



Drivers of treeline shift in different European mountains

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ABSTRACT: A growing body of evidence suggests that processes of upward treeline expansion and shifts in vegetation zones may occur in response to climate change. However, such shifts can be limited by a variety of non-climatic factors, such as nutrient availability, soil conditions, landscape fragmentation and some species-specific traits. Many changes in species distributions have been observed, although no evidence of complete community replacement has been registered yet. Climatic signals are often confounded with the effects of human activity, for example, forest encroachment at the treeline owing to the coupled effect of climate change and highland pasture abandonment. Data on the treeline ecotone, barriers to the expected treeline or dominant tree species shifts due to climate and land use change, and their possible impacts on biodiversity in 11 mountain areas of interest, from Italy to Norway and from Spain to Bulgaria, are reported. We investigated the role of environmental conditions on treeline ecotone features with a focus on treeline shift. The results showed that treeline altitude and the altitudinal width of the treeline ecotone, as well as the significance of climatic and soil parameters as barriers against tree species shift, significantly decreased with increasing latitude. However, the largest part of the commonly observed variability in mountain vegetation near the treeline in Europe seems to be caused by geomorphological, geological, pedological and microclimatic variability in combination with different land use history and present socio-economic relations.

KEY WORDS: Vegetation zone shift · Climate change · Climate models · Treeline ecotone · European mountains · Ecosystem services

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1. INTRODUCTION

Mountain regions are crucial areas for studying the impact of climate change on vegetation communities; steep climatic gradients enable testing of ecological, ecophysiological and evolutionary responses of flora to changing geophysical influences related to climate change. In addition, most of the species living there grow in conditions classified as their ecological limits (Körner 2012). Vegetation in European mountainous regions has been subjected to severe changes during the remote (e.g. Kullman 1988) and recent pasts (e.g. Vrška et al. 2009, Boncina 2011, Bodin et al. 2013, Elkin et al. 2013, Schwörer et al. 2014). Changes in species distribution and plant community composition have been the most often observed, although evidence of complete community exchange has not yet been registered.

A strong elevational zonation is typical of montane vegetation, caused mainly by steep climatic gradients. Vegetation zones are characterized by a specific structural-functional type of phytocoenosis constructed by particular main plant species (edificators) and roughly following latitude (latitudinal vegetation zones) or altitude (altitudinal vegetation zones or vegetation belts). Climatic zones along altitudinal gradients are compressed, with large habitat and species diversity in successive altitude vegetation zones. In these steep gradients, species richness decreases with increasing altitude, although topographic isolation results in increased levels of endemism (Pedrotti 2013).

The most obvious vegetation boundary at high elevations is that of the upper forest limit (Harsch & Bader 2011). Owing to its diffuse character, it might be better to refer to the treeline ecotone, which consists of the belt between the boundary of the closed forest stand–timberline and the uppermost or northernmost scattered and stunted individuals of the forest-forming tree species regardless of their growth form and height (Holtmeier & Broll 2005). Within this ecotone, the treeline (i.e. the line connecting the tallest patches of forest composed of trees of ≥ 3 m height) is often delimited; at this elevation, the mean temperatures for the growing season are ca. 6.4°C (Körner 2012). Climate is one of the most important limiting factors defining the spatial distribution of any species (Pearson & Dawson 2003, Wieser et al. 2014). Temperature, especially summer mean temperature and temperature sums, is the primary factor causing the formation of treelines at the global scale (Grace et al. 2002, Moen et al. 2004), although it may be substantially affected by several

other non-climatic factors, e.g. mass elevation effect (Ellenberg 1988), past land use or forest management (Gehrig-Fasel et al. 2007). The main factors affecting the expansion and/or retreat of tree stands at their upper limits are scale-dependent (Holtmeier 2009). At the global scale, treeline position is determined by growing-season temperatures (Körner & Paulsen 2004), whereas at the landscape scale, second-order factors (i.e. climatic stress caused by wind or precipitation, natural disturbances and geomorphological factors), in addition to temperature, significantly affect treeline elevation and dynamics (Holtmeier & Broll 2005, Hagedorn et al. 2014, Treml & Chuman 2015). A recent review on the causes producing the upper limits of tree occurrence, introduced 6 current concepts: climatic stress (e.g. frost damage, winter desiccation), disturbances (e.g. wind, ice blasting, avalanches), insufficient carbon supply, limitation to cell growth and tissue formation, nutritional limitation and limited regeneration (Wieser & Tausz 2007). Air temperature, as the strongest factor, influences the treeline in 2 different ways: temperatures during the warm part of the year are the main control of treeline elevation while temperatures during the cold part of the year can damage the living tissue of the trees (evergreen or deciduous species) (Jobbágy & Jackson 2000). Climate change is likely to trigger latitudinal and elevational vegetation zone shifts, mainly by altering species mortality and recruitment, by exceeding physiological thresholds and changing natural disturbance regimes (Gonzalez et al. 2010).

Vegetation shifts need to be considered as an inherent adaptation mechanism allowing populations to track climatically suitable sites. Such shifts, however, can be limited by a variety of non-climatic factors, such as nutrient availability, soil conditions, landscape fragmentation or species-specific traits, including dispersal capacity, competition with ground vegetation, presence of mycorrhizal fungal symbionts or increasing virulence of pests and pathogens (Camarero et al. 2015b). In particular, species geographic ranges are expected to shift depending on their habitat preferences and their ability to adapt to new conditions. A growing body of evidence suggests that processes of treeline upward expansion, drought-induced retraction of species distributions and shifts of some dominant tree species may occur in response to global climate change (Kullman 1999, Kittel et al. 2000, Hansen et al. 2001, Payette et al. 2001, Theurillat & Guisan 2001). Using a meta-analysis, treeline advance was recorded in 52% of 166 sites around the world (Harsch et al. 2009). On the other hand, there is

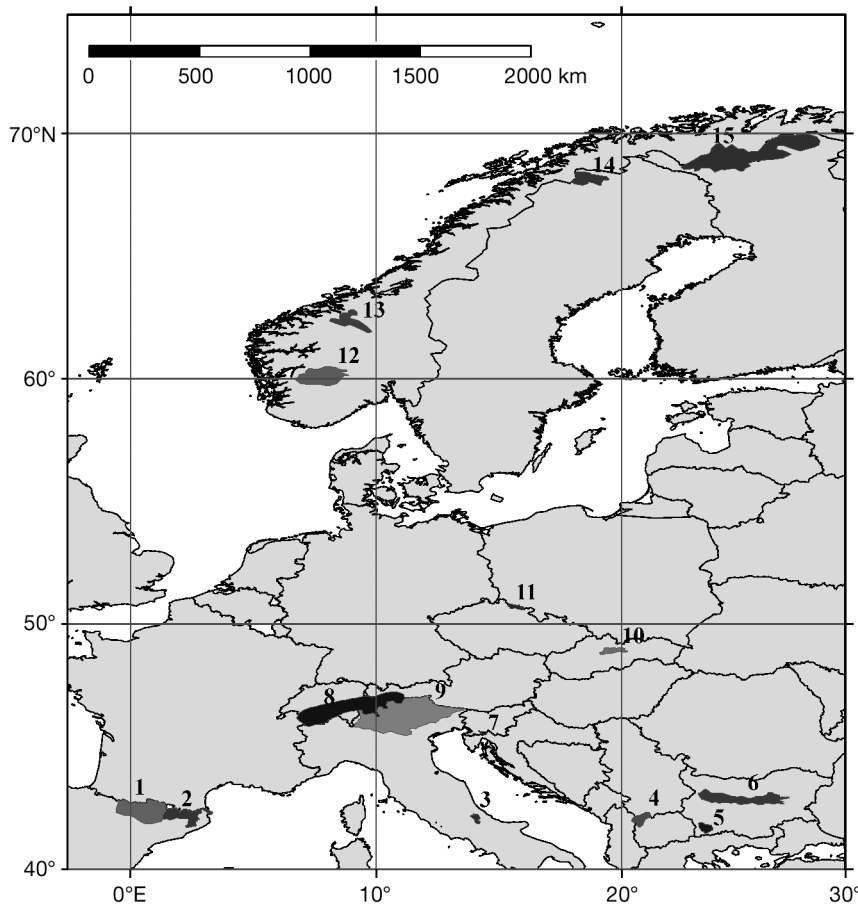


Fig. 1. Selected European mountains. Grey shading differentiates mountain areas. 1 Central Pyrenees (CP), 2 Eastern Pyrenees (EP), 3 Apennines (AP), 4 Shara Mts. (SH), 5 Pirin (PI), 6 Central Balkan Mts. (CB), 7 Northern Dinaric Mts. (DI), 8 Central Alps (CA), 9 Eastern Alps (EA), 10 Low Tatra Mts. (LT), 11 Giant Mts. (GM), 12 Hardangervidda (HG), 13 Dovre (DO), 14 Northern Swedish Lapland (NS), 15 Inner Finnmark/northernmost Finnish Lapland (FL)

evidence that treelines have always been dynamic and influenced by climate change and forest development cycles in the past (Kullman 1988, 2007, Gehrig-Fasel et al. 2007, Vladovi et al. 2014, Treml & Chuman 2015).

There are 3 main aspects of environmental change to which trees are likely to respond: increasing temperature, rising concentrations of CO_2 and increasing deposition of nitrogen (Grace et al. 2002, Lindner et al. 2014). The trees at the treeline accumulate carbohydrates, because autotrophic respiration is more limited by low temperature than photosynthesis. This means that factors such as temperature and nitrogen abundance, both of which affect the capacity of a tree to use the products of photosynthesis, will probably be more important than factors directly affecting photosynthesis, such as elevated CO_2 (Fajardo et al. 2012).

However, climate signals can be confounded with the effects of human activity. Stronger treeline dynamics due to a coupled effect of climate change and highland pasture abandonment frequently occur in European mountain ranges (Ellenberg 1988). Other human-related influential factors, such as (overly) intensive forest management, pasture and grazing, may be regionally important as well. Direct human-related factors may be crucial in changing the species composition and structure of mountain forests, especially in treeline ecotones where climate change does not represent the key factor (Alados et al. 2014).

The aims of this study were to evaluate the effects of geographical position and different regional climatic and other site conditions on treeline ecotone characteristics of selected European mountain areas, to identify the natural and anthropogenic drivers of treeline shift. We further discuss the effects of climate and land use changes on biodiversity in forests below the treeline.

2. METHODS

To demonstrate and discuss the possibilities and limits of treeline species shift, including latitudinal and longitudinal heterogeneity, the current situation in 11 mountain areas from Italy to Norway and from Spain to Bulgaria were analysed (Fig. 1). To determine the influence of mountain massif size on the mesoclimatic and vegetation conditions, including treeline formation, we included large mountain complexes (Pyrenees, Alps, Scandes) as well as relatively small, separated mountains (Pirin and Giant Mountains) in this study. The characteristics of the treeline ecotone, including historical and recent human impacts on mountain ecosystems for the 11 mountain areas of interest, are summarized in Table 1. Extensive mountain massifs (Pyrenees, Alps, Scandes) were further divided into more homogeneous units (Central Pyrenees, Eastern Pyrenees, Central Alps, Eastern Alps, Hardangervidda, Dovre, Northern Swedish Lapland, Inner Finnmark/northernmost Finnish Lapland). To esti-

Table 1. Timberline and treeline parameters and characteristics of human activities, changes according to climatic models and limits to climate change induced species shifts in selected European mountains. A1B, A2: emissions scenarios (IPPC); A.a.: *Abies alba*; A.p.: *Acer pseudoplatanus*; F.s.: *Fagus sylvatica*; L.d.: *Larix decidua*; P.a.: *Picea abies*; P.c.: *Pinus cembra*; P.h.: *Pinus heldreichii*; P.m.: *Pinus mugo*; P.p.: *Pinus peuce*; P.s.: *Pinus sylvestris*; P.u.: *Pinus uncinata*; T: timberline; Tr: treeline; TSL: tree species limit; VZ: vegetation zone; C: century; mng: management. Elevation range of T and Tr: mean (min–max)

Country; part of mountains	Coordi- nates of central site	Elevation range of T (m a.s.l.)	Elevation range of Tr (m a.s.l.)	Range of tree species limit (m a.s.l.)	Annual altitudinal shift of T or Tr (m yr ⁻¹)	Area of study (km ²)	VZs near Tr (m a.s.l.)
Spain; Spanish Pyrenees	42°37'N; 0°27'E	1930 (1800–2050)	No data	P.u. 2700	0.49 (T; 1956–2006)	15 800	Pine with A.a., P.s. and F.s. (1400–2050); subalpine with P.u. (1800–2300)
Italy; Majella Massif, part of Apennines	42°05'N; 14°05'E	1800 (1700–1850)	No data	F.s. 2100, P.m. 2300	1 (Tr [P.m.]; 1954–2007)	741	Beech forest (800–1850); mixed beech–dwarf pine (1800–2000); dwarf pine (2100–2300)
Macedonia; Shara Mountain (Balkan Peninsula)	41°47'N; 20°33'E	1850 (1800–1900)	1900 (1850–1950)	P.a. 2100, P.p. 2200	~1 (T;) 1934–2010	829	Mixed fir–beech– spruce (800–1900); beech (1600–1900); dwarf pine (1600–2200)
Bulgaria; Pirin	41°42'N; 23°31'E	1900 (1800–2100)	2100 (1900–2300)	P.p. 2500	No data	384	Beech (1000–1500); coniferous forest (P.s., P.p., P.h., P.a., 1300–2300); dwarf pine (2000–2500)
Bulgaria; Central Balkan Mts.	42°47'N 24°36'E	Beech T 1600 (1500–1700)	1600 (1500–1850)	F.s. 1700, P.a., A.a. 1850	No data	717	Beech (800–1700); coniferous (P.a., A.a., 1500–1850); juniper (1500–1850)
Slovenia; Northern Dinaric Mts.	45°36'N; 14°28'E	1540 (1455–1600)	1600 (1550–1650)	F.s. 1650, P.a. 1700, A.a. 1650	No data	~200	Mixed fir–beech–spruce (600–1400); beech (1300–1550); dwarf pine with small groups or individual trees of F.s., P.a., A.a., A.p. (1500–1700)
Switzer- land, Italy; Central and Eastern Alps	46°46'N; 9°52'E; 46°17'N; 11°45'E	1900 (1700–2150)	2100 (1850–2300)	P.a. 2400, L.d. 2450	ca.1.3 (T; 1954–present)	~250 + ~750	Spruce with L.d. (1000–1900); forest with P.c., L.d. and P.a. (1700–2200); dwarf shrub vegetation, partly pastures (2200–2500)

Human influence in VZs in past and recently	Annual temperature (<i>T</i>) and precipitation (<i>P</i>) differences between 1961–1990 and 2021–2050; mean of CORDEX models	Limits to climate change induced species shift	References
Since 11th C: clear-cutting and grazing, moderate on irregular slopes and ridges; since 1930: significant release of influence but recovery mainly at moderate elevations	HIRHAM5 model: period $\Delta T_{2021-2050} = 1.5-2^{\circ}\text{C}$; $\Delta T_{2051-2080} = 4^{\circ}\text{C}$; $\Delta P_{2021-2050} = +5\%$; $\Delta P_{2051-2080} = +30\%$ compared to 1960–1990	Inadequacy of substrata (rocky); climatic constraints (including growing-season extreme events, such as late-spring freezing, summer drought, etc.)	Batllori et al. (2009), Alados et al. (2014), Gartzia et al. (2014), Camarero et al. (2015a)
Since 1000 BC: cutting, burning and grazing mng; since the mid-20th C: grazing intensity decreased; now occasionally managed and regeneration of P.m.	HadCM3_A2, period 2020–2080: $\Delta T_{\text{min-Jan2050}} = 1.7^{\circ}\text{C}$; $\Delta T_{\text{min-Jan2080}} = 3.1^{\circ}\text{C}$; $\Delta P_{2050} = -7\%$; $\Delta P_{2080} = -23\%$	Low density of F.s. in T, dispersal distances of F.s. seeds upslope; poor soils; excessive exposure to solar radiation in open areas	van Gils et al. (2008), Palombo et al. (2013, 2014)
Since 14th C: clear-cutting and grazing to enlarge alpine pastures and to produce charcoal; since 1970: abandonment of traditional agricultural practices	Mean of 4 GCMs (CSIRO/Mk2, HadCM3, ECHAM4/OPYC3, NCAR – PCM); $\Delta T_{2050} = 2.6^{\circ}\text{C}$; $\Delta T_{2100} = 5.3^{\circ}\text{C}$; $\Delta P_{2050} = -3\%$; $\Delta P_{2100} = -8\%$	Differences in soil types between subalpine beech and mixed forest (poor calcareous soils or rankers on silicate bedrock); cliffs and rocks; cattle grazing	Em (1986), Strid et al. (2003), Bergant (2006) Amidžić et al. (2012)
Since 680 AD: intensive fires, deforestation and grazing; since 1962: traditional mng has changed; last decades tourism impact has increased	HADCM3_A2, CGGM2, $\Delta T_{2050} = 1.7^{\circ}\text{C}$, $\Delta T_{2080} = 2.8^{\circ}\text{C}$; $\Delta P_{2080} = -15\%$	Rocky sites; extreme hydrothermal conditions; competition of shrubs and tree seedlings; locally intense pasturing	Velchev (1997), Grunewald & Scheithauer (2011), Raev et al. (2011)
Human impact (mostly burning) started in 17th C; excessive and improper forest mng; release of influence since 1980	HADCM3_A2, CGCM2, $\Delta T_{2050} = 1.7^{\circ}\text{C}$, $\Delta T_{2080} = 2.8^{\circ}\text{C}$; $\Delta P_{2050} = -15\%$; $\Delta P_{2080} = -15\%$	Low density of F.s. in T, dispersal distances of F.s. seeds upslope; pasture intensity, new expansion of juniper stands	Raev et al. (2011), Gikov et al. (2016), Zhiyanski et al. (2008, 2016)
15–18th C: slash, burn, grazing mng; 18–19th C: uncontrolled cutting; 20th C: irregular shelterwood systems and over-exploitation mng	DMI-HIRHAM5_A1B, period 2001–2100: $\Delta T_{2050} = 1.2^{\circ}\text{C}$; $\Delta T_{2100} = 2.5^{\circ}\text{C}$; $\Delta P_{2050} = +15\text{ mm}$; $\Delta P_{2100} = -18\text{ mm}$	Impact of wild large ungulates on tree seedlings (especially A.a.); shallow, nutrient-poor soils (i.e. ranker and rendzina)	Klopčič et al. (2010, 2015), Mina et al. (2017)
Since 12th C: slash, burn, grazing mng; 13–19th C: intensive forest mng; at the end of the 19th C: decrease in grazing	ENSEMBLES models_A1B, period 1980–2100: $\Delta T_{2050} = 1.2-1.8^{\circ}\text{C}$; $\Delta T_{2100} = 2.7-4.1^{\circ}\text{C}$; $\Delta P_{2050} = 0\text{ mm}$; $\Delta P_{2100} = -5\text{ mm}$	Frequent disturbances by snow avalanches and snow gliding; ongoing cattle grazing; game grazing in the coldest years	Tattoni et al. (2010), Kulakowski et al. (2011), Barbeito et al. (2012), Bebi et al. (2012), Dawes et al. (2015)

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Table 1 (continued)

Country; part of mountains	Coordi- nates of central site	Elevation range of T (m a.s.l.)	Elevation range of Tr (m a.s.l.)	Range of tree species limit (m a.s.l.)	Annual altitudinal shift of T or Tr (m yr ⁻¹)	Area of study (km ²)	VZs near Tr (m a.s.l.)
Slovakia; Dumbier Tatra (part of Low Tatra Mts)	48°55'N; 19°31'E	1400 (1350–1450)	1530 (1400–1630)	P.a. 1730	~0.3 (Tr; 1950–present)	~400	Spruce–fir–beech (1200–1350); spruce (1300– 1550); P.m. with individual P.a. trees (1400–1700)
Czech Republic; Giant Mts	50°42'N; 15°38'E	1250 (1130–1460)	1320 (1250–1460)	P.a. 1500	0.43 (Tr; 1936–2005)	550	Beech–spruce (700–1050), P.a. dominates with increasing altitude; spruce (1000–1400); P.m. with P.a. trees (1400–1560)
Norway Southern Scandes	60°10'N; 7°40'E; 62°20'N; 10°05'E	850	600–1050	1500	0.8 (Tr; 1915–2007)	40 600	Birch forest dominance at high altitudes, but with some scattered P.s. or P.a.; mixed birch–conifer below 800
Norway, Sweden, Finland Northern Scandes	68°20'N; 18°20'E; 69°50'N; 27°00'E	West: 650 East: 100	West: 750 East: 290	West: 1000 East: 0	0.6 (Tr ; 1958–2008)	35 000	Birch forest dominance at all altitudes, but with some scattered pines or pine stands on sandy soils

mate the geographical position of these mountain units, 1 value was used for the geographical latitude and longitude of the locus of the studied mountain units. The analysed parameters of these 15 mountain units are shown in Table 2.

In addition, we calculated the following climate characteristics for all mountain units: annual mean air temperature, annual sum of precipitation, the growing season length and the date of the onset of the growing season. These characteristics were then compared for 2 distinct periods, 1961–1990 and 1991–2015 (Table 3). The climate characteristics were derived from the E-OBS gridded dataset of station observations version 13.1 (Haylock et al. 2008). We used the E-OBS version on the regular longitude–latitude grid with a horizontal resolution of 0.25 degrees. The climate data from all grid points within the mountain units or near their geographical borders were considered.

Data processing for 15 mountain units was made on the basis of data obtained from the literature and

personal studies by the co-authors; these are summarized in Tables 1 & 2 and in Tables S1 & S2 in the Supplement at www.int-res.com/articles/suppl/c073p135_supp.pdf. In addition, a semi-quantitative valuation of abiotic, biotic and anthropogenic factors limiting an upward treeline shift was performed (Fig. 2). To answer the question how natural and anthropogenic factors have influenced treeline ecotone characteristics with a focus on treeline shift, redundancy analysis (RDA) was used to describe and test the effect of the explanatory variables (geographical position, size of the whole mountain massif, start of human influence and start of the decrease in human influence) on treeline ecotone characteristics (timberline elevation, width of the treeline ecotone, tree species forming the treeline and treeline shift per year) and identify groups of mountain units with similar variability of the dependent data (ter Braak & Šmilauer 2012). The whole data set for this analysis is shown in Table S2. We tested both their simple effects, which show how much variation every explan-

Human influence in VZs in past and recently	Annual temperature (T) and precipitation (P) differences between 1961–1990 and 2021–2050; mean of CORDEX models	Limits to climate change induced species shift	References
From 14th C to 1922: mining, forest change to spruce monocultures; from 13th C to 1978: pastures in upper parts of mountain	Average of 10 RCM_B1: $\Delta T_{2050} = 1.8^{\circ}\text{C}$; $\Delta T_{2100} = 3.7^{\circ}\text{C}$; $\Delta P_{2050} = +24 \text{ mm}$; $\Delta P_{2100} = -35 \text{ mm}$	More rocky and nutrient-poor soils; late frosts; steep slopes with avalanches; absence of mature trees	Körner (2003), Fridley et al. (2011), Hlásný et al. (2011, 2016)
9–11th C: forest clear cutting, grazing in dwarf pine VZ; since 18th C: forest change to spruce monocultures, since 19th C: artificially planted	ALADIN_A1B, period 1961–2100: $\Delta T_{2050} = 1.3^{\circ}\text{C}$; $\Delta T_{2100} = 3.4^{\circ}\text{C}$; $\Delta P_{2050} = +25 \text{ mm}$; $\Delta P_{2100} = -14 \text{ mm}$	Different soil types for F.s. and P.a. (cambisol versus podzol); only TSL of P.a. could elevate on ranker soils in P.m. VZ	Treml and Banaš (2000), Cudlín et al. (2013), Treml & Chuman (2015), Treml & Migo (2015)
Grazed and browsed by reindeer and livestock (sheep and cattle) over thousands of years	RegClim/MPI/Hadley: $\Delta T_{2050} = 1.2^{\circ}\text{C}$; $\Delta T_{2100} = 2.2^{\circ}\text{C}$; $\Delta P_{2050} = +23 \text{ mm}$; $\Delta P_{2100} = -12 \text{ mm}$	Sheep and reindeer grazing and episodic insect outbreaks (<i>Epirrita</i>)	Dalen & Hofgaard (2005), Wielgolaski (2005), Hofgaard et al. (2009), Kullman, Öberg (2009)
Grazed and browsed by semi-domestic reindeer for hundreds of years; increased grazing from year 1960	RegClim/MPI/Hadley: $\Delta T_{2050} = 1.6^{\circ}\text{C}$; $\Delta T_{2100} = 2.9^{\circ}\text{C}$; $\Delta P_{2050} = +18 \text{ mm}$; $\Delta P_{2100} = -10 \text{ mm}$	Continued grazing regime and frequent episodic insect outbreaks (<i>Epirrita</i>)	Dalen & Hofgaard (2005), Wielgolaski (2005), Tømmervik et al. (2005), Hofgaard et al. (2009), Aune et al. (2011), Mathisen et al. (2014)

atory variable can explain separately, without using the other variables, and their conditional effects, which depend on the variables already selected in the model. The statistical significance of the explanatory variables was tested using a Monte Carlo permutation test, and only predictors with $p \leq 0.05$ were included in the subsequent RDA (Šmilauer & Lepš 2014).

To find the drivers of biodiversity loss in forests, meadows and animal communities (dependent variables), the explanatory variables (geographical position, timberline elevation, tree species forming the treeline, start of human influence, start of the decrease in human influence and temperature increase between the 2 periods 1961–1990 and 2021–2050) were tested again by RDA in Canoco 5 as mentioned above (Figs. 3 & 4). The whole data set for this analysis—including additional information about tree-lines in the mountain areas of interest, with a focus on treeline shift (its rate, drivers, limits and problems with its assessment)—is presented in Tables S1 & S2.

Selected univariate graphs were constructed to visualize the data of relationships between the explanatory and dependent variables of all analyses, which were not seen distinctly from the results of the multivariate statistics or linear regression (Fig. 5).

3. RESULTS

3.1. Effect of environmental variables on treeline ecotone characteristics with a focus on treeline shift

The variation in the dependent variables (timberline elevation, width of treeline ecotone, tree species forming the treeline and treeline shift per year) was significantly affected only by latitude and size of the whole mountain massif (Fig. 3). The adjusted explained variability by all explanatory variables was 34.2% ($F = 4.6$, $p = 0.01$). The RDA diagram shows that in the mountains located more to the north, the

Table 2. Factors influencing treeline ecotone characteristics in selected European mountains. The mountain size is the size of the whole mountain massive, functioning as a mezoscale climate unit, not only the studied mountain area. Width of the treeline ecotone was determined by subtracting the value of the mean timberline elevation from the value of the upper tree species limit. C: conifers, B: broadleaved trees; HI: human influence

Mountain unit	North latitude	East longitude	Mountain size (km ²)	Timberline (m a.s.l.)	Width of treeline ecotone (m)	Tree species forming the treeline	Temperature increase between 1961–1990 and 1991–2015 (°C)	Treeline shift (m yr ⁻¹)	Start of HI (yr)	Start of HI decrease (yr)
Central Pyrenees (CP)	42°21'N	0°30'W	55 000	2250	300	C	0.8	1.92 (1956–2006)	1000 BC	1930
Eastern Pyrenees (EP)	42°28'N	1°30'E	55 000	2400	300	C	0.8	0.71 (1956–2006)	1000	1930
Apennines (AP)	42°05'N	14°05'E	50 000	1800	300	B	1.4	1 (1954–2007)	1000 BC	1950
Shara Mts. (SH)	41°47'N	20°33'E	1600	1850	350	C, B	0.7	1 (1934–2010)	1300	1970
Pirin (PI)	41°42'N	23°31'E	2585	1900	400	C	0.5	no data	680	1962
Central Balkan Mts. (CB)	42°47'N	24°36'E	11 600	1600	250	C, B	0.7	no data	1700	1980
Northern Dinaric Mts. (DI)	45°36'N	14°28'E	1000	1540	160	B	1.3	no data	1400	1900
Central Alps (CA)	46°46'N	9°52'E	180 000	2100	550	C	0.7	1.3 (1954–2015)	1300	1880
Eastern Alps (EA)	46°17'N	11°45'E	180 000	1800	400	C	0.9	1.3 (1954–2015)	1150	1950
Low Tatra Mts. (LT)	48°55'N	19°31'E	1240	1400	330	C	0.9	0.57 (1975–2016)	1400	1922
Giant Mts. (GM)	50°42'N	15°38'E	630	1250	250	C	0.7	0.43 (1936–2005)	1000	1963
Hardangervidda (HG)	60°03'N	7°47'E	9000	900	150	C, B	0.5	0.8 (1915–2007)	800	1970
Dovre (DO)	62°21'N	8°52'E	6000	1000	400	B	0.7	0.8 (1915–2007)	1000	no decrease
Northern Swedish Lapland (NS)	68°12'N	18°33'E	4000	700	300	B	1.1	0.6 (1958–2008)	1000	no decrease
Inner Finnmark/northernmost Finnish Lapland (FL)	69°10'N	25°12'E	60 000	290	90	B	1.0	0.6 (1958–2008)	1600	no decrease

treeline ecotone is narrower, treeline shift is smaller, the timberline occurs at lower elevations, and the treeline is formed more by broadleaved species. Higher values of treeline ecotone width and treeline shift were found in the mountains with a greater size of the whole mountain massif.

When every explanatory variable was tested separately, values of the start of the decrease of human influence in the mountains also had a significant effect on the variation of the tree line ecotone data (explained variation = 20.6%, pseudo- $F = 3.4$, $p = 0.024$). Some selected relationships of the explanatory and dependent variables, even those not showing significant effects on the variation in the tree line ecotone parameters, are depicted in Fig. 5.

3.2. Effect of recent changes in climate and land use on the biodiversity

Biodiversity loss in forests, meadows and animal communities, analysed by RDA, was explained by geographical position, treeline species composition and temperature increase between the 2 periods 1961–1990 and 2021–2050 (Fig. 4). The adjusted explained variation by all explanatory variables was 63.2% ($F = 5.8$, $p = 0.001$). The RDA results indicated that biodiversity loss in forest communities increased with increasing latitude and longitude as well as in the case where broadleaved species formed the treeline. In contrast, the highest biodiversity loss in meadows was found in the mountains positioned more to the south and with higher temperature increase. The biodiversity loss in animal communities was negatively correlated with longitude and temperature increase.

4. DISCUSSION

The comparison of several mountain areas situated across Europe shows a variation in understanding of what constitutes the treeline across countries. The primary issue is the different approach to the definition of forest when applying a tree height threshold. This threshold decreases from

Table 3. Differences of selected climatic parameters between the 2 study periods (1961–1990 and 1991–2015) in selected European mountains

	Length of growing period (d) ^a	Beginning of growing season (d) ^b	Mean annual temperature (°C)	Mean annual precipitation (%)
Central Pyrenees	13.5	−8.9	0.8	−10.7
Eastern Pyrenees	11.7	−9.1	0.8	−9.2
Apennines	28.4	−23.2	1.4	5.7
Shara Mts.	1.6	0.1	0.7	−10.0
Pirin	2.6	−1.4	0.5	2.7
Central Balkan Mts.	16.9	−13.6	0.7	7.6
Northern Dinaric Mts.	16.0	−9.5	1.3	−5.6
Central Alps	14.7	−8.6	0.7	6.2
Eastern Alps	12.5	−9.6	0.9	−3.3
Low Tatra Mts.	2.4	−3.4	0.9	−9.1
Giant Mts.	−1.0	1.3	0.7	5.5
Hardangervidda Blefjell	6.3	3.4	0.5	5.6
Dovre	13.8	3.2	0.7	6.4
Northern Swedish Lapland	8.1	0.5	1.1	−2.7
Inner Finnmark/northernmost Finnish Lapland	1.7	0.8	1.0	7.7

^aPositive numbers indicate a prolongation
^bNegative numbers indicate an earlier beginning

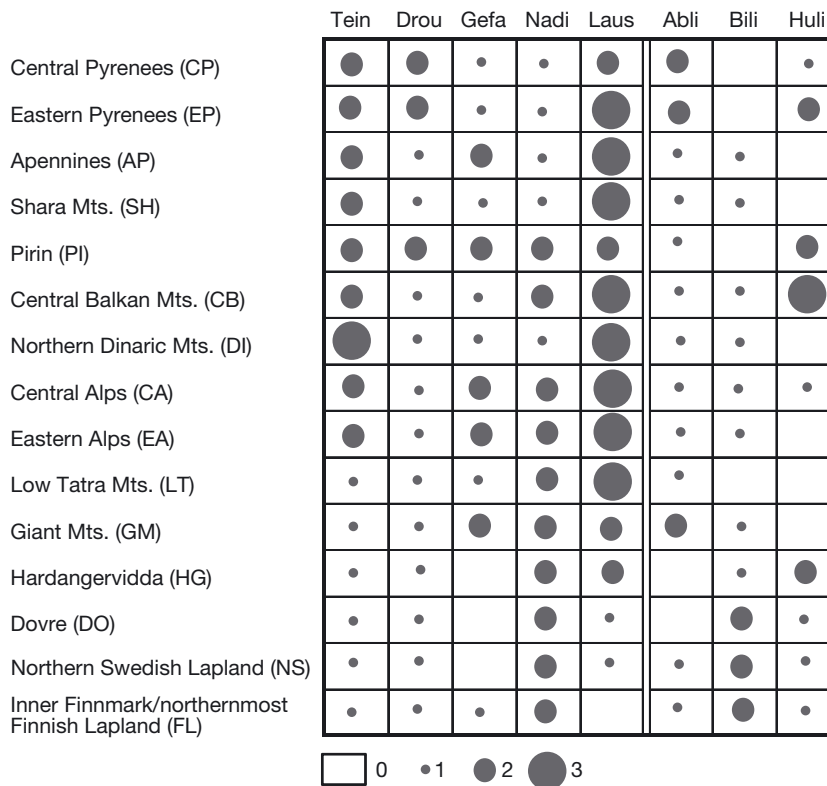


Fig. 2. Rates of treeline drivers (temperature increase [Tein], land use change [Laus] and treeline shift limits (drought [Drou], geomorphological factors [Gefa], natural disturbances [Nadi], other abiotic, biotic and human factors) in selected European mountains. Abli, Bili and Huli: abiotic, biotic and human treeline shift limits, respectively). Rate of treeline driver influence—0: no influence; 1: weak influence; 2: middle influence; 3: strong influence

5 m (Jeník & Lokvenc 1962) to 3 m (Körner 2012) in Northern and Central Europe to only 2 m (Holtmeier 2009) in Central and Southern Europe, where even shrubby stands (e.g. *Pinus mugo*) are considered as a forest in some countries, e.g. in Spain, Italy and Macedonia (Batllori et al. 2009). Another problem is a different designation of forest stands below the treeline: ‘upper montane forests’ in Central Europe and ‘subalpine forests’ in Southern Europe (Ellenberg 1988). Further differences are related to the tradition of different branches of science (e.g. a more traditional ‘geobotanical’ approach in Central Europe versus a more experimental approach in Western Europe), especially in the rate of applying new progressive methods (e.g. climatic modelling or molecular biological methods).

Our comparison of selected regions (Tables 1 & 2, Figs. 1 & 2) showed that southern mountains, compared to those located more centrally and in the north had (1) a longer and more profound exploitation by humans in the past; (2) greater differences in climatic parameters (temperature, length of growing period) between the 2 periods 1961–1990 and 1991–2015 (Table 3) and (3) more dramatic climate change scenarios, especially concerning temperature increases. Longitude also had some influence on the start and intensity of human influence, and on tree-line elevation and rate of tree-line shift (Table 2, Fig. 5). The occurrence of broadleaf tree species in the treeline ecotone in the northern (and to some extent the southern) countries distinguishes these from the Central European countries, where conifers prevail. It is interesting that grazing, an important factor shaping treeline ecosystems (Dirnböck et al. 2003,

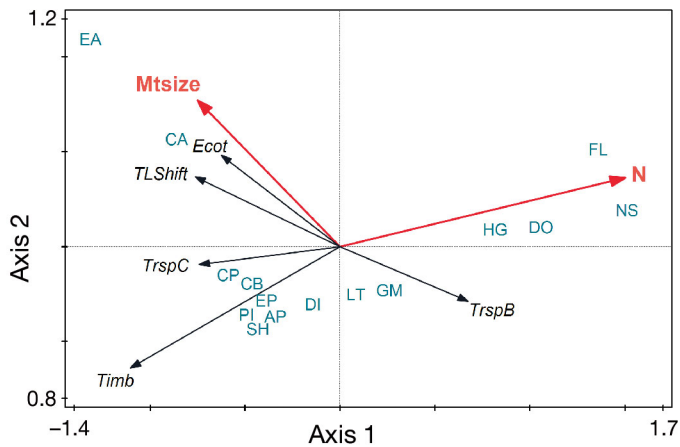


Fig. 3. Redundancy analysis diagram, with variation in timberline elevation, width of treeline ecotone, the tree species forming the treeline, and treeline shift used as dependent variables, explained by explanatory variables (latitude, mountain size). Mountain units (blue) are projected as the centres of abbreviations (see Table 2). Explanatory variables account for 43.6% of the total variation in the dependent data. The first canonical axis explained 46.6% of variation, the second axis explained 3.0% of variation. Dependent variables (black) are *Ecot*: altitudinal width of treeline ecotone, *TLShift*: treeline shift, *TrspC* (*TrspB*): treeline formed by conifers (broadleaved trees), *Timb*: timberline elevation. Explanatory variables (red) are *N*: north latitude, *Mtsize*: size of the mountain massif

Gehrig-Fasel et al. 2007), limits treeline shift in half of the countries of interest, regardless of latitude, longitude or recent political developments (Shara, Pirin, Central Balkans, Alps, Scandes; Fig. 2).

Despite the stated differences between studies looking at climate change impacts on the treeline, it is clear that current and future changes in temperature will seriously affect treeline ecotones in all mountain ranges of Europe. Winter is a period when treeline stands and individual trees have to survive severe, life-limiting conditions (Wieser & Tausz 2007). Therefore, winter warming might increase the chance of young trees surviving and passing the most critical period from seedling to sapling and further to the mature stage (Körner 2003). There is already much evidence worldwide that winter warming is one of the significant drivers of treeline advance (Harsch et al. 2009). Although it is expected that tree growth at the upper distributional margins (and in the northern European countries) will increase due to ongoing climate change (Peñuelas & Boada 2003, Chen et al. 2011, Hlásny et al. 2011, Lindner et al. 2014), extremes in temperature (e.g. black frosts, temperature reversals in the spring) or winter precipitation (e.g. lack of snow, drought) might also limit

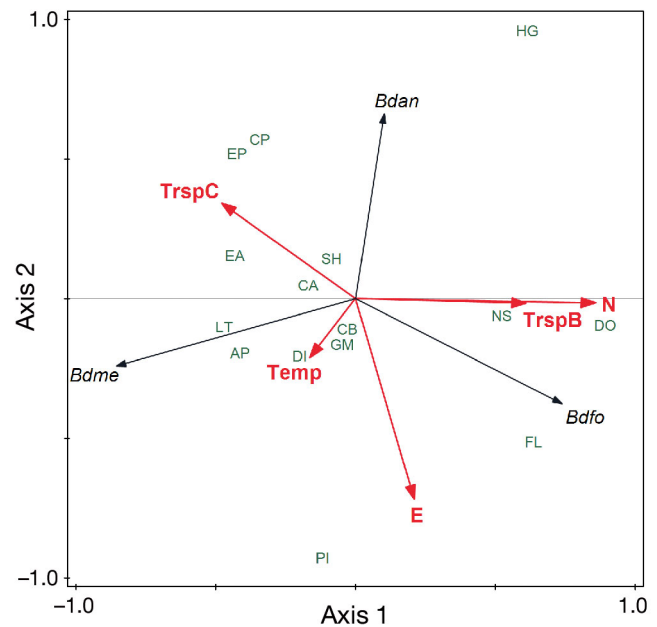


Fig. 4. Redundancy analysis diagram, with variation in biodiversity loss in forests, meadows and animal communities, used as dependent variables, explained by explanatory variables (geographical position, tree species forming the treeline and temperature increase between the 2 study periods [1961–1990 and 2021–2050]). Mountain units (green) are projected as centres of abbreviations (see Table 2). Explanatory variables account for 76.3% of total variation in the dependent data. The first canonical axis explained 48.4% of variation, the second axis explained 18.3% of variation. Dependent variables (black) are *Bdfo*/*Bdme*/*Bdan*: biodiversity loss in forests/meadows/animal communities. Explanatory variables (red) are *N*: north latitude, *E*: east longitude, *TrspC* (*TrspB*): treeline formed by conifers (broadleaved trees), *Temp*: temperature increase between the 2 study periods

this process in the future in some regions and local situations (Holtmeier & Broll 2005, Hagedorn et al. 2014). An earlier start to the growing period (especially in the Apennines, Central Balkan and Spanish Pyrenees; see Table 2) can play a negative role in the resistance of trees and seedlings to early spring frosts. On the other hand, at lower distributional margins (and in Southern European countries), it is expected that tree growth will decrease or forests will experience some level of dieback due to drought (Breshears et al. 2005, Piovesan et al. 2008, Allen et al. 2010, Huber et al. 2013). A serious implication is the positive effect that warming can have on root rot fungi and populations of bark beetles resulting in large-scale disturbances to temperate and also high-altitude forests (Jankovský et al. 2004, Elkin et al. 2013, Millar & Stephenson 2015).

Although recent upward advances of treeline ecotones are widespread in mountain regions (Harsch et

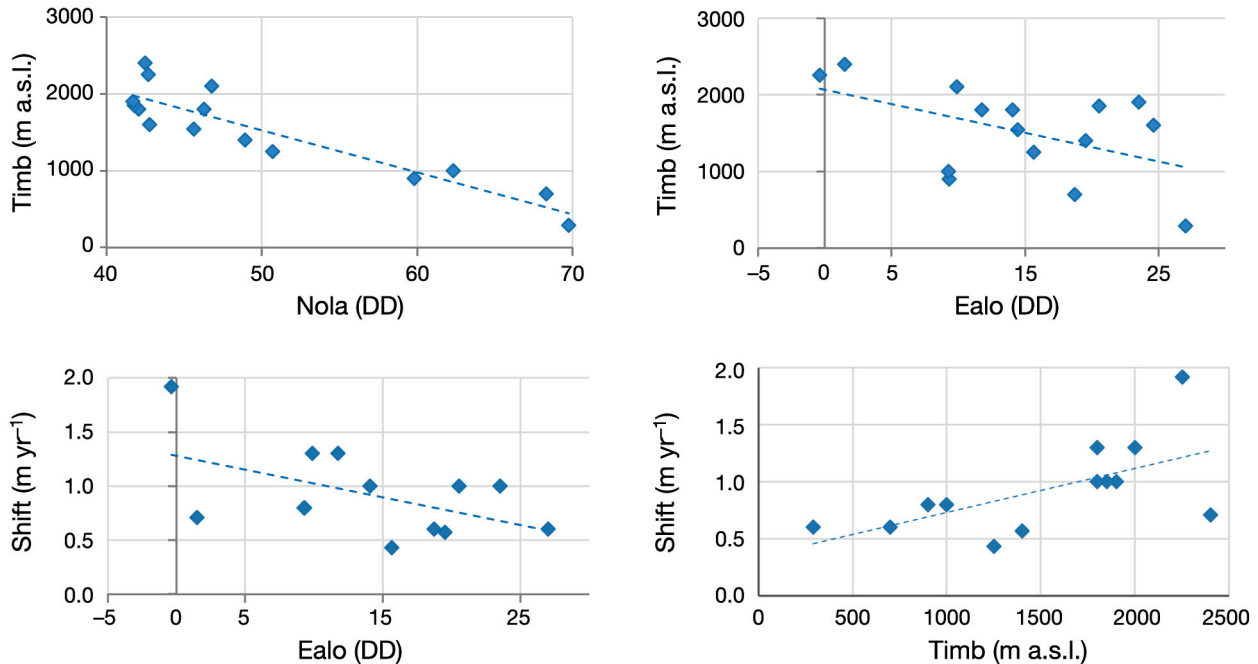


Fig. 5. Univariate graphs of the relationships of dependent variables, viz. timberline (Timb) and treeline shift per year (Shift), and their explanatory variables. Nola: north latitude; Ealo: east longitude; DD: decimal degrees

al. 2009), only a few published studies have included quantitative data about treeline shifts (Devi et al. 2008, Kullman & Öberg 2009, Diaz-Varela et al. 2010, Van Bogaert et al. 2011). Additionally, our knowledge of the spatial patterns in treeline ecotone shifts at the landscape scale is still surprisingly poor, except for some studies from subarctic areas, the Ural Mountains and the Alps (Lloyd et al. 2002, Diaz-Varela et al. 2010, Hagedorn et al. 2014). In the 15 studied mountain units, the values of treeline shift ranged from 0.43 to 1.9 m yr⁻¹, showing a rather distinct spatial pattern of the dynamics within European mountains. The observed treeline shift had a significant positive relationship only with northern latitude and a weak positive relationship with mountain-range size (i.e. the size of the whole mountain massif; Fig. 3). Nevertheless, this illustrates the importance of the mass elevation effect (Körner 2012), and partially explains why treelines could be at different altitudes at the same latitude. Small negative regressions with east longitude and timberline elevation are shown in Fig. 5. There was no apparent dependence of the treeline shift rate on climatic parameter changes between the periods 1961–1990 and 1991–2015.

A whole forest vegetation zone shift is a complex process, as not only the life strategies of an individual tree need to be considered, but plant, animal and microorganism species and their interrelationships, as well as the relationships to their specific microhab-

itats (including soil conditions), are also involved (Urban et al. 2012). Across all regions, we identified several important obstacles to treeline shifts, often related to site properties, such as significant rockiness, having shallow or low-nutrient soils, extreme relief causing disturbances by avalanches, snow gliding or wind damage (data from the Pyrenees, Apennines, Shara, Northern Dinaric, Low Tatra and Giant Mountains; see Fig. 2). Soil heterogeneity certainly has an important role in plant responses to climate change, and could also maintain the resilience of the community assemblages (Fridley et al. 2011). Another group of obstacles includes extreme climatic parameters, especially in winter (reported e.g. from the Pyrenees, Apennines, Pirin, Central Balkan, Northern Dinaric and Giant Mountains; Fig. 2). Their combination can result in edaphic and/or climatic unsuitability of habitats where species could potentially migrate. Climatically and edaphically suitable sites will likely decline over the next century, particularly in mountain landscapes (Bell et al. 2014). Therefore, trees in the treeline ecotone will colonize previously forested habitats. The colonization success of individual forest communities is affected by differences in species dispersal and recruitment behaviour (Dullinger et al. 2004, Jonášová et al. 2010). For these reasons, colonization of new forest habitats by the next tree generation may not be successful and may result in loss of species diversity (Honnay et al. 2002, Ibáñez et al. 2009, Dobrowski et

al. 2015), as reported from Macedonia, Slovenia, the Czech Republic, Slovakia and Norway (Fig. 4).

Another limiting factor is the existence of strong adaptation mechanisms of the dominant tree species which allow them to survive in their current distribution areas. Species migration is likely to be slow due to the limited quantity of climatically and edaphically suitable sites and the slow velocity of seed dispersal and tree regeneration, and will be hampered even more by fragmentation of high mountain landscapes caused by human activities, including brush invasion in abandoned meadows (Gartzia et al. 2014). A vertical shift in a vegetation zone involves not only single species of plants, animals and microorganisms, but also their interrelationships and links to soil conditions. The speed at which climatic conditions change will be different from changes in the soil conditions due to the slowness of soil-forming processes. Soil types and conditions (cambisol versus podzol) are crucial obstacles for the shift from a beech forest zone into the spruce forest zone in the Czech Republic (Vacek & Matjka 2010). According to other sources, the dominant tree species can influence soil formation processes (especially humus forms). Under favourable climatic and orographic conditions, beech is able to change its soil conditions over decades to centuries (J. Macku unpubl. data).

Significant changes in biodiversity must be expected in all of the mountain areas of interest. We found that biodiversity declined particularly in the southern regions of Europe, where the timberline is situated at higher elevations and human impact is mostly longer-lasting (Fig. 4). Similarly, Pauli et al. (2012) reported an increase in species richness of mountain grasslands across Europe except for Mediterranean regions, and assigned this different response of the southern regions to decreased water availability. On the other hand, ecosystems which exhibited biodiversity increases were not only enriched by migrant species, but the assemblages underwent thermophilization, i.e. cold-adapted species declined and more warm-adapted species spread (Gottfried et al. 2012). However, not all species are able to track climate changes. It is expected that around 40% of habitats will become climatically unsuitable for many mountain species, particularly endemic ones, increasing their extinction probability during this century (Dullinger et al. 2012). The abandonment of traditional land use forms is another source of this loss, which may be a more important driver than temperature increase (Fig. 4). Serious biodiversity losses in mountain meadows were reported from Spain, Italy, Macedonia, Bulgaria, Slovenia and Slovakia. There-

fore, controlled grazing must occur in order to maintain alpine grasslands (Dirnböck et al. 2003). Unfortunately, grazing is still active only in smaller parts of European mountains (e.g. in the Central Alps and the Central Balkan Mountains, but pasturing can also negatively affect vegetation diversity) and sometimes does not serve to maintain alpine grassland. The same is true for grassland management, which can help to maintain mountain species and decrease habitat loss. A serious biodiversity loss in mountain meadows was reported from the Pyrenees, the Apennines, and the Shara, Pirin, Central Balkan, Northern Dinaric and Low Tatra Mountains (Fig. 4).

In forests, species responses to climate change may be equivocal; some recent studies indicated contradictory shifts in species distributions (e.g. Lenoir et al. 2008, Zhu et al. 2012, Rabasa et al. 2013). This disparity is widely discussed and assigned to the great variety of non-climatic factors or even tree ontogeny (Grytnes et al. 2014, Lenoir & Svenning 2015, Máliš et al. 2016). Disturbances leading to tree mortality may also play an important role (Cudlín et al. 2013); changes in tree canopy cover modify light availability and microclimate and can induce the thermophilization of forest vegetation (De Frenne et al. 2015, Stevens et al. 2015). The loss of this microclimate buffering effect of forests may induce a biotic homogenization of forests (Savage & Vellend 2015) or the creation of novel non-analogical communities, such as oak–pine forests (Urban et al. 2012), which may be a new threat to forest biodiversity.

The observed changes in treeline forest ecosystems are often related to changes in land-use intensity (Theurillat & Guisan 2001, Alados et al. 2014). According to climate change predictions and the recent and future exploitation intensity of European mountains, trees and forest communities will shift upward due to land use change or climate change or both. Reduced land-use intensity certainly will interact with climate change by facilitating or inhibiting species occurrence, and will accelerate forest expansion above the present treeline, particularly to previously forested habitats (Theurillat & Guisan 2001). The simultaneous action of both main treeline shift drivers, viz. temperature increase and decrease in land use intensity, was recorded from all of our studied mountain areas. The extensive differences in timberline and treeline elevations in almost all studied mountains (Table 1) indicate the anthropo-zoogenic treeline type (according to Ellenberg 1998). In most mountains (e.g. in the Apennines, Shara Mountains, Central Balkans and Alps), land use is the prevailing factor influencing vegetation drift (Fig. 5). Previous

research showed that the upward shift of the treeline in the Swiss Alps was predominantly attributable to land abandonment, and only in some situations to climate change (Gehrig-Fasel et al. 2007). In the Apennines in the last few decades, tree establishment has been mainly controlled by land use, while tree growth has been controlled by climate, pointing to a minor role played by climate in shaping the current treeline (Palombo et al. 2013).

The impact of climate change and the connected land use change on biodiversity and ecosystem services provision in several European countries is summarized by Wielgolaski et al. (2017), and Kyriazopoulos et al. (2017) (both this Special), and Sarkki et al. (2016). One of the possible adaptive management options in response to climate change, assisted migration as human-assisted movement of species, has been frequently debated in the last few years (Stemarie et al. 2011). It is possible to apply it as a type of assisted colonization, i.e. intentional movement and release of an organism outside its indigenous range to avoid extinction of populations of the focal species (e.g. Macedonian pine species), or as an ecological replacement, i.e. the intentional movement and release of an organism outside its indigenous range to perform a specific ecological function (e.g. planting of *Pinus mugo* in the Alps; IUCN/SSC 2013).

5. CONCLUSIONS

The analysis of 11 mountain areas across Europe showed that with increasing latitude, the treeline and altitudinal width of the treeline ecotone significantly decreases, as do the significance of climatic and soil parameters as barriers against tree species shift. Although temperature is the overwhelming controlling factor of tree growth and establishment in temperate and boreal treeline ecotones, late-seasonal drought might also play a driving role in Mediterranean treeline ecotones. Longitude was less influential, mostly affecting climate and land use change effects on increased biodiversity loss, as well as the size of the area that forms one mesoclimate unit affecting altitudinal ecotone width. The biggest part of the commonly observed remaining variability in mountain vegetation near the treeline in Europe seems to be caused by geomorphological, geological, pedological and microclimatic variability in combination with different land use history and the present socio-economic relations. The observed differences in climatic parameters between the mountain areas of interest in comparison with the reference period

1960–1990 (0.9°C) have not explained the relatively high differences in the rate of treeline shift per year (1.49 m). The predicted variability in temperature increase due to global warming (1.2–2.6°C in 2050 and 2.2–5.3°C in 2100) could lead to a much bigger differentiation in treeline ecotone biodiversity and ecosystem processes between southern and northern European mountains in the future. Therefore, these differences must be taken into account by scientists and EU policy makers when formulating efficient adaptive forest management strategies for treeline ecosystems at the European level (e.g. assisted migration of adapted genotypes).

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