 10 m^3/ha, approximately 40%), selective logging (20%; with approximately half of the area dedicated to production of mixed beech–conifer, mixed beech–broadleaved and oak forests), shelterwood forests (28%; majority of Fagus, also the remaining mixed beech–conifer, mixed beech–broadleaved and oak forests) and clearcut forests (12%; mostly Norway spruce pure stands). Within each management area, management treatments (stand selection, harvesting periodicity, intensity, targeting species and cycle duration) were implemented based on stand composition and stand age.

2.5. Climate Change Scenarios

Three climate change scenarios were defined (Figure 2) based on the RCP 2.6, 4.5 and 8.5 emission scenarios [85]. For the model spin-up period (1901–2015), we used gridded climate data (precipitation, maximum and minimum temperature) from the Climate Research Unit Time Series (CRU TS) [86] high-resolution dataset. For the simulation period between 2015 and 2100, we used RCP projections from Climatic Data Generator (ClimGen) [87] based on the French National Centre for Meteorological Research CNRM-CN5 climate model [88]. For the simulation period between 2100 and 2140, for which there were no cli-

mate projections available, climate data were randomly resampled from the last 3 decades, the last climate normal period, of the corresponding CNRM-CN5 series. Climate series were extended to 2140 because of the species longevity and the long logging cycles used in Romanian forestry.
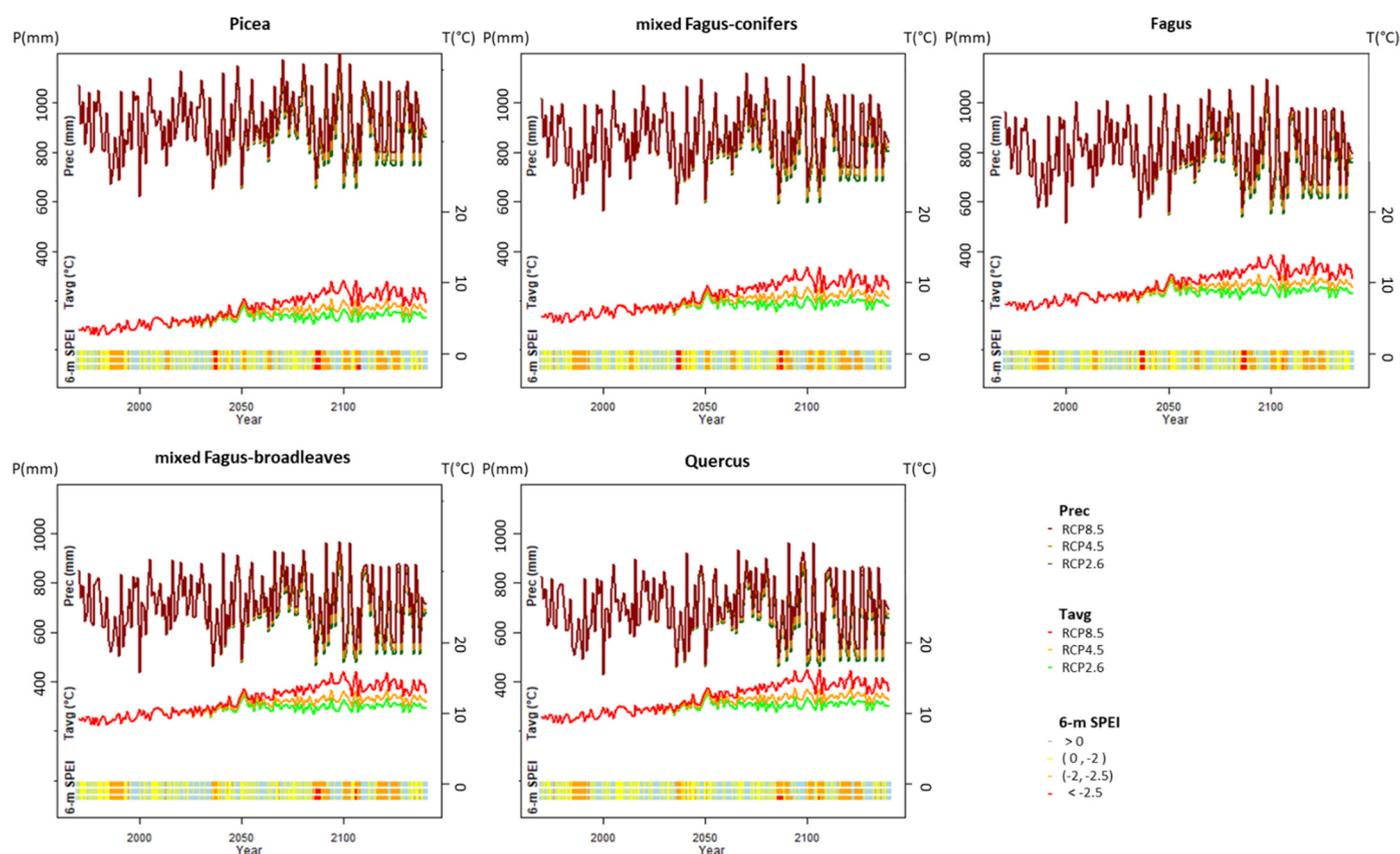

Figure 2. Comparison of climate change scenarios for the period 1970–2140 among the three RCP scenarios (RCP 2.6, RCP 4.5, RCP 8.5) in five main forest types representative of the altitudinal gradient (top to bottom). Precipitation (Prec), average temperature (Tavg) and standardized precipitation evapotranspiration index (SPEI index) (rows top to bottom represent RCP 2.6, RCP 4.5 and RCP 8.5, respectively).

Gridded 0.5° climate data were statistically downscaled following Moreno and Hasenauer [89] using a 30″ resolution gridded climate dataset from WorldClim 1.4 and 2.0 [68]. Mean annual CO_2 concentrations taken from van Vuuren et al. [85] differed among PCR scenarios but were assumed spatially constant. Similar to climate, CO_2 concentrations after 2100 were kept constant at the level of the last climate normal to prevent inconsistencies with resampled climate series. Photosynthetically active radiation (PAR), calculated from WorldClim 2.0 solar radiation [68], changed seasonally and spatially but did not differ across climate change scenarios.

2.6. Model Output and Validation

We simulated changes in forest biomass and species composition over a period of 125 years (2015–2140) under three climate change scenarios (RCP 2.6, RCP 4.5 and RCP 8.5), using 22 replicates of each scenario at a spatial resolution of the 200 m cell size. Model outputs included annual live, dead and harvested biomass throughout the simulation period. Forest net productivity was calculated as the change in biomass accounting for the harvesting. Model outputs for the period 2010–2020, when the management plans were released, were validated using Romanian forest yield tables [72,73] and forest management plans of the study area [37–46]. The simulated initial biomass per hectare (Figure 3) and

the extracted timber volume were within the ranges recorded in the management plans for all five forest types. As expected, compared to management, background natural disturbances had minor effects on the current landscape. The simulated windthrow impact was in accordance with volumes estimated from Popa [76] and the area affected by intense windthrows during the period 1986–2016 [79–81]. Insect outbreak occurrence and impact were also in accordance with the area affected by intense insect attacks in the study area in the period 1986–2016 [79–81], and the harvested volumes were in agreement with the management plans [37–46].
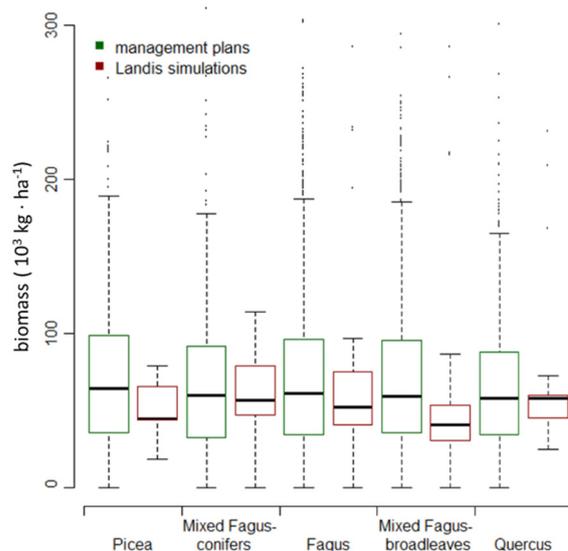
Figure 3. Boxplot diagram comparing the modeled biomass in the five main forest types in the initial Landis-II simulated landscape (year 2015) and the field-measured biomass data recorded from the management plans.

2.7. Statistical Analysis

Biomass results were spatially aggregated for the five main forest types. Differences across scenarios and forest types were assessed by linear mixed models (LME) [90], with changes over time fit to polynomial functions (up to 5 terms) and simulation replicates as a random factor. Natural disturbance outputs (i.e., mean damaged area, number of killed cohorts and severity) and harvested biomass were analyzed for the entire study area. Shifts in forest species composition at the landscape level were analyzed through the change in species biomass, using constrained redundancy analysis [91] with year and climate change scenario as constraining variables.

3. Results

3.1. Disturbances

Windthrows affected a minor percentage of the forest area (1%), with all of the effect located in the Norway spruce forest type. The affected area significantly increased over time ($p \leq 0.05$) such that by 2140, the area damaged was two-fold the area of 2015 (Figure 4a). A similar trend was observed in the severity and the number of cohorts killed by wind, with values increasing over time, and the number of cohorts killed being significantly lower for the RCP 8.5 scenario. These results are in accordance with the aging of Norway spruce forests, as the susceptibility to windthrows increases with tree age.
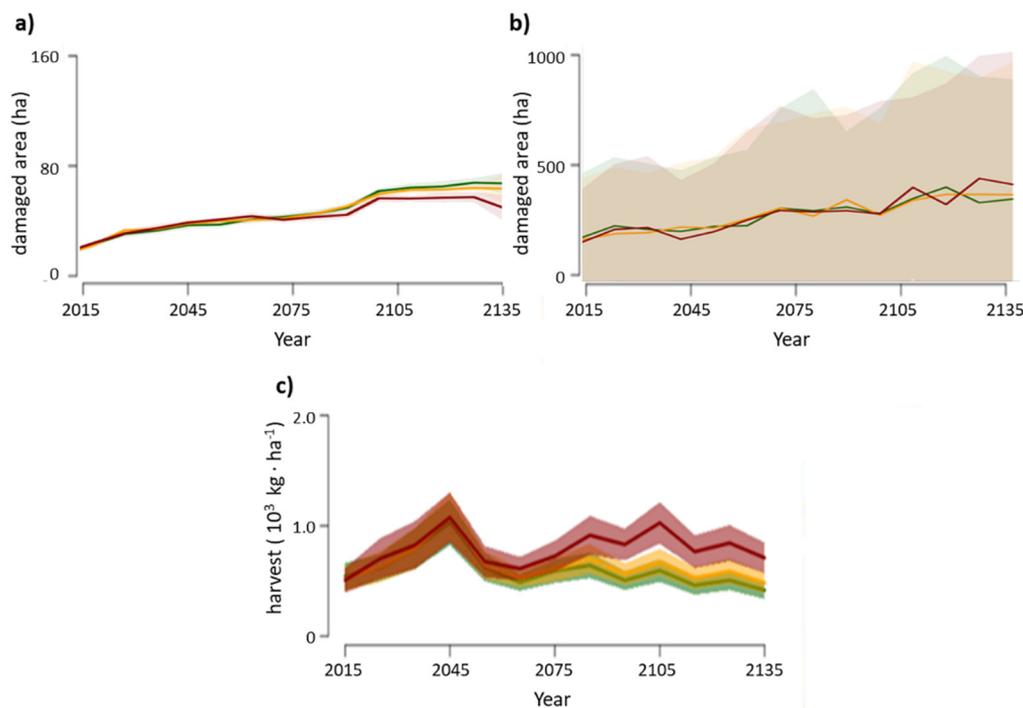
Figure 4. Variation in the average area damaged by (**a**) wind (**b**) and insects and (**c**) the harvested biomass across climate change scenarios. RCP 2.6 (green), RCP 4.5 (orange) and RCP 4.5 (red).

Insect outbreaks annually affected around 200 ha of the forest area (~1%), mostly in the spruce and mixed *Fagus* (beech)–conifer forests. The area and the number of cohorts killed by *Ips* insects, which target mature *P. abies* trees, increased over time ($p < 0.05$), also reflecting a change in the forest age structure. This trend was not observed for *H. abietis* (Figure 4b).

Harvesting occurred mostly in the *Fagus* and *Quercus* forest types, where annual means of 300,000 and 100,000 tons were extracted, respectively, with extraction rates of about 10 and 15% every 10 years (Figure 4c). Harvesting in the spruce and mixed beech–conifer forest types was mostly restricted to conservation works, with rates of extraction below 2%. Differences between climate change scenarios were noted from 2070, with biomass harvested in RCP 8.5 being greater, followed by RCP 4.5, and RCP 2.6, the lowest among all the scenarios. Given that harvesting prescriptions were constant over time, following the national Romanian regulatory framework, this indicates that differences in forest attributes developed over time among climate change scenarios.

3.2. Changes in Biomass across Climate Change Scenarios

Living aboveground biomass (Figure 5) tended to increase in all forest types and climate change scenarios throughout the simulation period, with fluctuations related to disturbance or harvesting events. Comparatively larger increases in biomass were observed for RPC 8.5, ranging from 21% in the *Quercus* forest type to 51% in the mixed beech–broadleaved forest type, than for RCP 4.5 (from 2% to 37%). The lowest change in biomass was observed in RCP 2.6, ranging from a decrease in total biomass (−15%) in the *Quercus* forest type to a 29% increase in the mixed beech–conifer forest type. The effect of climate varied across forest types: mixed beech–broadleaved forests showed the largest differences in the final biomass among scenarios, with RCP 8.5 showing a larger biomass than RCPs 4.5 and 2.6.
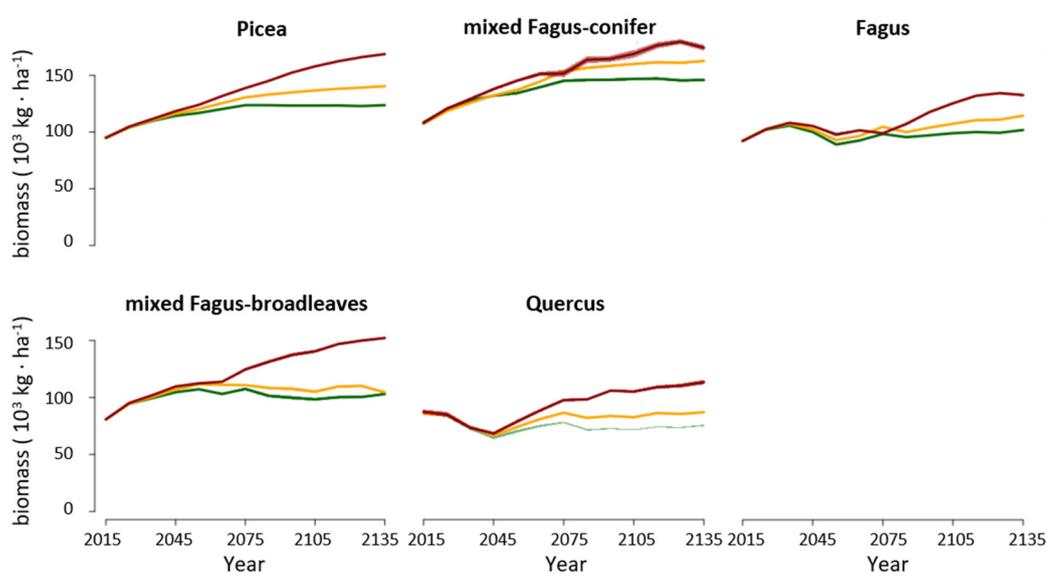
Figure 5. Mean (dashed line) and 95% confidence interval (shaded area) of the living biomass (-10^3 kg·ha^{-1}) measured in the forest belts over time under the three climate change scenarios: RCP 2.6 (green), RCP 4.5 (orange) and RCP 4.5 (red).

The analysis of the biomass at the species level revealed changes in species biomass through the simulation timespan and among climate change scenarios (Figure 6). The five main species, *P. abies*, *A. alba*, *F. sylvatica*, *Q. petraea* and *Q. frainetto*, showed significant biomass increments during the succession (*F. sylvatica* up to 2050) ($p < 0.05$). Of those five, all but *F. sylvatica* showed significant differences in biomass among the scenarios, with the largest biomass under RCP 8.5 ($p < 0.05$). Three species, *C. betulus*, *Q. petraea* and particularly *F. sylvatica*, showed short periods with strong reductions in biomass after 2050, which co-occurred in time with low SPEI values, although they tended to recover later.
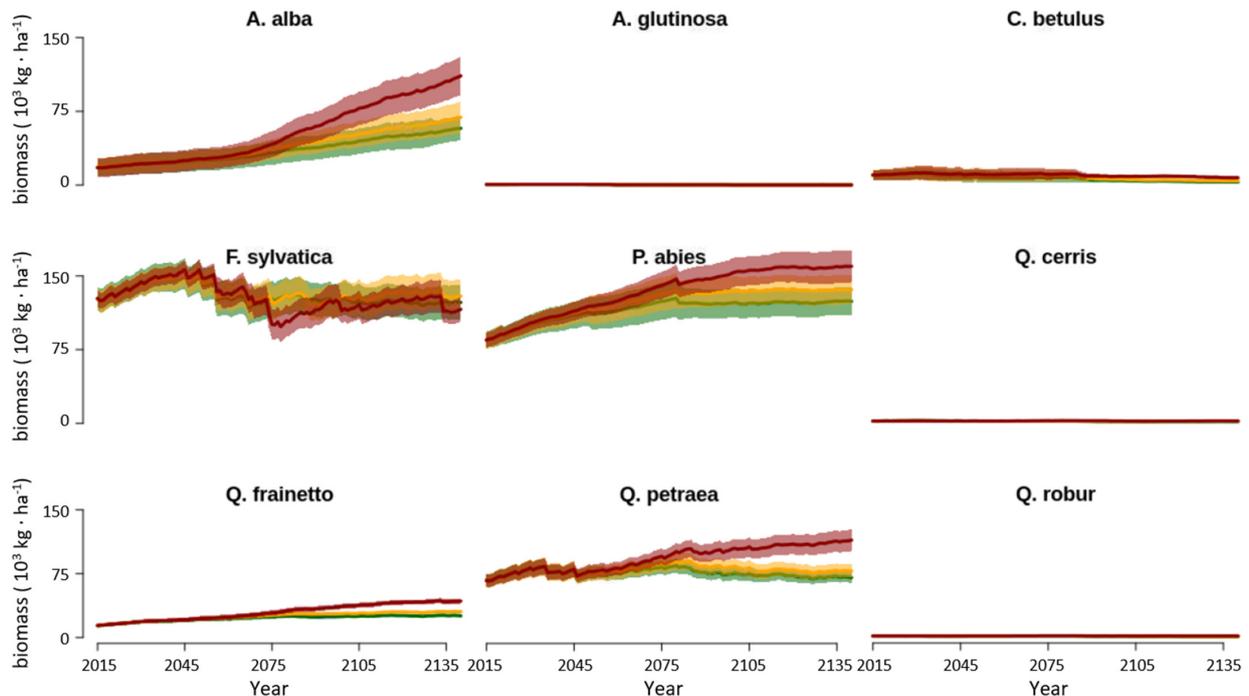
Figure 6. Mean (dashed line) and 95% confidence interval (shaded area) of the species living biomass ($·10^3$ kg·ha^{-1}) measured over time under the three climate change scenarios: RCP 2.6 (green), RCP 4.5 (orange) and RCP 4.5 (red).

The percentage of dead wood biomass relative to the total biomass showed a slight increase in all the forest types over time (Figure 7). Whereas the living biomass of Norway spruce and *Quercus* spp. differed among scenarios, the RCP scenario did not affect the percentage of dead biomass in these forests, which also showed a trend with very small interdecadal variations. Forest types with participation of *F. sylvatica* were subjected to strong variations in dead biomass over time, usually within the range 2.5–5.0%, which is also related to fluctuations in living biomass (Figure 5) and a low 6-month SPEI (Figure 2). The mortality events after drought temporally altered the proportion of live and dead biomass and occurred with a higher intensity in the RCP 8.5 scenario.
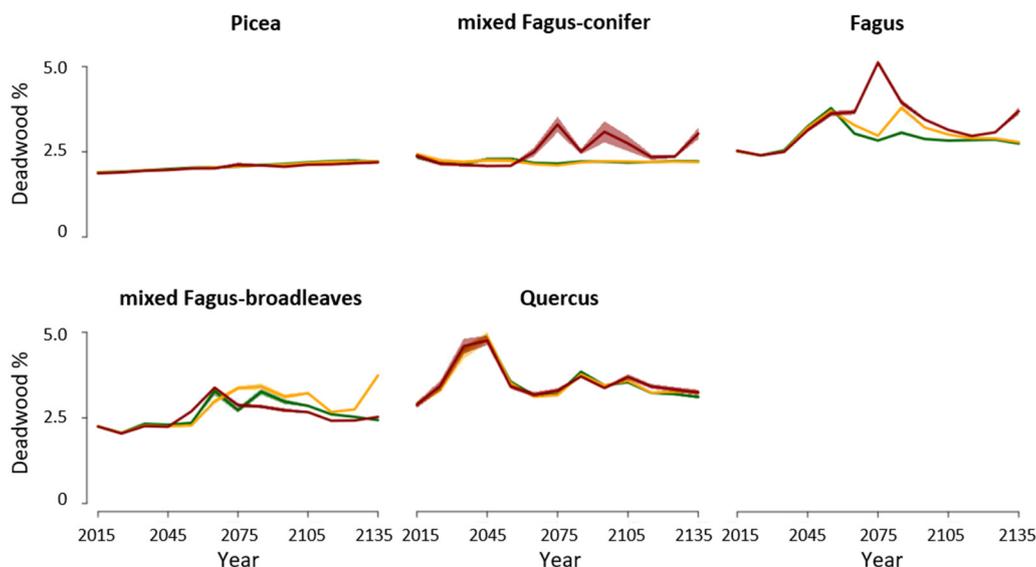

Figure 7. Percentage dead biomass relative to total biomass in the different forest types. Shaded areas indicate 95% confidence interval for every decade and climate change scenario: RCP 2.6 (green), RCP 4.5 (orange) and RCP 4.5 (red).

3.3. Productivity

The main forest types showed different aboveground net productivities, with Norway spruce and mixed forest productivity being typically lower than 15 kg/ha, that of beech pure forests being around that value and that of *Quercus* being usually above it. The aboveground net productivity tended to decrease slightly over time for all forest types. Productivity also differed among climate change scenarios, with the magnitude of the differences depending on forest type (Figure 8). Three forest types, Norway spruce, mixed beech–broadleaved and *Quercus*, showed significantly ($p < 0.05$) higher productivity under RCP 8.5 than under the other two scenarios. Beech forest productivity, despite having high temporal variations, showed significant differences between RCP 8.5 and RCP 4.5 ($p < 0.02$), usually being larger in RCP 8.5. The mixed beech–conifer forest productivity only showed significant differences between the RCP 2.6 and RCP 4.5 scenarios ($p = 0.035$).

3.4. Changes in Landscape Species Composition

Forest species composition varied over time and across climate change scenarios (Figure 9). During the first half of the simulations, the landscape species composition was similar among scenarios; in the following decades, the position of samples started to drift with the displacement increasing over time. This resulted in a significant differentiation in the species composition between RCP 8.5 and the other two scenarios. As shown by the ordination, and in accordance with the biomass analysis, RCP 8.5 was characterized by a greater biomass of *Q. frainetto*, *P. abies* and *A. alba*.
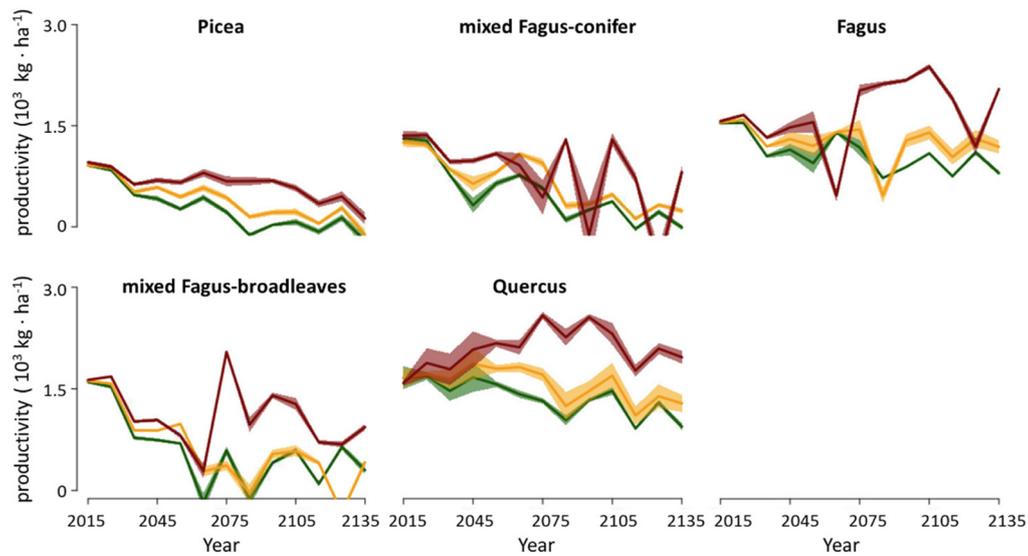
Figure 8. Productivity of the five main forest types (*Picea*, *Fagus*–conifers, *Fagus*, *Fagus*–broadleaved, *Quercus*) for the forecasts for every decade and climate change scenario: RCP 2.6 (green), RCP 4.5 (orange) and RCP 4.5 (red).
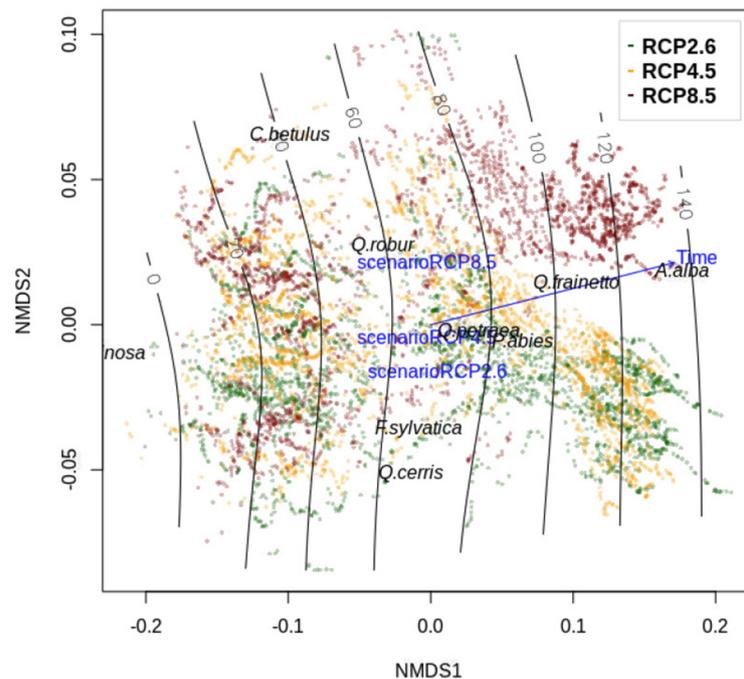
Figure 9. Ordination-based redundancy analysis of species biomass for the whole landscape, every year in the period 2015–2140 and every Landis-II simulation obtained for climate change scenarios RCP 2.6 (green), RCP 4.5 (orange) and RCP 8.5 (red), with the constraining variables year and RCP scenario.

4. Discussion

The simulation model implemented for temperate forests in the Romanian Southern Carpathians showed that climate change produces changes in forest biomass, productivity and species abundance. Such changes were particularly noticeable under RCP 8.5, the most extreme climate change scenario, and rendered an overall increase in the carbon carrying capacity of the studied Carpathian forests.

4.1. Forest Biomass and Productivity

The results of our Landis-II model adapted to Southern Carpathian forests showed an overall increase in forest biomass over time, with significantly greater biomass accumulation in the RCP 8.5 scenario. This is in line with Hubau et al. [10], who found that contrary to some tropical forests, temperate forests maintain a certain capacity to keep stocking carbon. The increased forest biomass accumulation and productivity predicted for the study area with intense climate change point to the raised CO_2 concentration [2,5] and warmer winters [3] as being the main drivers in the Carpathians, where precipitations do not change significantly for most of the area [23]. However, our simulations also indicate that the initial increase in biomass is limited, likely due to increasing drought and the stabilization of climate and atmospheric CO_2 concentrations. This trend suggests that the equilibrium already observed in some tropical forests [10] might occur in temperate forests somewhere at the end of the current century. Indeed, other authors have reached similar conclusions and timing, pointing directly to the proliferation of bark beetles as one of the main natural disturbances limiting carbon sequestration associated with climate change [92]. In the Southern Carpathians, climate change conditions overcompensate the negative effects of the disturbances at the beginning of the period but may not be able to do that after 2040, for most of the forests.

The main forest types studied responded differently to climate change, according to the ecophysiology of the species. Norway spruce and *Quercus* spp. forests had low productivity but higher stability, while mixed beech–conifer forests, beech forests and mixed beech–broadleaved forests were more prone to biomass changes, particularly after 2050. Indeed, low- and medium-altitude forests in the Southern Carpathians are very likely to be more affected by drought, while the precipitation in mountain tops, often covered by Norway spruce forests, might increase slightly [23]. Bouriaud el al. [16] also predicted forest biomass increments for the Romanian Eastern Carpathians but found a decreasing trend for conifer forests. This discrepancy among Bouriaud et al.'s [16] results and ours is likely due to three causes: (a) climate change effects on forests vary in type and intensity at the global, regional and local levels [15,23,93], as do the local conditions and climate change projections of the study areas in the Eastern and Southern Carpathians; (b) the modeling approach, with PnET and Landis-II models also accounting for complex ecophysiological responses to photosynthetically active radiation, atmospheric CO_2 concentration, etc.; and (c) the climate models used [16,94–97]. Indeed, the CNRM-CN5 model [87,88] used here is one of the least limiting climate models regarding water availability in the study area.

The predicted increase in the impact of the main natural disturbances in the Southern Carpathians: windthrows and bark beetle attacks, particularly *Ips* sp., is in agreement with other studies [6,98]. Even though some variations may be caused by harvest and aging forests, the periods with low productivity are likely associated with drought, since the SPEI value tends to decrease within the same periods. Drought events also occur simultaneously with raised mortality and deadwood biomass increments. This is the case of Norway spruce forests and beech forests after 2040. Natural disturbances induce organic carbon release, and hence it is common that disturbance regimes and ecosystem resilience determine forests' carbon sequestration capacity [10,99–102]. A net increase in temperate forest biomass caused by climate change has been forecasted for areas where disturbances and extreme climate events have a limited impact [54,103]. These disturbances usually damage conifer forests [6], and aging forests will likely contribute to it [52]. In our model, *H. abietis* had a minor impact, as a consequence of the low biomass of the cohorts they target, and because the selection harvesting management implemented in mixed beech and silver fir (*A. alba*) stands prevents *H. abietis* outbreaks [104]. The change in wood harvest observed here was also predicted by Bouriaud et al. [16], Ciceu et al. [105] and Chivulescu et al. [33] and concentrated in the intermediate- and low-altitude forests, having consequences for the forest structure. This increment in harvested timber is directly associated with both forest aging and the application of logging cycles [78]. As a result of all previous processes, around the year 2050, forests are expected to reach the carbon sequestration limit. Such

an idea is supported by Bouriaud et al.'s [16] and Hubau et al.'s [10] studies. Nabuurs et al. [19] also found evidence of carbon sink saturation in European forests.

4.2. Forest Composition

The Landis-II projections predicted shifts in forest species composition and abundance under the RCP scenarios in Romanian Southern Carpathian temperate forests, with the five main species showing significant biomass increments over time (*F. sylvatica* only up to 2040). Indeed, the reduction in the cohorts killed by windthrows under RCP 8.5 compared to RCP 4.5 and RCP 2.6 is likely due to the success of *A. alba* and the intense modification of the forest structure under RCP 8.5. However, only *F. sylvatica* showed differences among the RCP scenarios, with the highest biomass accumulation under RCP 8.5. Some species, particularly *F. sylvatica*, showed short periods with strong reductions in the biomass after 2050 that co-occurred, and thus are likely associated, with drought conditions. Climate change may alter local environmental conditions, making them no longer suitable for a given species and altering the interspecific competition [18,96], ultimately resulting in a change in species abundance [1]. For instance, Musselman and Fox [14] indicated that drought-tolerant species are expected to succeed at the global scale under the new conditions, and this is likely going to occur for *A. alba* in the Southern Carpathians, as predicted here.

Previous studies have indicated that the intensity of the change in climate is proportional to the magnitude of the impact on forests [16,33]. The intensity of such a change in the Southern Carpathians is expected to be relatively small, as the climate conditions do not strongly depart from the current conditions under the analyzed RCPs. However, some forest types are more vulnerable to changes than others [18,96]. Norway spruce forests at the upper limit will gain from the temperature rise [15], and, as suggested by Landis-II models, at the lower limit, they will also benefit from *F. sylvatica*'s vulnerability to drought. At lower altitudinal belts, conifers coexist with beech. Beech and conifer mixed forests are more successful than pure beech stands [25,26], but Norway spruce grows more and remains relatively unaffected compared to *F. sylvatica* during drought [106–108]. *A. alba* is also less susceptible to warmer and drier conditions than *F. sylvatica* [25]. Thus, at the stand level, the association between *F. sylvatica* and *A. alba* is not only advantageous for enduring drought [25,26,106,107] but also for sunlight use [104,109]. Our results for the Southern Carpathians suggest that climate change will contribute to *A. alba* encroachment in *F. sylvatica* pure forest stands. Indeed, there is strong evidence that beech forests have already been affected by climate change-induced drought in recent decades [20]. Moreover, Broadmeadow et al. [4] recently highlighted beech's vulnerability in temperate forests across Europe.

Conifer and beech forests aside, *Quercus* spp.-dominated forests will partially benefit from the temperature rise and *F. sylvatica* decline. *Quercus* species are relatively drought resistant. According to the Landis-II simulations, and as also supported by previous studies [110], the most thermophile and drought-resistant species in the Southern Carpathians such as *Q. frainetto* [36] will benefit from climate change and increase their biomass during succession, while *Q. petraea* will eventually suffer the impact of drought events.

5. Conclusions

Here, we simulated the changes in the composition and structure of the temperate forests of the Southern Carpathians under three climate change scenarios. Our results indicate that climate change may contribute, overall, to increasing temperate forest productivity and biomass, mainly due to the combination of increasing temperatures and thus extended growing periods in the uplands and only a mild reduction in rainfall across the landscape. Fluctuations in this trend associated with strong biomass reductions and temporary deadwood rise were related to drought periods. However, it is likely that increased drought events may eventually counteract such positive trends.

Climate change selectively affected areas and species, thus contributing to changes in species abundance. *P. abies* benefitted from warmer conditions, whereas forests dominated by *F. sylvatica* were vulnerable to climate change, with drought periods associated with large mortality events. The *A. alba* abundance increased under the new climate conditions at the expense of *Fagus*'s decline. Our results suggest that under the upcoming climate, mixed *F. sylvatica*–conifer (namely Norway spruce and silver fir) stands will have greater resistance and resilience than those of pure *F. sylvatica* stands, a finding that will help in guiding future forest management practices.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/f12111434/s1, Figure S1: Distribution of the ecoregions within the study area. Ecoregions represent areas of homogeneous climate, soil and forest types, Table S1: Characteristics of the defined ecoregions within each forest type: main species composition, elevation range, soil attributes and main natural disturbances affecting the ecoregion. Disturbances: It: *I. typografus*; Id: *I. duplicatus*; Ha: *H. abietis* [34,35,111,112].

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