Forests dynamics in the montane–alpine boundary: a comparative study using satellite imagery and climate data

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ABSTRACT: Over the past decades, the altitudinal and latitudinal advance of forest lines has increased due to global warming and the abandonment of less productive areas previously subject to agricultural activities. The intensity and speed of the forest line advance also depend on numerous physical, biological and human factors that are region-specific. It is important to fully understand the mechanisms behind forest line behaviour, as existing studies do not report global figures. We selected 4 study areas in which to analyse the temporal and spatial behaviour of the forest line and of forest cover based on selection criteria such as minimal human interference and maximal representativeness at the European level. The sites were located in national parks that were evenly spread across some of the dominant European mountain ranges such as the Pyrenees, Alps and Carpathians, at comparable altitudes and latitudes, and with similar land cover proportions in the year 1970. Methodologically, we used cloud-free Landsat satellite images that were acquired in the same month during the growing season. A post-classification comparison technique, using all bands but the thermal one, was implemented to evaluate forest line behaviour, while the accuracy of image classification was evaluated by random sampling. Four time frames were used to evaluate forest cover behaviour in relation to the non-forested areas: 1971−1980, 1981−1990, 1991−2000 and 2001−2014. Also, climate and topography data were included in this study, which enabled comparison and computation of dependence relations. Our results indicate significant differences between the analysed areas. For instance, for the same reference period (1981−1990), the greatest differences in terms of forest cover change were specific to the Austrian Alps (28%), whereas the lowest differences were those from the Spanish Pyrenees (1%). Similar forest line shifts were found in the Austrian Alps and in the Romanian Carpathians, whereas the lowest altitudinal advancement was specific to the Spanish Pyrenees. According to this study, the temperature trend could have significantly influenced tree line behaviour.

KEY WORDS: Remote sensing · Tree lines · Mountains · National park

1. INTRODUCTION

Forested areas are increasing in many developed countries due to the combined effects of more intensive agriculture, abandonment of less productive areas and increasing awareness regarding the environmental importance of forests (Müller et al. 2009, Kozak 2010, Lambin & Meyfroidt 2010, Baumann et

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Klinge et al. 2015) combined Landsat image classification and spatial modeling to understand the distribution patterns. Both studies used multi-temporal image analysis. Dynamics of mountain tree lines and forest lines vary across the globe. Previous studies reveal an average northward advance of 156 and 71 m for birch and pine forest lines in Norway during the 20th century, respectively (Hofgaard et al. 2013). Shifts in tree lines were more pronounced in birch (340 m yr\(^{-1}\)), whereas pine advance was very limited (10 m yr\(^{-1}\)). In Russia's Khibiny Mountains, the mean tree line advance of birch and pine was 29 and 27 m in altitude (0.6 and 0.5 m yr\(^{-1}\)), respectively, between 1958 and 2008 (Mathisen et al. 2014). In the Italian Alps, tree lines shifted upwards by 115 m between 1901 and 2000 (Leonelli et al. 2011). Overall, analysis of historical and recent forest delineation data shows a very restricted advance rate compared to the predictions of dynamic global vegetation models (ACIA 2005, Kaplan & New 2006).

Complex interactions between factors affects the patterns of mountain tree lines (e.g. exposure to wind, snow depth, animals, mass outbreak of insects) and forest lines. Tree line responses to climate change are dependent on a multitude of interacting abiotic and biotic drivers in a site-specific manner (Holtmeier & Broll 2005, Holtmeier 2009, Hofgaard et al. 2012), with characteristics determined by multiple variables (Holtmeier & Broll 2007, Hofgaard et al. 2012), dominated by temperature, precipitation, wind and herbivory (Sveinbjörnsson et al. 2002, Cairns & Moen 2004, Holtmeier & Broll 2005). A change in the regeneration capacity in the tree line ecotone has caused its main features, forest line, tree line and species line (limit of tree saplings and seedlings) to move back and forth over time in accordance with long- and short-term climate changes.

Ameztegui et al. (2015) parameterised and used an individual based, spatially explicit model of forest dynamics (SORTIE-ND) to investigate the role of species-specific differences in juvenile performance induced by climate change (juvenile growth and recruitment ability) in the dynamics of mixed forests located in the montane–subalpine ecotone of the Pyrenees. Batllori & Gutiérrez (2008) found that past and recent synchronous recruitment trends (mid-19th century, second half of the 20th century) were apparent at the tree line over the studied area of the Pyrenean range. Altitudinal treeline ecotone, growth and establishment has been occurring since the 1950s in the context of climatic warming and substantial land-use abandonment; both gradual and step-like transition patterns in tree age and size along the ecotone have been observed. Gehring-Fasel et al. (2007) found a significant increase in forest cover between altitudes of 1650 and 2450 m in the Swiss Alps. Above 1650 m, 10% of the new forest areas were identified as true upward shifts, whereas 90% represented in-growth, and both land use and climate change were identified as likely drivers. Most upward shift activities occurred within a band of 300 m below the potential regional tree line, indicating land use as the most likely driver. Only 4% of the upward shifts were identified to rise above the potential regional tree line, thus indicating climate change. In this context, the present study aimed to (1) quantify forest dynamics in the montane–alpine belts over the past 40 yr, using 4 protected European representatives of mountain forest ecosystems; (2) investigate whether there were significant changes in forest line and forest cover; and (3) understand the relationship between these forest changes and climate modification over the past 40 to 50 yr. For this purpose, multi-temporal analysis with Landsat satellite data was performed. Regression models between forest line and cover, using baseline climate data from 1901 to 1970, were established.

2. MATERIALS AND METHODS

2.1. Study areas

The boundaries between the montane and alpine belts in 4 European mountain areas (Fig. 1) were considered for analysis. The areas shared homogeneous minimum human influence and protected status (in the core areas of national parks), and were located in the Austrian Alps, Slovak and Romanian Carpathians, and Spanish Pyrenees at similar altitudes and comparable un-forested surfaces in 1970 (pastures, alpine hollows, etc.): 19.945 ha (Ordesa, Spain), 18.945 ha (Nockberge, Austria), 10.436 ha (Tatra, Slovakia) and 15.175 ha (Rezat, Romania). The latitudinal range of the selected areas was 4° (between 43 and 47° N), while the general aspect (orientation) was eastern–western.

The Ordesa and Monte Perdido National Park, located in the central Pyrenees (Spain), covers 15 608 ha and was established in 1918. Altitude ranges between 700 and 3355 m above sea level, and Monte Perdido is Europe’s highest calcareous peak. Average annual rainfall is 1688 mm, and average maximum and minimum temperatures are 8.7 and 1.5°C, respectively (Góriz Refuge Meteorological Station at 2200 m between 1992 and 2012, both included). Natural vegetation is dominated by coniferous forest Pinus sylvestris, beech Fagus sylvatica and several oak species at lower altitudes. At higher altitudes, P. uncinata forests have been replaced by Buxus sempervirens, Echinospartum horridum and Juniperus communis shrublands, followed by alpine grasslands. At altitudes below 2100 m, grasslands were created by humans to obtain pastures for livestock during summer. Since the Middle Ages, the Pyrenees forest line has been artificially lowered to increase grassland availability for livestock summer pastures (Monserrat-Martí 1992). But since 1930, a marked reduction in agro-pastoral activities in mountain areas has taken place (Alados et al. 2014, Gartzia et al. 2016b), which has also affected the Ordesa and Monte Perdido National Park, where the grazing activity was maintained as part of the conservation programme (Gartzia et al. 2016a). Consequently, we are facing important changes in the land cover in the national park, mainly below the 2100 m, where approximately 30% of shrubland has turned to forest and 12% of grasslands have become shrubland. Above 2100 m, the woody encroachment of grasslands is low (Gartzia et al. 2014).

The Nockberge Biosphere Park (Austria) was established initially as national park in 1987. It covers 18 300 ha and is among the oldest and most interesting upland formations in Europe. Altitude ranges between 600 and 2441 m, with the highest peak at Mt. Eisenhut in Styria (2441 m). The climate is continental dry, due to its central location in the European land mass. Average annual rainfall and temperature are 1100 mm and 7°C, respectively. The region boasts the Eastern Alps’ largest pine P. sylvestris, larch Larix decidua and spruce Picea abies forests. Wind throw is
the main factor that influences tree lines and their advance.

The Low Tatra National Park (Slovakia) was created in 1978 and covers 72,842 ha. The first attempt to create this national park was between 1918 and 1921. Altitude ranges between 700 and 2043 m, with the highest peak at Dumbier (2043 m). The mountains are characterised by continental mountain climate on the slopes and a slightly cold climate at the foothills. Average annual temperature is 4°C and average annual precipitation 1200 mm. Dwarfed pines *P. mugo*, mountain ashes *Sorbus aucuparia* and small pines *P. sylvestris* occupy the park’s highest areas. The constant interaction between natural forces and human effects (mainly destructive activities) has significantly influenced the tree line of the Tatra Mountains, (as well as of other important mountains regions of Slovakia). As a general rule,
tree lines in Slovakian mountains are not situated at their natural elevation. For example, nowadays, the tree line is situated on average at altitudes of 1185 to 1430 m. Furthermore, strong winds affected the forest stands near the tree line from the Tatra Mountains in 2004, which was followed by a damaging fire.

The Retezat National Park (Romania) was created in 1935. With an area of 38 138 ha, it shelters one of Europe’s last remaining intact old-growth forests and the continent’s largest single area of pristine mixed forest. Altitude ranges between 600 and 2509 m, with the highest peak at Peleaga (2509 m). Average annual temperature is 6°C and average annual precipitation is 1400 mm. The main tree line species are Norway spruce \textit{P. abies}, mountain pine \textit{P. mugo} and alpine stone pine \textit{Pinus cembra}. Wind throw is the main factor that influences tree lines and their advance.

2.2. Forest line and forest cover quantification using satellite imagery data

The tree line was defined in this study as the pixels classified as forest (according to the FAO definition) near the non-forest pixels located in the upper area of the massif. Assessing the expansion of forest line over time is a typical problem of change detection, and many approaches can be found in the literature (Singh 1989, Almutairi & Warner 2010, Canty 2010, Hecheltjen et al. 2014), each with specific advantages and disadvantages.

Change detection methods can be grouped into 6 categories (Lu et al. 2004): algebra (which includes image differencing, vegetation indexes, change vector analysis); transformation (e.g. principal component analysis); classification; advanced models (where image reflectance values are often converted to physically based parameters); GIS approaches; and visual analysis. Generally, it is not possible to establish \textit{a priori} which method of change detection is the most convenient, so the choice is often made on a pragmatic and application-driven basis (Coppin et al. 2004).

2.2.2. Image processing

\textit{Atmospheric correction}. Images acquired on different dates are affected to some extent by the presence of haze and dust in the atmosphere, a fact that could mask real changes in a given territory. In order to reduce this effect, images were corrected atmospherically using the European Cooperation in Science and Technology (COST) model developed by Chavez (1996), which employs the cosine of the solar zenith angle, representing a good approximation of atmospheric transmittance.

\textit{Topographic correction}. To remove the relief effects, images were normalised using the Shuttle Radar Topographic Mission (SRTM) digital terrain model downloaded from http://earthexplorer.usgs.gov/. SRTM is a key breakthrough in digital mapping and provides a major advance in the accessibility of high-quality elevation data worldwide.
The sun-canopy-sensor (SCS) topographic correction method was used to remove topographic effects. SCS correction (Gu & Gillespie 1998) is based on SCS geometry and it can be expressed as:

\[ L_m = L \frac{\cos \theta \cdot \cos \alpha}{\cos i} \]  

where \( L_m \) is the normalised radiance, \( L \) is the uncorrected radiance, \( \theta \) is the solar zenith angle, \( i \) is the incident angle and \( \alpha \) is the slope of the surface.

All images have been thus co-registered to UTM, WGS84, and the accuracy of image registration was assessed using topographic plans and local cartographic products based on terrestrial measurements and aerial surveys, according to the acquisition period (Fig. 2).

Owing to the different characteristics of spectral sensors (i.e. TM and ETM+) in the Landsat image series, we also corrected the spectral reflectance between images acquired by different sensors (MSS, TM, ETM+ and OLI). The empirical line approach for reflectance factor retrieval from Landsat-5 TM and Landsat-7 ETM+ was used for this purpose (Moran et al. 2001). All operations were performed in ENVI 5.0.

2.2.3. Mapping and change detection in forest line and cover

Temporal and spatial dynamics in forest covers and lines within the montane–alpine elevation belts (>900 m) were measured using post-classification comparison (PCC) change detection with independently classified images. This method compares, pixel by pixel, 2 independent classified images acquired on different dates, using a change detection matrix (Jensen 2004). PCC minimises the influence of sensor variation in the detection of change. Results depend on the accuracy of initial classifications (Coppin & Bauer 1996). The method locates changes and provides ‘from–to’ change information. Here, the source for PCC change detection was land cover data created for each Landsat scene. Land cover classification was performed using a supervised classification with maximum likelihood algorithm supported by forest management data that provided information on the spatial distribution of forest and other additional variables (e.g. stand age, height or diameter). Two land cover classes were considered (forest and pasture), and all bands were used for classification, except the thermal band. The approach included the 3 steps: training site selection, classification and assessment of results (Lillesand et al. 2008).

Reference data for training and validation were collected based on high-resolution satellite images or air photos available in Google Earth that cover the complete study area (Knorn et al. 2009, Baudron et al. 2011). We sampled 200 random training areas and classified those as either forest or non-forest, based on visual interpretation. Areas were considered forested if tree cover exceeded 60% and forest

### Table 1. Summary of satellite data used for multi-temporal mapping of forest dynamics in the mountain study sites. NIR: near-infrared band; SWIR: shortwave infrared band

<table>
<thead>
<tr>
<th>Year</th>
<th>Ordesa</th>
<th>Nockerge</th>
<th>Low Tatra</th>
<th>Retezat</th>
<th>Band-to-band registration accuracy</th>
<th>Geometric accuracy and registration successa</th>
</tr>
</thead>
<tbody>
<tr>
<td>1970</td>
<td>Soviet Topographic Map</td>
<td>Soviet Topographic Map</td>
<td>Soviet Topographic Map</td>
<td>Soviet Topographic Map</td>
<td>–</td>
<td>5 m</td>
</tr>
<tr>
<td>1980</td>
<td>1975-07-26</td>
<td>1979-05-22</td>
<td>1979-09-03</td>
<td>1980-09-21</td>
<td>0.2 pixel</td>
<td>(90%)</td>
</tr>
<tr>
<td>1990</td>
<td>GLS 1975</td>
<td>Landsat 2</td>
<td>Landsat 2</td>
<td>Landsat 3</td>
<td>0.2 pixel</td>
<td>(90%)</td>
</tr>
<tr>
<td>2000</td>
<td>1989-07-17</td>
<td>1988-08-07</td>
<td>1990-07-16</td>
<td>1988-08-29</td>
<td>0.2 pixel</td>
<td>(90%)</td>
</tr>
<tr>
<td>2014</td>
<td>1989-07-17</td>
<td>1988-08-07</td>
<td>1990-07-16</td>
<td>1988-08-29</td>
<td>0.2 pixel</td>
<td>(90%)</td>
</tr>
<tr>
<td>Spatial resolution (m)</td>
<td>30</td>
<td>30</td>
<td>30</td>
<td>30</td>
<td>0.2 pixel</td>
<td>(90%)</td>
</tr>
</tbody>
</table>

NIR: near-infrared band; SWIR: shortwave infrared band

aAccording to Landsat metadata files
patches were larger than 1 Landsat pixel (900 m²) (Kuemmerle et al. 2009).

Classification accuracy was evaluated through a confusion matrix based on a minimum of 100 ground truth sites for each image, other than the training sites, established through a random sampling strategy based on field recommendations (Congalton & Green 2009, Vorovencii 2014). In order to emphasise the changes in land cover classes over the 1970–2014 period, the classified images were compared by cross-tabulation, which resulted in the change matrix that estimates quantitative change (Fig. 3). Using
2.3. Historical climate data

Climate data retrieved from Climate Explorer Utility (http://climexp.knmi.nl) were used to pattern climate conditions across each study area from 1900 to 2014 (we took monthly station data, introducing the coordinates of the national parks, from the 10 nearest meteorological stations to that point). To reconstruct climate condition trends during the analysed tree line period (1970–2014), climate data between 1901 and 1970 were taken as a baseline. Climate conditions were represented by average temperature, precipitation and de Martonne aridity index (de Martonne 1926). However, preliminary correlation analysis showed an insignificant statistical relationship between growth in forest area and the last 2 variables, which led to their exclusion from the analysis. This was expected, as precipitation in forest line ecosystems is not a limiting factor (Leal et al. 2007, Grytnes et al. 2014).

2.4. Statistical analysis

Temperature evolution was analysed using simple graphical trends for the studied regions. The reference mean temperature values calculated as simple arithmetic means of periods covering 10 to 15 yr each were used to plot the trends. A clear growth trend was observed, so further analyses were carried out to estimate the relationship between temperature increase and both forest cover growth and altitudinal forest line migration. The percentage of forested cover growth and the forest line altitudinal migration were plotted versus the relative temperature increment during the studied period. Furthermore, the dependence between the percentage of forest cover growth and forest line altitude migration, with respect to temperature variation in the studied period, were modelled using least-squares simple regression.

3. RESULTS

3.1. Forest line and forest cover dynamics across the montane–alpine boundary

The error matrix obtained for each land cover classification is presented in Table 2. Overall accuracy values reached the minimum average standard of 85% recommended by the USGS classification scheme (Anderson et al. 1976), which indicates a strong link between map classification and ground reference data.

The accuracy values can be grouped (Congalton & Green 1999) into (1) strong link (>0.80; >80%); (2)
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Moderate link (0.40–0.80; 40–80%); and (3) weak link (<0.40; <40%).

All study sites showed changes in forest line and forest cover. Highest and lowest change in elevation of the upper forest limit (altitude growing) occurred in the Alps (Nockberge) and Pyrenees (Ordesa), respectively. Surface forest growth indicated differences between sites. The largest forest expansion was registered in the Alps (28%; Nockberge) and the lowest in the Pyrenees (1%; Ordesa) for the period 1981–1990. The largest forest line advance was recorded in the Alps (Nockberge) and the Carpathians (Retezat), while the lowest was found in the Pyrenees (Ordesa) (Table 3).

Table 2. Summary of forest class accuracies (%) of land cover maps (see Fig. 4) obtained with maximum likelihood supervised classification of Landsat satellite data (years 1980, 1990, 2000 and 2014), along with Kappa statistics. PA: producers’ accuracy; UA: users’ accuracy

<table>
<thead>
<tr>
<th>Year</th>
<th>Ordesa (ES)</th>
<th>Nockberge (AU)</th>
<th>Low Tatra (SK)</th>
<th>Retezat (RO)</th>
</tr>
</thead>
<tbody>
<tr>
<td>PA</td>
<td>UA</td>
<td>PA</td>
<td>UA</td>
<td>PA</td>
</tr>
<tr>
<td>1980</td>
<td>90</td>
<td>85.60</td>
<td>86.64</td>
<td>82.10</td>
</tr>
<tr>
<td>1990</td>
<td>85</td>
<td>78.40</td>
<td>84.70</td>
<td>79.40</td>
</tr>
<tr>
<td>2000</td>
<td>94</td>
<td>89.40</td>
<td>97.50</td>
<td>94.30</td>
</tr>
<tr>
<td>2014</td>
<td>95</td>
<td>91.50</td>
<td>88.12</td>
<td>98.70</td>
</tr>
<tr>
<td>Mean</td>
<td>86.23</td>
<td>88.63</td>
<td>89.25</td>
<td>91.00</td>
</tr>
<tr>
<td>Kappa statistics</td>
<td>0.84</td>
<td>0.87</td>
<td>0.88</td>
<td>0.90</td>
</tr>
</tbody>
</table>

Fig. 4. Spatial and temporal dynamics of forest line and cover in 4 European mountain sites obtained from supervised land cover classification of Landsat satellite data between 1970 and 2015. Dynamics are represented using a 10 yr time-step interval for (a) Ordesa and Monte Perdido National Park, Spain; (b) Nockberge Biopshere Park, Austria; (c) Low Tatra Park, Slovakia; and (d) Retezat National Park, Romania.
Forest expansion also varied across exposure classes and study sites. In the Austrian Alps (Nockberge) and the Romanian Carpathians (Retezat), expansion was strongly skewed to northerly slopes, while in the Slovakian Carpathians (Low Tatra), it occurred mostly on southerly slopes (Table 4).

### Table 3. Summary of changes in forest line and forest cover across the study areas between 1970 and 2014, and average annual temperatures registered during this period

<table>
<thead>
<tr>
<th>Exposition</th>
<th>Nockberge</th>
<th>Retezat</th>
<th>Low Tatra</th>
</tr>
</thead>
<tbody>
<tr>
<td>N</td>
<td>18</td>
<td>14</td>
<td>15</td>
</tr>
<tr>
<td>NE</td>
<td>18</td>
<td>12</td>
<td>12</td>
</tr>
<tr>
<td>E</td>
<td>11</td>
<td>10</td>
<td>7</td>
</tr>
<tr>
<td>SE</td>
<td>6</td>
<td>11</td>
<td>20</td>
</tr>
<tr>
<td>S</td>
<td>5</td>
<td>9</td>
<td>22</td>
</tr>
<tr>
<td>SW</td>
<td>8</td>
<td>11</td>
<td>10</td>
</tr>
<tr>
<td>W</td>
<td>16</td>
<td>14</td>
<td>3</td>
</tr>
<tr>
<td>NW</td>
<td>19</td>
<td>20</td>
<td>9</td>
</tr>
</tbody>
</table>

### Table 4. Spatial distribution of the expansion in forest cover (%) across topographic exposure classes in the study areas

<table>
<thead>
<tr>
<th>Exposition</th>
<th>Nockberge</th>
<th>Retezat</th>
<th>Low Tatra</th>
</tr>
</thead>
<tbody>
<tr>
<td>N</td>
<td>18</td>
<td>14</td>
<td>15</td>
</tr>
<tr>
<td>NE</td>
<td>18</td>
<td>12</td>
<td>12</td>
</tr>
<tr>
<td>E</td>
<td>11</td>
<td>10</td>
<td>7</td>
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<tr>
<td>SE</td>
<td>6</td>
<td>11</td>
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<tr>
<td>S</td>
<td>5</td>
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<td>22</td>
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<td>11</td>
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<tr>
<td>W</td>
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<td>14</td>
<td>3</td>
</tr>
<tr>
<td>NW</td>
<td>19</td>
<td>20</td>
<td>9</td>
</tr>
</tbody>
</table>

Historical climate data evidence an increase in average annual temperature between 1950 and 2014 across all sites. Overall, the average increase was 1.1°C, with the Carpathian sites showing both the highest (Low Tatra; +1.4°C) and the lowest (Retezat; +0.89°C) increases (Fig. 5). In 3 of the studied areas, mean temperatures of the past 50 yr showed a continuously growing trend (Table 3, Fig. 5). Regression models showed strong linear relationships between forest cover increment and altitudinal migration of forest line across all sites with respect to mean annual temperature rise (Fig. 5). The increment of dependent variables had a lower magnitude in the Romanian Carpathians (Retezat), significantly contrasting with the magnitude in the Alps (Nockberge), which was the highest. Fig. 5 illustrates the magnitude of the dependencies between dependent and independent variables.

### 3.2. Relationship between average annual temperature and forest line and cover dynamics

In this study, we combined multi-temporal satellite image analysis and observed the impacts of climate on forest cover and forest line dynamics in the montane–alpine...
boundary across European mountains between 1970 and 2014. Four protected areas, distributed along a west–east longitudinal gradient and enclosed in 3 emblematic European mountain ranges (Pyrenees, Alps and Carpathians), were considered. These areas were located in national parks that were created before the oldest satellite images considered for analysis. Therefore, human influence (cattle grazing, tree cutting, etc.) in the period of analysis was minimised, and changes in forest cover and line were mostly driven by natural processes. The influence of natural disruptive factors (windfalls, fires, insect attacks, etc.) was not accounted for in this study. The accuracy values of imagery classification were predominantly above the average standard (85%) suggested by the USGS classification scheme (Anderson et al. 1976) and in line with previous studies using Landsat data in mountain regions (Kharuk et al. 2010, Hagedorn et al. 2014). Lower accuracy values in some scenes, which can slightly influence the estimations, are related to common factors influencing multi-temporal satellite studies in mountain areas (e.g. spatial resolution, atmospheric anomalies and cloud cover), including in tree line studies (Wang et al. 2006).

Forest change analysis revealed a considerable expansion in forest cover and altitudinal migration of forest lines in the montane–alpine boundary across all sites, particularly in the central eastern mountains. The expansion of forest cover and increase in altitude of the upper forest line are 2 common patterns in Northern Hemisphere mountains in the past decades (Boll et al. 2006, Gehring-Fasel et al. 2007, Harsch et al. 2009, Schickhoff et al. 2015). Both forest cover and forest line were below their potential ranges (Gehring-Fasel et al. 2007), especially in mountains where humans have social and economic interests (Motta et al. 2006), as in the case of our study sites. The combination of atmospheric warming and decreased human activities at high altitudes promoted forest cover expansion and forest line shifts (Motta et al. 2006, Gehring-Fasel et al. 2007, Leonelli et al. 2011). Our patterns of upward shifts of the forest line were not uniform and varied across sites (Harsch et al. 2009). Registered upward shifts of forest lines were below (Low Tatra), in line with (Retezat) or above (Nockberg) the 70 to 100 m belt previously proposed (Moiseev et al. 2010). Forest cover expansion also differed among sites and topographic exposure. While the western forest (Pyrenees) was slightly altered, central and eastern sites showed a considerable forest cover expansion of up to 28%. Dynamics in the forests of central and eastern Europe have been widely discussed in the past few years (e.g. Gherig-Fasel et al. 2007, Hartl-Meier et al. 2014, Pretzsch et al. 2014, Munteanu et al. 2016).

The anthropogenic effect on forest expansion is reinforced by asymmetric historical distributions of the largest expansion periods across the study areas. While in the Romanian Carpathians (Retezat), large expansion occurred until the 1980s, in the Austrian Alps (Nockberg) and the Slovak Carpathians (Low Tatra), the high expansion periods were registered in and after the 1990s. Moreover, large tree line upward shifts occurred in the early 1980s. This asymmetry within study sites under the same trend (increasing average temperatures during the last century) suggests that average temperature is not the only factor impacting forest and forest line expansion. Indeed, anthropogenic activity determines European mountain tree lines (Dirnböck et al. 2003, Kuehmer et al. 2008).

Several alpine tree line studies document altitudinal shifts and tree density increase during the 20th century (Kullman 1979, MacDonald et al. 1998), although only 51% out of 166 sites reviewed by Harsch et al. (2009) showed tree line advance. The main factors responsible for those changes were climate warming and land-use modification. In the Pyrenees, increases in temperatures between 1882 and 1970 were observed at the Pic du Midi meteorological station (Bücher & Dessens 1991). In parallel, grazing pressure has been declining drastically since the 1950s (Alados et al. 2014). In spite of these changes, we did not observe the expected tree line upward shift. Previous studies (Camarero & Gutiérrez 2004, Camarero et al. 2015) also show that the tree line remained static in the central Pyrenees, while tree density increased within the ecotone.

A careful reading of the overall effects of mean temperature increase on forest expansion (1.31°C; 1970–2014) is therefore required (Körner 1998), as alpine vegetation can tolerate temperature increases only between 1 and 2°C without major changes (Theurillat & Guisan 2001), and the response of the tree line to observed climate warming is still globally inconsistent (Harsch et al. 2009, Schickhoff et al. 2015). Nonetheless, a strong statistical relationship between tree line expansion and annual increased average temperatures was found, with sites experiencing increased temperatures showing a large advance in tree line. The temperature trend is consistent with the general constant increasing trend in average temperatures across European mountain ranges (Kullman 2007, Leonelli et al. 2011, González de Andrés et al. 2015). The impacts
of temperature on tree lines are well known (Körner 1998), but the significant responses are mostly related to early or late growing seasons (Rammig et al. 2010, González de Andrés et al. 2015) or even winter temperatures (Kullman 2007). Our findings suggest that increasing annual average temperatures favour the expansion of tree cover and line in the Austrian Alps, Low Tatra and the Romanian Carpathians. Annual average temperatures may influence tree cover and line due (to a lesser effect) to factors affecting plant growth (e.g. wind, snow cover), improvement of microsite conditions (Leonelli et al. 2011, Pardo et al. 2013) and the favouring of seed viability and seedling emergence at higher temperatures (Kullman 2007).

In conclusion, rising mean annual temperatures in mountainous European areas have influenced tree line advance, especially in areas with reduced human intervention (national parks). This mechanism was stronger in the mountainous areas located in central Europe (Alps, Carpathians) and weaker in the warmer European areas (Pyrenees). However, uncertainty in the definition of line position suggests that interpretations should be carried out carefully. The accuracy with which the location of forest lines can be measured in historical data is influenced by the georeferencing accuracy of the data sources and the accuracy of the mapping technique in the definition of line position (Hofgaard et al. 2013). Our data include estimated uncertainties of 0.2 pixels band-to-band, which indicate a relative misregistration of less than 1/3 pixel in the position of forest lines due to misregistration of Landsat imagery. In addition, uncertainty due to misclassification of forest class has also occurred. Mean uncertainty due to misclassification amounted to 11.2%, with the Pyrenees (Ordesa) presenting the higher values. Interpretation in sites with limited change in forest line (e.g. Ordesa) and high uncertainty therefore requires caution.

Overall, open access to historical forest maps and multispectral satellite imagery archives combined with accurate pre-processing and classification is well suited to multi-site comparative analysis on forest line and forest cover dynamics. Comparative analysis of forest lines in protected areas can be a good strategy to better understand the response of natural systems to changes in climate conditions. The consideration of novel variables can further enhance the benefits of understanding mountain forest lines.

Acknowledgements. This article is based on work from COST Action ES1203 SensFor, supported by COST (European Cooperation in Science and Technology, www.cost.eu).

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Editorial responsibility: Nils Chr. Stenseth, Oslo, Norway

Submitted: April 8, 2016; Accepted: December 27, 2016

Proofs received from author(s): April 4, 2017