


Article

Expected Impacts on Mediterranean Forest Species Under Climate Change

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Abstract: Climate change affects tree species, altering their growth and distribution, with effects varying by region, although mostly negative in the Mediterranean. This study examines 27 tree species in central Iberia, in a continental Mediterranean climate, using GISs and climate models. It investigates changes in net primary productivity (*NPP*) under different climate scenarios, identifying species that are endangered or vulnerable. Currently, only 2.4% of forest stands are endangered, but 51.2% are vulnerable; by 2100, these figures could rise to 35.4% and 85.2%, respectively. A correlation between altitude and threat level was found, with mountain species facing lower risks. Species with higher threat levels are linked to high *NPP* or low *NPP* variability. Four species currently have no threatened stands, though they may in the future, except one introduced in high-elevation areas, which will be favoured by climate change. Climate change will induce migrations to higher altitudes, but these movements depend on the rate of change, population size, fragmentation, and human alteration of the environment. Migration will be more challenging for low-altitude species in heavily human-impacted areas.

Keywords: climate change; net potential productivity; Spain; tree species

1. Introduction

There is overwhelming scientific evidence that the climate is changing as a result of human activity [1–3]. Anthropogenic emissions increase the greenhouse effect, leading to global warming, which also influences other climatic patterns, such as the abundance and distribution of precipitation, and, on a larger scale, affects global atmospheric circulation as well as the frequency and intensity of extreme events [4].

The Mediterranean region is particularly sensitive to the effects of climate change, experiencing the highest temperature increases in Europe [5]. In this region, droughts and heat waves, which are common, are becoming increasingly frequent and prolonged [6]. These climatic changes are altering the distribution and abundance of forest trees in a region where many species also reach their southern distribution limit [7,8]. Significant declines in tree growth have been recorded over the past years [9], with projections indicating further decreases due to climate change [10]. Additionally, climate change increases the risk of disturbances such as wildfires and insect outbreaks, even in non-water-limited environments, while extreme droughts and heat waves lead to high tree mortality [9,11–14]. These processes act synergistically, causing regression in some Mediterranean forests, which are approaching the limits of their ability to cope with increases in drought frequency and intensity [15,16].

The effects of climate change on tree species can be both positive, by expanding suitable habitats, and negative, by reducing them, resulting in ‘loser’ and ‘gainer’ species



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and in forest recession or expansion, depending on the region and climate change scenario [17,18]. In the Eastern Mediterranean, increased tree mortality has been observed at lower elevations during years of reduced precipitation, while higher altitudinal and latitudinal zones have shown improved growth due to rising temperatures [19]. In the Western Mediterranean, sharp declines in growth and carbon sequestration by up to 28% occur at lower elevations but disappear with increasing altitude [10]. Meanwhile, in the Mediterranean zone, tree growth may become smaller due to projected drier conditions, and, in temperate and boreal areas of Central and Northern Europe, where water is not strongly limiting, climate warming is expected to primarily enhance forest growth [20–25].

As a result, the effects of climate change vary greatly depending on latitude and altitude and can affect forest species differently across regions. An example of this variability is the beech (*Fagus sylvatica* L.), with a wide distribution across Europe, for which various studies have predicted global [12] or local [8] expansion, a partial threat [26], or a decline in its growth [25,27] or distribution, favouring other species such as *Quercus cerris* L., *Q. petraea* (Matt.) Liebl., or *Q. robur* L. [28–30]. This range of results, due to its wide distribution, reflects a great variability in the expected future climate conditions.

The importance of trees in the vegetation landscape makes their response to climate change a vital global concern [31]. As noted, the influence of climate change is highly species- and region-specific and cannot be extrapolated. It is therefore essential to have adequate predictions of the potential impacts of climate change on different regions and for as many species as possible; the response of the same tree species can vary greatly from one region to another. Information is currently available for certain species and regions, but more data are needed to tailor forest management in each region to its specific problems. The aim of this work is to analyse in a global and systematic way the impacts of climate change on all tree species that form forest stands in a continental Mediterranean region, in the centre of the Iberian Peninsula.

2. Materials and Methods

2.1. Study Area

The study area is the Community of Madrid, located at the geographical centre of the Iberian Peninsula (Figure 1). The territory covers an area of 8030 km², with an elevation ranging from 430 m to 2430 m. The climate is continental Mediterranean, with cool to cold winters and very dry, hot summers. The significant altitudinal range causes both temperature and precipitation patterns to vary greatly, with average temperatures ranging from 3 to 13 °C, and rainfall from 400 to 1500 mm [32]. Geologically, the western and north-western parts of the region are siliceous, primarily granites and gneisses in the mountains and arkoses at their foot, while the eastern and south-eastern parts are calcareous, with Quaternary materials in river valleys and some gypsum outcrops on slopes. Orographically, the northern and western areas of the region are included in the Central Range, with numerous peaks exceeding 2000 m. In the southern and eastern areas, calcareous plateaus and plains dominate, with large river valleys running through the territory; the Tagus River, one of the most significant in the Iberian Peninsula, flows south of the area.

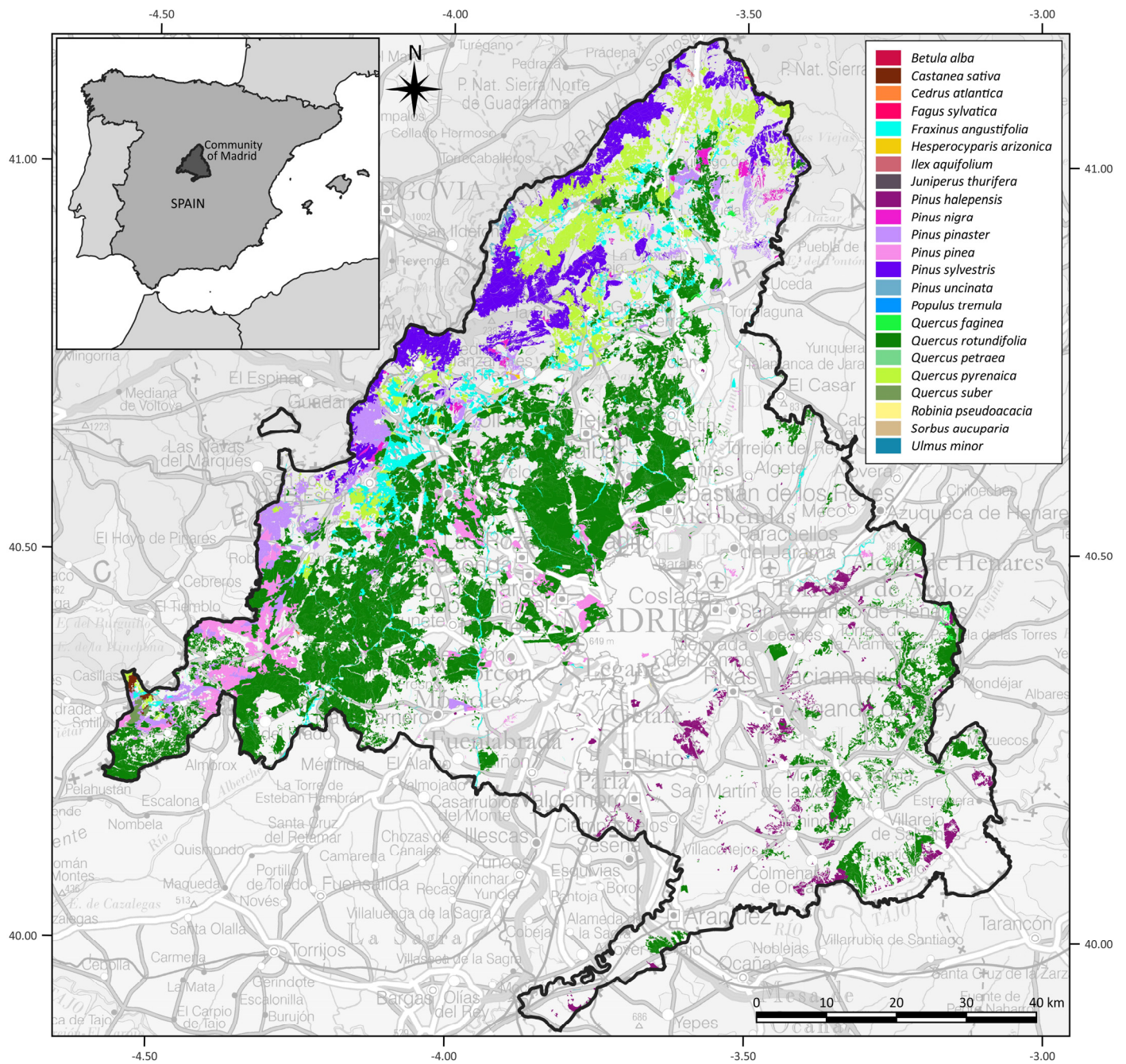


Figure 1. Study area and forests.

2.2. Analysed Species

A total of 31 forest tree species have been considered, both native and introduced to the region, which grow either as a dominant or accompanying species. The presence of these species is highly variable, occupying areas ranging from just a few hectares to several thousand. The species considered are as follows: *Acer monspessulanum* L., *Alnus glutinosa* (L.) Gaertn., *Betula alba* L., *Castanea sativa* Mill., *Cedrus atlantica* (Endl.) Manetti ex Carrière, *Cupressus sempervirens* L., *Fagus sylvatica* L., *Fraxinus angustifolia* Vahl, *Hesperocyparis arizonica* (Greene) Bartel, *Ilex aquifolium* L., *Juniperus thurifera* L., *Pinus halepensis* Mill., *P. nigra* J.F. Arnold, *P. pinaster* Aiton, *P. pinea* L., *P. sylvestris* L., *P. uncinata* Ramond ex DC., *Populus alba* L., *P. nigra* L., *P. tremula* L., *Quercus faginea* Lam., *Q. petraea* (Matt.) Liebl., *Q. pyrenaica* Willd., *Q. rotundifolia* Lam., *Q. suber* L., *Robinia pseudoacacia* L., *Salix alba* L., *Sambucus nigra* L., *Sorbus aucuparia* L., *Taxus baccata* L., and *Ulmus minor* Mill.

2.3. Software

Three main programmes were used for the management of the information. Spatial data were handled with a Geographic Information System (GIS), which combines georeferenced spatial information with a database. In this case, QGIS 3.28 Firenze, an open-source software, was employed. The GIS not only allows the management of information obtained from various sources but also enables its modification, both spatially and in terms of its attributes, and its completion by creating new fields, performing geoprocessing between different thematic layers, and incorporating formulas for automatic calculation. Once the base spatial layer has been prepared, managing the database is much more efficient in a spreadsheet. The original format of this database is *.dbf, and it has been converted into an Excel spreadsheet, which has been used and divided as explained later. Finally, for the variables that require statistical analysis, Excel spreadsheets have been prepared with an appropriate format for reading and handling with Statgraphics 19 Centurion, the software used for these calculations.

2.4. Initial Data and Preliminary Manipulation

To analyse tree species, the forest map of the Community of Madrid, available in vector digital format for GIS [33], was used as the starting point. This map consists of 56,935 polygons, covering the entire territory of the Community of Madrid. As a first step, 23,279 polygons representing agricultural, urban, or pasture areas without woody vegetation were removed. Subsequently, polygons lacking tree species, either as primary or secondary vegetation, were excluded, leaving a layer with 21,148 polygons encompassing all areas with tree species, either in stands or scattered. These polygons cover 308,692 hectares (3087 km²), accounting for 38% of the territory of the Community of Madrid. For each polygon, information is available for up to three main tree species (with one, two, or three species recorded), including their coverage within the parcel. The extent of the polygons was calculated automatically using three-dimensional areas in the EPSG: 25830 reference system.

To determine the elevation of each polygon, a digital elevation model (DEM) in raster format from the National Cartographic System [34] was used. The DEM used has a grid pitch of 1000 m and was created using airborne LiDAR sensors. Elevations were assigned through vector–raster geoprocessing; in this process, a vector layer (forests) is intersected with a raster layer (elevations), and the operation automatically assigns each vector polygon the raster value corresponding to its centroid.

To determine climatic values, raster cartography from the Integrated Precipitation-Contribution Modelling System (SIMPA), developed by the Centre for Hydrographic Studies of CEDEX, was used. This dataset provides raster layers with a grid pitch of 1000 m for the entirety of Spain with annual mean temperature and annual precipitation values for the periods 1941–2006 and 1981–2006 [35]. As in the previous case, a vector–raster geoprocessing process was performed, assigning to the centroid of each vectorial polygon a value for annual mean temperature and annual precipitation for both the 1941–2006 and 1981–2006 periods.

2.5. Determination of Future Climatic Parameters

This study aims to determine the potential impact of climate change on forest tree species. To achieve this, it is necessary to establish the expected future climate conditions in the region based on climatic scenarios. For this purpose, the regionalised climate change scenarios developed by the Government of Spain [36], and updated in 2024, were applied. These scenarios are based in the representative concentration pathways (RCPs), which are projections of greenhouse gas (GHG) concentration in the atmosphere, which will result in

increased radiative forcing (RF) relative to pre-industrial levels. In this study, it has been applied the RCP8.5 scenario, which considers an RF greater than 8.5 W/m^2 and a CO_2 concentration of 935.9 ppm in 2100 [37,38]. This is the scenario with the highest increase in GHG emissions, often referred to as ‘business as usual’. Therefore, its application involves considering the most severe effects that climate change could produce in tree species, based on current scenarios.

Regressions were applied to the variation in precipitation and temperature for the regionalised RCP8.5 scenario (Figure 2). In both cases, the variation is statistically significant at a 95% confidence interval ($p < 0.05$), with an R^2 value of 52.37% for precipitation and 97.38% for temperature. Based on this modelling, the expected precipitation and temperature for each vegetation polygon were calculated automatically.

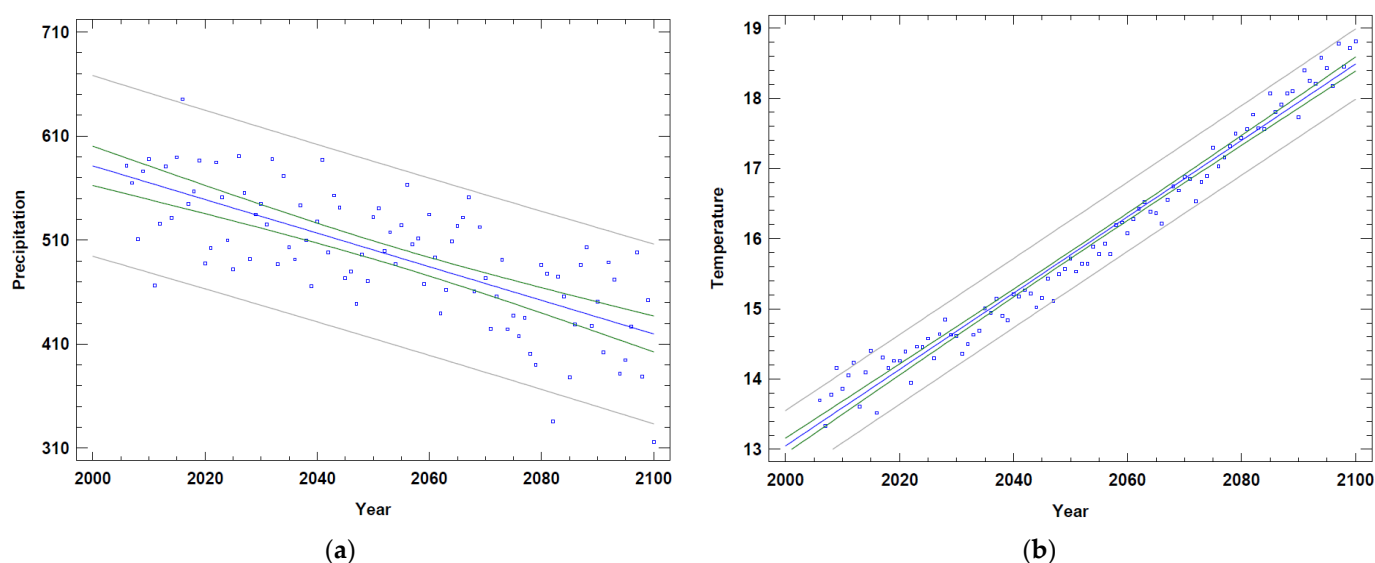


Figure 2. Regressions of precipitation (a) and temperature (b) in Madrid under the RCP8.5 scenario. Blue lines: linear regression; green lines: confidence interval; grey lines: prediction interval.

2.6. Calculation of Study Variables

To analyse the potential impacts in vegetation as a consequence of climate change, it is necessary to employ an indicator that relates the primary data of precipitation and temperature to growth or biomass production. For this study, we considered net primary productivity (NPP), according to the formula (Equation (1)) by Rosenzweig [39], which is well suited to the conditions of the Iberian Peninsula. In addition, the use of this indicator is common in studies that link growth with climate change [10,40–43].

$$\log NPP = 1.66 \cdot \log AE - 1.66 \quad (1)$$

where NPP —net primary productivity; and AE —actual evapotranspiration.

This formula has the advantage of determining productivity based on actual evapotranspiration (AE), which is in turn dependent on precipitation (P) and temperature (t) and therefore highly sensitive to the effects of climate change. Consequently, to determine NPP , it is necessary to first calculate AE . The formula by Turc [44] was used (Equation (2)), which adapts well to the available input data (P , t), yielding results quite similar to those obtained with the more complex Thornthwaite method [45].

$$AE = P / \{(0.9 + (P^2/L^2))^{1/2}\} \quad (2)$$

where AE —actual evapotranspiration; P —precipitation; and L —thermal indicator, calculated based on temperature (t) according to the following expression (Equation (3)):

$$L = 300 + 25 t + 0.05 t^3 \quad (3)$$

Using the initial data, and the climatic predictions for 2100, and incorporating Equations (1) to (3) into the GIS, AE and NPP were calculated for each polygon during the periods 1941–2006, 1981–2006, and 2100.

2.7. Data Processing

The starting point is a GIS vector layer, containing information on the area of each polygon, tree cover, elevation, as well as precipitation, temperature, AE , and NPP during the periods 1941–2006, 1981–2006, and 2100. The database associated with the GIS vector file was exported to a spreadsheet for easier handling.

Each polygon contains one, two, or three main species, with information of their cover in the polygon, as usual, in the forest map of Spain. In the spreadsheet, this database was exploited into a continuous list of species with their corresponding cover; this means that, when more than one species exists in a polygon, each species is separated into a separate row, which increases the number of records. However, not all resulting species are tree species, so a further cleaning of the data was carried out by removing non-tree species. As a result, a database with 26,862 records was obtained. This global database was divided into 31 spreadsheets, one for each species considered.

For each polygon and species, the actual area occupied was calculated by multiplying the total area of the polygon by the tree cover percentage of the species. The ratio between the total actual occupied area of the species and the total area of the polygon represents where it was present and indicates the average cover degree of each forest species, which is an indicator of its primary or accompanying character.

A common issue in extensive data series like these is the presence of outliers, which can have a considerable impact on the results [46]. Therefore, the data were filtered to remove outliers, using the IQR method. In this method, the first quartile (Q1) and the third quartile (Q3) were first calculated, and, with this, the interquartile range (IQR) was obtained, which is the difference between them (Equation (4)).

$$IQR = Q3 - Q1 \quad (4)$$

With this value, the normal lower and upper limits were calculated (Equation (5)).

$$\text{Lower boundary} = Q1 - (1.5 \cdot IQR) \quad \text{Upper boundary} = Q3 + (1.5 \cdot IQR) \quad (5)$$

This filtering was applied to the reference NPP (1941–2006); the data situated outside this range were considered outliers and were removed.

For the statistical treatment of elevation and NPP data, the results were weighted according to the actual species occupancy in each polygon, which allows for unbiased and consistent results [47], with greater weight given to areas with higher presence and/or dominance of the species. For each data series, the mean, maximum, minimum, standard deviation, standard error, and Q1 and Q3 were calculated.

2.8. Studied Scenarios

Four scenarios were considered in this study:

Scenario 1 (reference)

This is the scenario adopted as a reference, that is, as the normal conditions for the forest species. In this study, the period 1941–2006 was adopted, as a high-reliability raster layer was available. This period captures the normal variability of much of the 20th century, with a moderate climate change influence. The RF relative to 1750 during this period ranged between 0.87 and 2.63 W/m², with a mid-period value (1974) of 1.50 W/m² [48,49].

Scenario 2 (current)

This scenario represents the current situation. In this study, the period 1981–2006 was adopted, as a high-reliability raster layer is available. Although these are not the most up-to-date climate data, they capture the peak of GHG emissions and temperature rise, and the period is sufficiently long (25 years) to be significant in climatic terms. The RF relative to 1750 during this period ranged between 1.80 and 2.63 W/m², with a mid-period value (1994) of 2.45 W/m² [48,49], which represents a 63% increase compared to the baseline scenario. Recent RF figures are 2.72 W/m² in 2019 and 2.91 W/m² in 2022 [50], meaning that the situation in 2025 could reflect an RF increase of approximately 20% compared to this scenario and 95% compared to the reference scenario.

Scenario 3 (RCP8.5 in 2100)

The first future scenario corresponds to the RCP8.5 in 2100. As noted above, this scenario assumes an RF in 2100 greater than 8.5 W/m², with the probability of this occurring being very low, at just 0.5%; however, this scenario is useful for calibrating damage functions [51]. The regionalised data series up to 2100 are statistically significant for temperatures in both RCP4.5 and RCP8.5 but are only significant for precipitation in RCP8.5 [10], due to its pronounced irregularity in the Mediterranean region. Therefore, while RCP8.5 is unlikely, it is statistically reliable, whereas RCP4.5 is more probable but has an unacceptably margin of error for prediction series.

Scenario 4 (expected in 2100)

Current projections suggest that an RF of 5.1 W/m² is likely to be reached by 2100 [51]. This scenario aligns more closely with RCP4.5 than RCP8.5, but the former is not statistically significant in this region. For this study, it was estimated proportionally based on the results of Scenario 2 and 3. While the results are not statistically significant, they provide a fairly reliable approximation of the real situation that could be reached by 2100: Scenario 3 offers a reliable projection with a low probability of occurrence, whereas Scenario 4 provides a less reliable projection with a high probability of occurrence.

2.9. Study Hypotheses

Three threat categories were proposed to establish the expected impacts on forest species, which are related to the reference ranges of *NPP* for Scenario 1:

Endangered species

A species is considered endangered in a polygon when the expected *NPP* under Scenarios 2 to 4 is below the minimum or above the maximum range for the species in Scenario 1. The species will be outside its suitable range, so if these conditions persist—particularly a reduced *NPP*—it would face severe climatic limitations, likely leading to its eventual disappearance.

Vulnerable species

A species is considered vulnerable in a polygon when the expected *NPP* in Scenarios 2 to 4 falls between the minimum and Q1, or between the maximum and Q3 of Scenario 1.

These areas are less climatically favourable for the species; its presence is effective but with a significant vulnerability.

Non-threatened species

A species is considered not threatened in a polygon when the *NPP* in future scenarios remains within the normal range for Scenario 1, that is, between Q1 and Q3. In such cases, no climatic risks are identified.

2.10. Threat Global Assessment

The global endangerment and vulnerability in the current and future scenarios were quantitatively determined for each species based on the actual area within each threat category (endangered or vulnerable). For the qualitative assessment, five classes were established for both categories: very high (80–100%), high (60–80%), medium (40–60%), low (20–40%), or very low (0–20%).

2.11. Statistical Analysis

Regressions were conducted on the results of the global threat assessment for each species, considering both risk and vulnerability and relating them to the occupied area, the average polygon size, mean elevation, and mean *NPP* in different scenarios, to identify statistically significant relationships.

2.12. Error Prediction

This study predicts the impact of climate change on forest species, based on a series of assumptions, and is therefore subject to statistical errors as well as errors dependent on the assumptions made. These errors are cumulative and species-specific, affecting the overall accuracy of the predictions.

Climatic errors (E_{CL})

The *NPP* calculations are based on climate data, and, therefore, their error depends on the error assumed in those data. In Scenarios 1 and 2, real climate data were used, so the assumed error was considered negligible. However, in Scenario 3, regionalised predictions for the RCP8.5 scenario were used. This resulted in two types of errors. The first was related to the probability of occurrence of this scenario, which, as mentioned earlier, was very low. Nevertheless, it was adopted to consider the maximum expected impact. On the other hand, the variation in precipitation and temperature in this scenario was modelled applying a regression, as noted above, with an error of 8.61% for precipitation (E_{CL-P}) and 1.55% for temperature (E_{CL-T}).

Scenario 4 is useful for informational purposes, but it is not statistically significant. As noted, it represents a probable approximation to a very likely scenario. In this case, a specific error cannot be established, but the margin of certainty would be moderate.

Azonality error (E_{AZ})

Zonal vegetation is primarily influenced by climatic factors, whereas local factors play a greater role than climate in azonal vegetation [52]. Considering the forest vegetation of the study area, the main azonality is hydromorphy, whether due to riparian or phreatic moisture. The proposed model is consistent for zonal species but less consistent when the presence of species is influenced by hydromorphy. To evaluate this error, an azonality index (I_{AZ}) was proposed, similarly to other studies [52]; this index coincides with the azonality error (E_{AZ}). The I_{AZ} establishes the dependence of species on azonality, in this case, on hydromorphy. The values to this index were applied in a reasoned manner. Four categories of species were established:

- Zonal species, with no appreciable azonality. $I_{AZ} = E_{AZ} = 0\%$.
- Primarily zonal species, which can be riparian or phreatophytes in drier environments (*Betula alba*, *Populus tremula*). $I_{AZ} = E_{AZ} = 20\%$.
- Phreatophyte species, associated with areas with groundwater moisture but also with significant climatic influence (*Fraxinus angustifolia*, *Ulmus minor*). $I_{AZ} = E_{AZ} = 30\%$.
- Riparian species where climatic influence is lower than azonality influence (*Alnus glutinosa*, *Populus alba*, *P. nigra*, *Salix alba*). $I_{AZ} = E_{AZ} = 70\%$.

Global error

To determine the propagation of the error, that is, the global error, the formula applicable to independent variables (Equation (6)) was considered [53]:

$$E_G = (E_1^2 + E_2^2 + E_3^2 \dots)^{1/2} \quad (6)$$

where E_G is the global error, and E_n is the error of variable n , in this study precipitation, temperature, and azonality.

3. Results

3.1. Reliability of Predictions

For the vast majority of species, the prediction error reaches 8.7%, primarily due to the precipitation. For species that are occasionally hydrophytic (*Betula alba*, *Populus tremula*), the error increases to 21.8% and for phreatophytic species (*Fraxinus angustifolia*, *Ulmus minor*) to 31.2%. Finally, for riparian species (*Alnus glutinosa*, *Populus alba*, *P. nigra*, *Salix alba*), the error reaches 70.5%. In this latter group, the predictions are of no practical use, as the probability of being incorrect exceeds that of being accurate.

3.2. Occupation, Coverage, and Altitudinal Range

The first set of results includes the altitudinal range of the species, the associated *NPP*, the degree of tree coverage, and the actual absolute and relative occupation (Table 1). The elevation and *NPP* values presented correspond to the normal range for the species (between Q1 and Q3), under Scenario 1. In the results, the four riparian species, with an unacceptable error, have been excluded.

Seven species account for 97.15% of the studied woodland area. By far, the most prominent species is *Quercus rotundifolia*, comprising more than half of the area (51.67%). This is followed by *Pinus sylvestris* (11.68%) and *Quercus pyrenaica* (11.02%). Species with a smaller presence include *Fraxinus angustifolia* (7.71%), *Pinus pinaster* (6.02%), *Pinus pinea* (6.01%), and *Pinus halepensis* (3.03%). Three species have a very narrow altitudinal distribution (less than 100 m), considering the interquartile Q1–Q3 range: *Castanea sativa*, *Cupressus sempervirens*, and *Pinus halepensis*. The first two are non-native to the region, while the latter is only sporadically native and predominantly planted. Conversely, the species with the widest altitudinal range is *Populus tremula* (667–1162 m).

In terms of *NPP*, the species with the lowest associated values are *Pinus uncinata*, *Robinia pseudoacacia* and *Ulmus minor*, while the highest values are associated with *Fagus sylvatica*, *Juniperus thurifera*, *Castanea sativa*, and *Quercus suber*. The smallest variability in *NPP* is observed in *Sambucus nigra* and *Juniperus thurifera*, while the highest is found in *Sorbus aucuparia*, *Hesperocyparis arizonica*, *Pinus uncinata*, and *Ilex aquifolium*.

Table 1. Elevation, net potential productivity, tree cover, and occupation of the analysed species.

Species	Elevation (m)	Net Potential Productivity (g/m ² /year Dry Matter)	Tree Cover (%)	Area	
				Absolute (ha)	Relative (%)
<i>Acer monspessulanum</i>	847–1137	432–493	10.5	89	0.05
<i>Betula alba</i>	1293–1611	444–475	18.5	25	0.01
<i>Castanea sativa</i>	824–912	529–592	48.0	383	0.20
<i>Cedrus atlantica</i>	825–1156	449–537	12.2	28	0.02
<i>Cupressus sempervirens</i>	870–962	448–507	23.8	20	0.01
<i>Fagus sylvatica</i>	1314–1438	481–550	20.1	37	0.02
<i>Fraxinus angustifolia</i>	861–1080	450–495	44.2	14,600	7.71
<i>Hesperocyparis arizonica</i>	634–991	377–509	27.0	356	0.19
<i>Ilex aquifolium</i>	1375–1596	408–509	6.7	567	0.30
<i>Juniperus thurifera</i>	1126–1272	513–524	43.0	46	0.02
<i>Pinus halepensis</i>	621–703	361–390	63.7	5742	3.03
<i>Pinus nigra</i>	1047–1262	459–524	39.7	1608	0.85
<i>Pinus pinaster</i>	858–1115	472–521	43.7	11,388	6.02
<i>Pinus pinea</i>	651–785	396–483	38.3	11,367	6.01
<i>Pinus sylvestris</i>	1281–1581	418–517	68.0	22,112	11.68
<i>Pinus uncinata</i>	1653–1774	328–447	47.1	191	0.10
<i>Populus tremula</i>	667–1162	383–462	13.8	91	0.05
<i>Quercus faginea</i>	757–862	400–454	25.1	770	0.41
<i>Quercus petraea</i>	1344–1476	449–544	21.8	107	0.06
<i>Quercus pyrenaica</i>	1036–1240	468–515	58.3	20,853	11.02
<i>Quercus rotundifolia</i>	652–871	392–467	52.2	97,797	51.67
<i>Quercus suber</i>	775–934	558–594	43.2	443	0.23
<i>Robinia pseudoacacia</i>	658–791	375–410	14.5	36	0.02
<i>Sambucus nigra</i>	860–1106	457–468	6.6	5	0.00
<i>Sorbus aucuparia</i>	1404–1620	407–545	5.2	349	0.18
<i>Taxus baccata</i>	1496–1611	409–444	5.0	63	0.03
<i>Ulmus minor</i>	613–729	373–441	18.7	196	0.10

3.3. Endangerment and Vulnerability

The NPP in Scenarios 2 (current), 3 (2100-RCP8.5), and 4 (2100-expected) was compared with the NPP of Scenario 1 (reference), considering the threat categories based on the range in which they fall (Table 2). Scenario 4 is an interpolation of Scenarios 2 and 3, not statistically significant, but a reasonably reliable prediction for a very likely scenario.

Table 2. Tree species threat in the current and future scenarios.

Species	Endangered			Vulnerable		
	Scenario 2 Current	Scenario 4 * 2100-Expected	Scenario 3 2100-RCP8.5	Scenario 2 Current	Scenario 4 * 2100-Expected	Scenario 3 2100-RCP8.5
<i>Acer monspessulanum</i>	10.8%	27.1%	48.1%	46.7%	68.4%	96.2%
<i>Betula alba</i>	12.8%	23.2%	36.5%	29.2%	32.4%	36.5%
<i>Castanea sativa</i>	57.1%	68.9%	83.9%	64.6%	76.4%	91.5%
<i>Cedrus atlantica</i>	12.3%	30.5%	53.9%	53.5%	61.1%	70.9%
<i>Cupressus sempervirens</i>	17.0%	20.6%	25.2%	23.5%	57.0%	100.0%
<i>Fagus sylvatica</i>	75.5%	80.9%	87.9%	75.5%	84.9%	97.0%
<i>Fraxinus angustifolia</i>	9.6%	37.4%	73.0%	68.6%	81.4%	97.8%
<i>Hesperocyparis arizonica</i>	23.9%	41.0%	62.8%	60.2%	64.0%	68.9%
<i>Ilex aquifolium</i>	1.1%	0.6%	0.0%	39.4%	42.2%	45.7%
<i>Juniperus thurifera</i>	99.4%	99.7%	100.0%	99.4%	99.7%	100.0%
<i>Pinus halepensis</i>	8.4%	48.2%	99.2%	72.5%	84.5%	100.0%
<i>Pinus nigra</i>	0.6%	9.7%	21.4%	33.2%	54.2%	81.1%
<i>Pinus pinaster</i>	6.9%	30.2%	60.1%	66.1%	79.0%	95.5%
<i>Pinus pinea</i>	2.8%	17.0%	35.1%	39.0%	61.0%	89.1%

Table 2. Cont.

Species	Endangered			Vulnerable		
	Scenario 2 Current	Scenario 4 * 2100-Expected	Scenario 3 2100-RCP8.5	Scenario 2 Current	Scenario 4 * 2100-Expected	Scenario 3 2100-RCP8.5
<i>Pinus sylvestris</i>	0.0%	0.4%	0.8%	30.1%	27.4%	24.0%
<i>Pinus uncinata</i>	2.6%	1.5%	0.0%	5.9%	3.7%	0.8%
<i>Populus tremula</i>	0.0%	1.5%	3.4%	67.0%	72.3%	79.0%
<i>Quercus faginea</i>	20.7%	47.8%	82.6%	55.7%	73.4%	96.2%
<i>Quercus petraea</i>	15.3%	15.3%	15.3%	48.2%	53.9%	61.2%
<i>Quercus pyrenaica</i>	1.9%	21.4%	46.4%	52.6%	67.7%	87.0%
<i>Quercus rotundifolia</i>	0.4%	12.6%	28.3%	51.8%	70.6%	94.8%
<i>Quercus suber</i>	21.8%	56.1%	100.0%	79.3%	88.4%	100.0%
<i>Robinia pseudoacacia</i>	18.7%	52.2%	95.2%	82.6%	90.2%	100.0%
<i>Sambucus nigra</i>	37.2%	64.7%	100.0%	100.0%	100.0%	100.0%
<i>Sorbus aucuparia</i>	0.0%	0.0%	0.0%	33.2%	33.2%	33.3%
<i>Taxus baccata</i>	0.0%	2.3%	5.2%	82.8%	74.6%	64.2%
<i>Ulmus minor</i>	10.1%	39.2%	76.6%	59.9%	75.0%	94.4%
Weighted mean	2.4%	16.9%	35.4%	51.2%	66.1%	85.2%
	Null 0%	Very low 0.1–20.0%	Low 20.1–40.0%	Medium 40.1–60.0%	High 60.1–80.0%	Very high 80.1–100%

* Informative: interpolated between Scenarios 2 and 3 for RF 5.1 W/m². Threat categories by colour.

The proportion of endangered forests under the current Scenario (2) is very low (2.4%), although nearly half (51.2%) are vulnerable. In the most unfavourable scenario by 2100 (3), threatened forests rise to 35.4%, and the majority of them (85.2%) would become vulnerable. The likely predictions for 2100 (Scenario 4) point to 16.9% of forest stands threatened and two-thirds (66.1%) vulnerable. Figure 3 shows the expected changes in each of the species studied in Scenarios 1 to 3.

To explore the potential relationship between the endangerment and vulnerability for each species and their area, elevation, and *NPP*, regressions were performed. First, the threat indicators were related to the total area of each species and the average polygon size. None of the scenarios or combinations yielded statistically significant regression results, leading to the rejection of such a relationship.

Secondly, threat indicators in different scenarios were related to the mean elevation at which each species occurs (Table 3).

Table 3. Statistical indicators of the regressions between threat and elevation.

		Endangerment			Vulnerability		
		Scenario 2	Scenario 4	Scenario 3	Scenario 2	Scenario 4	Scenario 3
Elevation	<i>p</i> -value	0.7054	0.0348	0.0006	0.0287	0.0002	0.0000
	<i>r</i>	−0.0076	−0.4077	−0.6149	−0.4211	−0.6588	−0.7895
	<i>R</i> ²	0.5817	16.6181	37.8118	17.7356	43.3957	62.3277

p-value for 95% confidence (significant if *p* < 0.05); and *r*—Pearson’s correlation coefficient.

The relationship between danger and elevation is significant in future scenarios but not in the current one, while the relationship between vulnerability and elevation is always significant. Pearson’s coefficient is negative, indicating a threat reduction as elevation increases, with an increasing *R*² value as scenarios become more adverse, and higher values for vulnerability compared to risk.

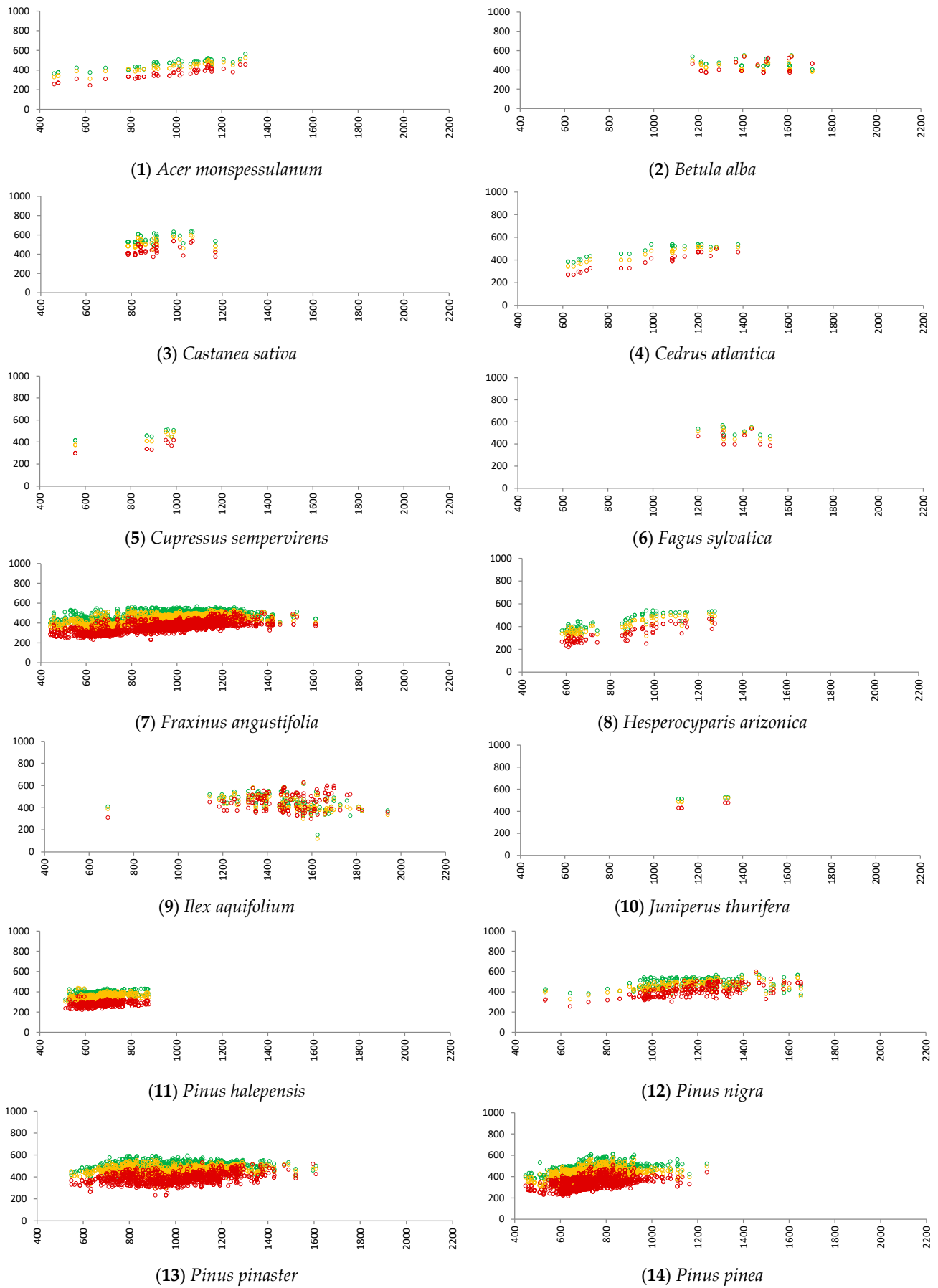


Figure 3. Cont.

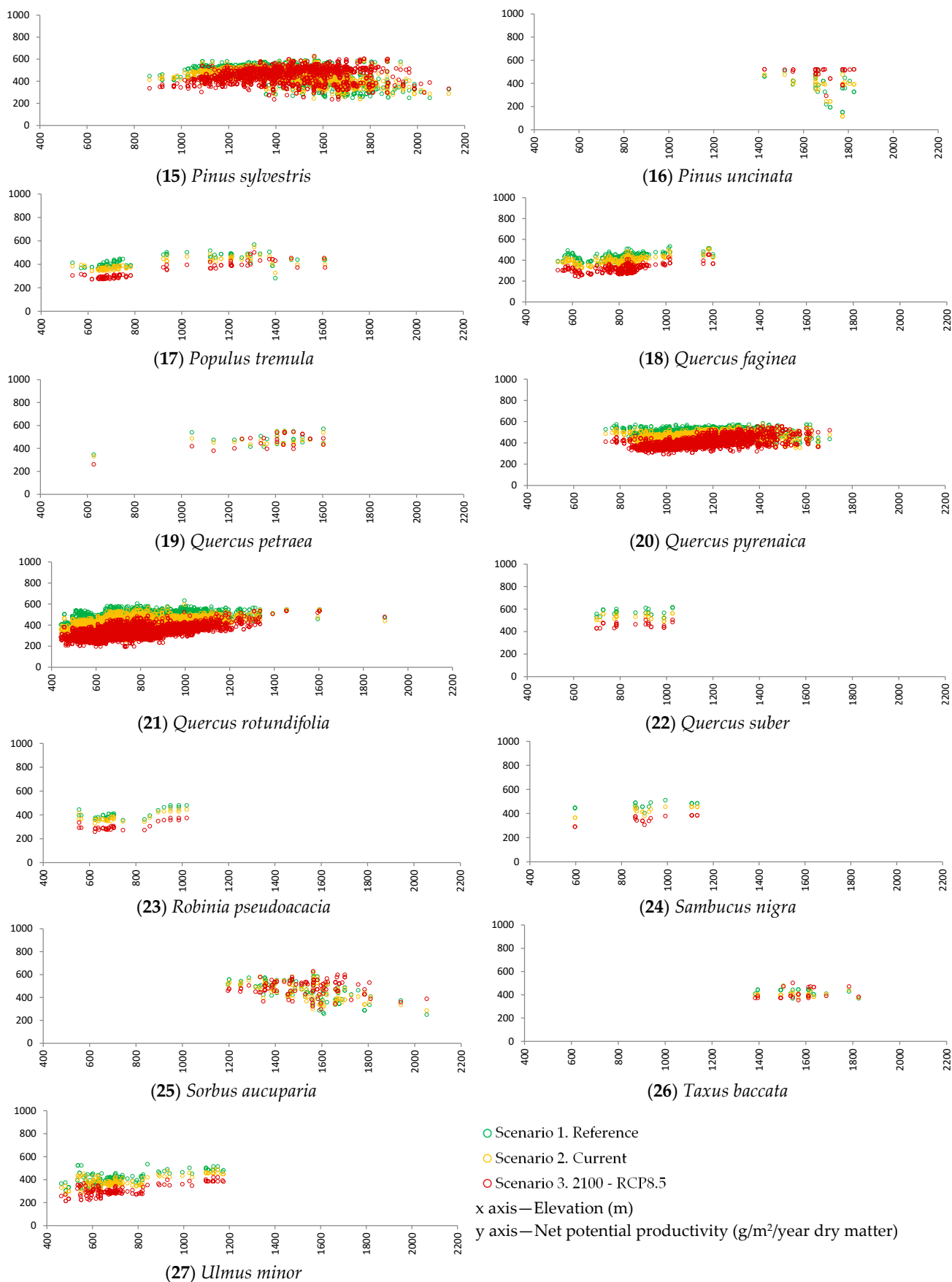


Figure 3. Variation in net potential productivity by species in Scenarios 1 to 3.

Additionally, the threat indicators have been linked to the *NPP* values in Scenarios 2 and 3 (Table 4).

Table 4. Statistical indicators of the regressions between threat and *NPP*.

		Scenario 2		Scenario 3	
		Endangerment	Vulnerability	Endangerment	Vulnerability
Net potential productivity	<i>p</i> -value	0.0438	0.9899	0.0278	0.0003
	<i>r</i>	0.3910	−0.0026	−0.4234	−0.6378
	<i>R</i> ²	15.2845	0.0007	17.9232	40.6792

p-value for 95% confidence (significant if $p < 0.05$); and *r*—Pearson’s correlation coefficient.

The results are variable. The relationship between danger and *NPP* is significant in both scenarios, but, in Scenario 2, risk increases as *NPP* increases, while, in Scenario 3, the opposite is true. The relationship between *NPP* and vulnerability is not statistically significant in Scenario 2, but it is strongly significant in Scenario 3; in the latter case, vulnerability decreases as *NPP* increases.

4. Discussion

4.1. Endangerment and Vulnerability

This study is based on predictive climate models and scenarios, and, therefore, its predictions are subject to a margin of error, mainly associated with the uncertainty in the evolution of precipitation in a region where it is extremely variable. Even so, prediction error is considered in general to moderate, except for riparian species. The future dynamics of these species will be determined by the flow rates in the rivers more than by the regional climate. Climate change is expected to have adverse effects in Mediterranean rivers, with a mean estimated reduction in flows in Central Spain of 10–15% for 3 °C of temperature increase [54]; just 2 °C of warming may reduce fresh water availability in the Mediterranean countries by 2–15%, among the largest decreases in the world [55]. However, the model proposed in this paper is unable to capture these changes, so riparian species have been excluded.

Our results predict, for 2100, in the most unfavourable scenario, that 35.4% of forest would be threatened and 85.2% would become vulnerable. In Andalusia (Southern Spain), the climate exposure of the forests will range between 32% for the RCP4.5 and 98% for the RCP8.5 by the end of the century [56]. There are other predictions in different regions, mostly negative, although they are very site-dependent. In China, tree vulnerability in 2070 ranges between 23% and 57%, depending on whether universal migration is considered, with a minimum of 18% even in the most favourable scenarios [57]. In North America, it is estimated that 30% of species ranges was deemed vulnerable in the period 1976–2006, similar to Scenario 2 in this study [58]. In Canada, it is estimated that only 37% of its forests will remain within its current climate range in 2071–2100 [59]. Even in rainy regions, such as the Amazon, climate change could cause a 31–37% decline in tree species by 2050 [60].

Threat indicators by species were related to the elevation at which they occur, indicating that elevation mitigates the effects of climate change. The same results have been reported in several regions of the world, predicting increased forest growth at high elevations and an upward shift in the area without growth limitations for trees due to climate change [61–64].

The current danger is very low to low, but three species stand out clearly: *Juniperus thurifera*, with an almost maximum risk and vulnerability; *Fagus sylvatica*, with high risk and very high vulnerability; and *Castanea sativa*, with medium risk that will rise to high and very high vulnerability. These three species are associated with a high *NPP* and *Juniperus*

thurifera with a very low *NPP* range. As noted above, results for *Fagus sylvatica* across Europe are highly variable, ranging from an expansion to a decline, although a dominant regression is expected in Southern Europe [27,30], except in the Orocantabrian mountain area [8]. Other species with similar characteristics regarding *NPP* face the same issue: *Quercus suber* is also associated with high *NPP*, and *Sambucus nigra* has a limited *NPP* range. In both cases, their current risk is medium but increases sharply by 2100, with vulnerability reaching 100%. Consequently, the need for a high *NPP* or a very narrow *NPP* range are factors that seem to be associated with a greater threat due to climate change, as future variations can easily push these species outside their optimal range. It is noteworthy that all these species, except *Castanea sativa*, which is not native to the region, are included in the regional catalogue of threatened species [65]. Consequently, the applied model effectively identifies those species that are currently rare or in decline.

Only four species currently face no risk: *Pinus sylvestris*, *Populus tremula*, *Sorbus aucuparia*, and *Taxus baccata*.

Pinus uncinata would improve its position with respect to climate in the future; it is currently slightly endangered but will no longer be by 2100. However, it is a non-native species in the region (although it is in high mountain areas of Northern Spain), used very locally for reforestation at high elevations, in pure stands or mixed with *Pinus sylvestris*. The high elevations at which it has been planted prevent it from being affected by climate change, although it is subject to strong competition from *Pinus sylvestris*, whose stands in this region are adapted to withstand drought [66].

Sorbus aucuparia shows virtually no change across the three scenarios. Other species close to this point of equilibrium, with only slight changes expected in risk or vulnerability, include *Betula alba*, *Ilex aquifolium*, *Pinus sylvestris*, *Populus tremula*, *Quercus petraea*, and *Taxus baccata*. Three of these species, *Sorbus aucuparia*, *Pinus uncinata*, and *Ilex aquifolium*, exhibit the greatest variability in *NPP*, which appears to be a factor that reduces their threat. In *Pinus sylvestris*, short-term negative effects are expected in warmer climates and positive in colder ones, although long-term negative impacts are expected to diminish, while positive impacts are likely to increase in most Eurasian stands [67]. It has also been pointed out that most of the Spanish populations of this species are adapted to drought, so the influence of climate change would be less than in other regions [66].

All these species are mountain dwelling, with an optimal range between 1281 and 1774 m, which explains their relatively favourable or slightly unfavourable dynamic. A study on pine forests in this region [10] concluded that, by 2100, under the RCP8.5 scenario, there would be a shift in the *NPP* trend at 1646 m, with a decrease below this threshold and an increase above it. This is because the rise in productivity at higher altitudes, driven by an extended growing season during colder months due to warming, outweighs the reduction caused by the lengthening of the hot and dry summer period. However, in lower areas, warming intensifies summer droughts, reducing the growing season and productivity. Another study predicted a moderate *NPP* gain in continental and mountainous zones and no change in oceanic zones [40].

Pinus nigra is found at a slightly lower altitude than *Pinus sylvestris*. It currently faces very low risk and low vulnerability, but, by 2100, its risk increases somewhat, and its vulnerability rises sharply. In Turkey, a loss of distribution areas of this species is projected by 2100, although it may be accompanied by the emergence of new suitable areas [41]. The same could happen in the studied region as, being a mid-mountain species, it might compensate for the loss of suitable areas at lower areas with more favourable ones at higher elevations. However, the vast majority of forest stands belong to an alien subspecies, which faces challenges in natural regeneration, making adaptation difficult.

A subsequent group of species, occupying slightly lower elevations, will be much more affected by climate change. *Acer monspessulanum*, *Quercus pyrenaica*, *Fraxinus angustifolia*, and *Pinus pinaster* currently have very low risk, which will increase to medium for the first two and high for the latter two; in all cases, their future vulnerability will be very high. *Quercus faginea* is an example of adaptation of a deciduous oak to Mediterranean-type climates, slightly more thermophilic than other deciduous oaks, but still dependent on moisture [68]; it has a low current risk that will rise to very high in the future.

The three most typically Mediterranean species, *Quercus rotundifolia*, *Pinus pinea*, and *Pinus halepensis*, currently face very low risk. For the first two species, the risk will increase slightly, but, for *Pinus halepensis*, it will rise sharply to 99.4%; in the Eastern Mediterranean, high mortality of this species has already been detected in dry years [19]. It is worth noting that *Pinus halepensis* is almost non-native to the region (barely native to a single point in the extreme south), so its high future risk aligns with its natural absence in the region, despite being native and common in neighbouring provinces. In these species, future vulnerability will be very high, although the way in which temperature increase and changes in precipitation affect each of them varies due to specific phenological adjustments [15]. Another species of low areas, *Ulmus minor*, will face a significant increase in threat by 2100. However, it is a phreatophyte and is already severely affected by phytosanitary problems today.

A group of alien species introduced to the region (*Cedrus atlantica*, *Cupressus sempervirens*, *Hesperocyparis arizonica*, *Robinia pseudoacacia*) exhibit irregular behaviour, with very low to low current risk, which will increase to medium to very high. As they are alien and have a very limited presence, predictions are less reliable.

The concepts of ‘winner’ and ‘loser’ species have been applied in relation to climate change [17,68]. The first group includes, in Europe, species such as *Abies alba*, *Fagus sylvatica*, *Fraxinus excelsior*, *Quercus robur*, or *Quercus petraea*, and, in the second group, *Betula pendula*, *Larix decidua*, *Picea abies*, or *Pinus sylvestris* [69]. However, the situation across boreal, temperate, and Mediterranean regions is so varied that such distinctions cannot be universally applied. For instance, in the studied region, *Fagus sylvatica* would clearly be a ‘loser’, while *Pinus sylvestris* would be almost neutral.

4.2. Migration Possibilities

Tree species migrations are a natural process in response to environmental changes; many species have shifted multiple times since the last glacial period [70]. The response to these changes varies by species and even within the same species. A small change in water availability can lead to changes in the growth, composition, or distribution of species [71]. Species with high mortality rates and populations subjected to periodic disturbances such as storms or fires may be the quickest to adapt to a warmer climate [72]. As the climate warms, there is an altitudinal shift in the optimal development conditions for species, with new suitable habitats appearing at higher altitudes, allowing the migration of colonising genotypes, while increasing stress occurs at lower altitudes, where genotypes capable of withstanding drought and thermal stress would be favoured [73]. The best adaptive response of species is associated with large populations and high genetic variability [74]. Species growing at high elevations, in the limits of their altitudinal range, will not be able to migrate anywhere, presenting a significant risk of decline [75].

Climate change is expected to force species to shift towards the poles or move uphill, in a process that will result in the dissociation and reassociation of species, potentially leading to new types of forests, with some species disappearing or being restricted to isolated refuges, while others could expand [76]. Changes in suitable habitat will vary greatly by area. For example, subtropical habitats in Thailand are expected to decline by 12–50%,

while tropical habitats are expected to expand by 45–80% [77]. In the Rocky Mountains of the US, predicted habitat losses will be more than offset by projected gains, although not for all species [78].

These migration processes present a high level of uncertainty. Some authors have pointed out a lack of evidence for climate-mediated migration [79], while others provide specific data, such as a latitudinal shift of approximately 3 km in temperate and boreal forests of North America [80]. Furthermore, several factors affect the actual possibilities for migration. On the one hand, the speed at which the climate is changing means that many species would need to migrate at a rate faster than their natural ability [81]. On the other hand, even if suitable new habitats for the species exist, in many cases, they will not be able to colonise them due to the large dispersal distances [29]. Additionally, the anthropisation of the environment is critical; advances in tree lines are likely in the near future, except where prevented by human activity [82]. Assuming these limited migration possibilities, most species will lose a significant portion of their potential range [66].

Vegetation succession is a slow process, with average species replacement periods ranging from just over 100 years to nearly 800 years [83]. However, extreme events such as droughts or heat waves, causing high tree mortality [11–14,19], can accelerate these replacement processes or lead directly to the disappearance of forests. The Mediterranean region is located at the transition between temperate and arid climates, and a modification of the climate could irreversibly shift ecosystems towards drier states [84].

For the tree species studied, the greatest difficulties for altitudinal migration will occur in species outside of mountain areas (below 1000 m) and with scattered populations, such as *Acer monspessulanum*, *Castanea sativa*, *Pinus halepensis*, *Quercus faginea*, *Q. suber*, *Sambucus nigra*, or *Ulmus minor*. This is due to the discontinuity of suitable habitats in lowland areas, with numerous agricultural, urban, or pasture areas, which limit the effective migration possibilities of the tree species. Species from lowland areas with abundant presence, particularly *Quercus rotundifolia* and, to a lesser extent, *Pinus pinea* (especially in the southwest of the region, where it is native), compensate for habitat fragmentation problems with greater abundance. In mountain areas, above 1000 m, the continuity of forest habitats is higher, which may allow for a more effective migration of tree species to higher areas, especially for the more abundant ones, such as *Pinus sylvestris*, *P. pinaster*, or *P. nigra*. *Pinus uncinata* is very scarce and is already planted at a high elevation, with little room for further migration, although it is the only species that would be favoured by climate change in this region. Although a more unfavourable situation for conifers is expected across Europe, many of them are located in mountain areas, which mitigate the rate of habitat change [85]. *Quercus pyrenaica* is common in mid-mountain areas, but its altitudinal shift in this region would involve direct competition with existing pine plantations. Other species, such as *Betula alba*, *Fagus sylvatica*, *Ilex aquifolium*, *Quercus petraea*, *Sorbus aucuparia*, or *Taxus baccata*, although typical of less disturbed mountain areas, have very small and fragmented populations, making their ability to migrate highly uncertain.

The adaptive capacity of tree species has two components, one related to the inherent adaptive capacity of trees and forests, and another connected to socioeconomic factors [86]. The inherent adaptability is determined by genetic, anatomical, physiological, and phenological mechanisms that enable plants to adjust to changing climatic conditions. Evidence suggests genetic adaptation to local climate in most species (79%), more common in conifers (87.5%) than in broadleaf species (67%) [87]; as noted, there is evidence that Spanish *Pinus sylvestris* stands are better adapted to drought than those in other regions [66]. There is evidence of rapid morpho-anatomical adjustments in some plant species as a result of particularly dry years [88]. Among physiological aspects, differences exist, for example, in the capacity of trees to relocate stored water between tissues, which makes them more or

less resistant to droughts [89]. Plant species exhibit phenotypic plasticity in response to changing climatic conditions. Climate change is altering plant phenology, with an especially intense response in the Mediterranean region [90]. These phenological changes may lengthen the vegetative period but can also increase tree desiccation at lower altitudes [91], with variable responses even within the same species depending on their specific location [92]. Moreover, there is a risk of decoupling in plant–animal interactions, particularly with pollinators and herbivores [93]. In addition to these adaptations, trees may also show varying responses to disturbances exacerbated by climate change, such as pests and wildfires. The socioeconomic component determines the ability to implement planned adaptation measures, strongly limited in the Mediterranean region due to less intensive forest management [86].

The varying adaptability of species may alter forest community composition in the future and affect long-term forest succession patterns. Although plants can adapt to changing conditions, it is uncertain whether they can do so sufficiently rapidly to cope with the fast-paced contemporary climate changes [94].

An important aspect to consider in the studied region, as in much of Europe, is the abundance of forest stands originating from conifer reforestations, many with uncertain provenance regions. This may lead to additional adaptation challenges. A notable example in the studied area is the cited widespread use of *Pinus nigra* subsp. *nigra* instead of the native lineage, *P. nigra* subsp. *salzmannii*, which could severely reduce its adaptation capacity. The diversification of forests with a mix of tree species, and especially of monospecific conifer stands, converting them in mixed stands with broadleaf species, would increase their resilience [95,96]. However, if forest management continues to take the potential natural vegetation of the 20th century as a reference, future adaptation may be inadequate [86].

Assuming the difficulties that species will face in adapting spontaneously, especially through migration, due to anthropisation of the environment, human intervention would be required to help mitigate the negative effects of climate change. One proposed solution is assisted migration [81,97], which can be achieved through forestation or through silviculture that allows the progressive displacement of species to more favourable areas. These actions need to take into account the identified risks of invasiveness and maladaptation [97]. Other forest management measures proposed to achieve adaptation to climate change include changes in the tree species composition, rotation period, and stand density [98]. The application of assisted adaptation measures in forest stands can ensure forest persistence, except in areas with particularly adverse climates. Nevertheless, they do not guarantee the persistence of specific forest types, as their future composition may change significantly [99].

5. Conclusions

Currently, the proportion of forest stands at risk in the studied region is still low, although nearly half are vulnerable. In the worst scenario for 2100 (RCP8.5), over one-third of forest stands could be at risk, with the vast majority classified as vulnerable. The most likely scenario for 2100 falls in between, with 17% of stands at risk and two-thirds considered vulnerable. There is a clear correlation between altitude and risk, with higher altitudes reducing the level of risk.

Some species already face a significant threat from climate change, which is expected to increase considerably in the future. This threat is especially high for species that require high *NPP*, and for those that grow in a narrow range of *NPP*, as future variations may push them out of their optimal range.

Only four species currently face no threat. Some mountain species may experience little change as they are in a zone of equilibrium; at lower altitudes, *NPP* would decrease due to climate change, while, at higher altitudes, it would increase. Species living at higher altitudes could benefit, but they represent a very small proportion compared to the vast forested areas that will face negative impacts.

To adapt to new conditions, tree species would need to migrate to higher altitudes, thus compensating for the effects of climate change. However, despite the existence of large areas of climatically suitable habitats, their ability to adapt is limited by habitat fragmentation, the dispersal of forest stands, and human activity, especially in lowland areas, which are more degraded and subject to greater human presence. Mountain species benefit from habitat continuity, but even they face constraints in their upward shifts due to competition and small population sizes. Additionally, species growing at high elevations, in the limits of their altitudinal range, will not be able to migrate anywhere. One adaptation option is assisted migration, although it carries certain risks. It may be preferable to accept that future forest stands will differ from those of today and begin managing them accordingly.

Succession processes can be lengthy, spanning several hundred years. Nevertheless, extreme events such as droughts and heat waves may accelerate tree mortality and replacement, particularly in the Mediterranean. However, there is a serious risk of ecosystems shifting irreversibly towards arid states.

Trees and forests face a significant adaptive challenge due to climate change, further exacerbated by ongoing environmental anthropisation and intense human intervention in many forests. Effective forest management is crucial to support this adaptation. However, its success depends on a solid research foundation that must continue to explore and deepen understanding of this topic.

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Abbreviations

The following abbreviations are used in this manuscript:

<i>AE</i>	Actual evapotranspiration
GHG	Greenhouse gas
GIS	Geographic Information System
<i>LiDAR</i>	Light Detection and Ranging
<i>NPP</i>	Net potential productivity
Q1/Q3	First quartile, third quartile
RCP	Representative concentration pathway
RF	Radiative forcing

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