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NOT ONLY CLIMATE: INTERACTING DRIVERS OF TREELINE CHANGE IN EUROPE

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Abstract

Treelines have long been recognized as important ecotones and likely harbingers of climate change. However, over the last century many treelines have been affected not only by global warming, but also by the interactions of climate, forest disturbance and the consequences of abrupt demographic and economic changes. Recent research has increasingly stressed how multiple ecological, biophysical, and human factors interact to shape ecological dynamics. Here we highlight the need to consider interactions among multiple drivers to more completely understand and predict treeline dynamics in Europe.

Key words

Picea • Larix • disturbance interactions • subalpine forests • climate • climate change • topography • pollution • snow avalanche

Introduction

Treelines have long been recognized as important ecotones and likely harbingers of climate change (Stevens & Fox 1991). Important work in Europe and elsewhere has elucidated the effects of temperature and precipitation on tree establishment and growth at elevational and latitudinal limits (Körner & Paulsen 2004; Harsch et al. 2009). However, over the last century in Europe, as well as on other continents, most shifts in treelines have occurred in response to both global warming and abrupt demographic and economic changes at high elevations (Hofgaard 1997; Motta et al. 2006). In this context, some lines of research have increasingly stressed how multiple ecological, biophysical, and human factors interact to shape ecological dynamics, including those at treeline. Here we do not aim to review the extensive literature on treeline dynamics, rather we highlight the need to consider interactions among multiple drivers to more completely understand and predict treeline dynamics in Europe.

Climatic drivers of treeline position

At broad spatial scales, positions of treeline globally have long been understood to be a function of climate with temperature and/or precipitation limiting tree establishment and growth (Troll 1973). In particular, summer temperatures during the vegetation growing period are considered as critical for treeline position worldwide because the lower threshold of temperature for tissue growth and development is thought to be in a restricted range of 5.5-7.5°C (Körner 1998). However, other climatic parameters such as winter temperatures (Kullman et al. 2007), precipitation (Daniels & Veblen 2003; Ohse et al. 2012) or the duration of snow cover (Hallinger et al. 2010; Barbeito et al. 2012) may be as important for tree survival and treeline positions as summer temperatures. For example, tree survival and height growth have been shown

to require different environmental conditions and even small changes in the duration of snow cover, in addition to changes in temperature, have been shown to strongly impact tree survival and growth patterns at tree-line (Barbeito et al. 2012; Li & Yang 2004). Because of the importance of these climatic drivers, treeline dynamics are widely associated with changing temperatures (e.g., Hagedorn et al. 2014) and/or precipitation (Ohse et al. 2012), which are being used to model future treeline dynamics (Dullinger et al. 2004; Paulsen & Koerner 2014). The relative importance of different climatic drivers varies spatially across different species and compositions of tree-lines in Europe. Although most treeline in Europe is dominated by coniferous species (mainly spruce, larch and pine), broad-leaf species (especially beech) are also regionally important (e.g. in the Apennines and the Carpathians; Czajka et al. 2015b).

The relative importance of climatic and other drivers for treeline position changes during the lifetime of a tree. Early seedling establishment is often limited by the availability of seeds, by the quality of seedbeds and by interactions with herbaceous vegetation (Dullinger et al. 2004; Grau et al. 2012). Young tree seedlings tend to be highly susceptible to drought, high radiation during daytime and cold night-time temperatures (Smith et al. 2009). Furthermore, during cold but snow-free periods, reduced wind speed close to the ground, relatively warm soil temperatures close to the soil surface, as well as terrestrial thermal radiation increase the effective temperatures for seedlings compared to taller trees with deeper roots (Grace et al. 1989). When tree seedlings grow taller, the relative importance of variables for tree mortality and growth can change rapidly, especially when tree height exceeds snow cover (Barbeito et al. 2012), at which point the stems increasingly become more exposed to surrounding air temperatures and to mechanical damage and abrasion caused by wind and blowing snow or ice (Aulitzky et al. 1982; Kharuk et al. 2010). With increasing size, taller seedlings and younger trees become

increasingly more vulnerable to cold air and soil temperatures, while differences in the microsite become increasingly less important (Körner 2012). For older trees at treeline, the relative importance of drought as a limiting factor may increase again, in particular where competition or biogenic disturbances are also important (Allen et al. 2010; Schuster & Oberhuber 2013). Therefore, the effects of climate on mortality and growth should be carefully evaluated according to the age of the trees, with explicit recognition of the changing relative importance of critical drivers during the developmental stages of the tree as well as the ecosystem in question.

Beyond the direct influence of climate

Although climate is clearly important for treeline dynamics, recent research has increasingly expanded the focus beyond climate being the only important variable (Fig. 1). For example, in the context of global climate change, CO₂ concentrations have been shown to interact with warming temperatures to promote growth of some treeline species in Switzerland (Dawes et al. 2011, 2013). While broad-scale treeline position is largely associated with temperature,

much of the finer-scale variation in treeline reflects a combination of thermal variables, physiological stress, landuse, and natural disturbances (Körner 1998; Case & Duncan 2014). Similarly, even if climate changes to allow upward expansion of treeline, that potential may be limited by physiographic setting or geomorphic processes (Garbarino et al. 2009; Holtmeier & Broll 2012; Macias-Fauria & Johnson 2013). Furthermore, the complexity and interactions of treeline drivers include interactions between climate and pathogens. For example, the 2000s bark beetle outbreak in Western Carpathians initially only affected low elevation planted spruce forest, but eventually spread to subalpine forests, including the treeline ecotone, which is also influenced by climate (Fig. 2).

The position of treeline can also vary locally due to disturbances such as snow avalanches, fires, or pathogens, which can suppress treelines below their climatic limit (Figs. 3, 4) (Bebi et al. 2009; Barbeito et al. 2013; Johansson & Granstrom 2014). As most natural disturbances are driven by climate, it follows that climate can affect treeline dynamics not only directly (e.g. by temperature or precipitation affecting tree demography) but also indirectly by altering disturbance regimes. In fact, in European temperate mountain ranges it is likely that

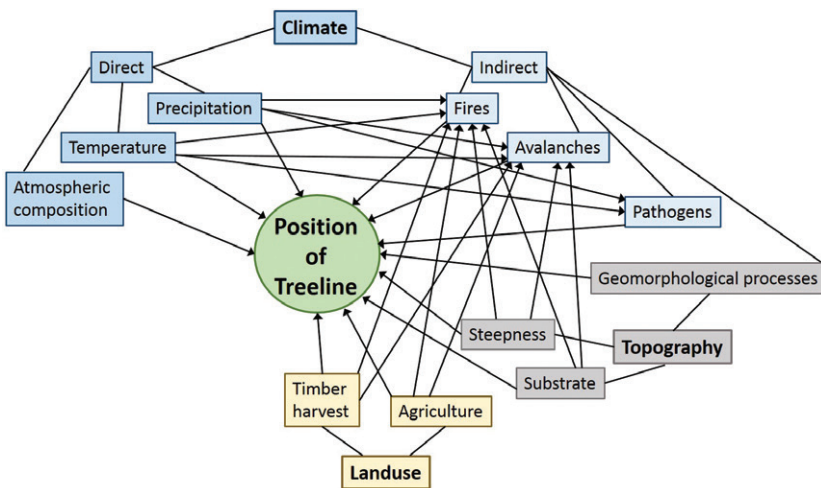


Figure 1. Treeline is determined by complex interactions among climatic, topographic, landuse, and other drivers – each of which directly affects treeline and also affects the other drivers



Figure 2. The complexity and interactions of treeline drivers include interactions between climate, snow avalanches and pathogens. Here, the 2000s bark beetle outbreak in the Western Carpathians, which initially only affected low elevation planted spruce forest, but eventually spread to subalpine forests, including the treeline ecotone, which is also influenced by climate (Photo by R. Kaczka)

future climate change could result in changes in snowfall and temperature, which may affect local avalanche regimes, especially in lower elevation subalpine forest. Future climate scenarios may also be characterized by lower overall precipitation and higher temperatures, which may fundamentally alter fire regimes and outbreaks of tree-killing insects and pathogenic fungi, even in regions that have not been affected by these disturbances over the past decades to centuries. Consequently, such changes in these disturbance regimes may set the stage for novel interactions among disturbances that could affect treeline position and ecosystem trajectories. Additionally, regeneration following these altered disturbance regimes may also be affected by the direct effects of climate on tree demography. Thus, changes in climatically-driven disturbances, including fires and insect outbreaks are critical to treeline dynamics but are likely to differ between broadleaf and coniferous species (Piermattei et al. 2012).

Influence of human activities on treeline shifts

In addition to potential changes in climatically-driven disturbances, changes in land use and forest management also affect the dynamics of many European treelines.

For example, while avalanches can suppress treeline below its climatically-determined limit, anthropogenic suppression of avalanches by the construction of snow-supporting structures can dampen this effect, leading to a greater influence of climate on tree growth near treeline (Kulakowski et al. 2006) and an overall upward expansion of treeline (Fig. 3) (Kulakowski et al. 2011).

Agricultural use of alpine and subalpine areas has an important effect on treelines. For example, wild and domesticated ungulates can interact with climate to impact treeline dynamics (Dufour-Tremblay & Boudreau 2011; Herrero et al. 2012; Munier et al. 2014). Over the Holocene, treeline vegetation in Switzerland has been affected by a combination of anthropogenic fire, human land use, and climate (Berthel et al. 2012; Rey et al. 2013; Schwörer et al. 2014). Across the European continent, treeline dynamics continue to be affected by browsing in many areas (Speed et al. 2011). However, as agriculture becomes less profitable in developed countries, browsing and grazing pressure from domesticated ungulates is decreasing. This change in herbivore pressure can reduce constraints on climatically-determined position of treeline (Gehrig-Fasel et al. 2007; Kulakowski et al. 2011; Czajka et al. 2015a). Similarly, following cessation of logging at high



Figure 3. The position of treeline can vary due to the effects of disturbances such as snow avalanches (left), fires (right), or pathogens, which can suppress treelines below their climatic limit (Photo by P. Bebi)



Figure 4. While avalanches can suppress treeline below its climatically-determined limit (right), anthropogenic suppression of avalanches by the construction of snow-supporting structures can dampen this effect, leading to a greater influence of climate on tree growth near treeline and an overall upward expansion of treeline (left)

Source: Photo courtesy of Swiss Federal Institute for Forest, Snow and Landscape Research (WSL) Institute for Snow and Avalanche Research (SLF)

elevations, climate has been shown to drive forest expansion (Carlson et al. 2014; Kaczka et al. 2015a). However, in some less developed regions such as the Eastern Carpathians of Ukraine and Romania, the deforestation of subalpine forests has increased due to commercial logging and growth of tourist infrastructure (Mihai et al. 2007; Kuemmerle et al. 2009; Knorn et al. 2012).

Beside the direct influence of land-use on trees, the legacies of former land-use can include altered site conditions or succession pathways. For example, a gradual decrease of grazing pressure can lead to relatively dense

shrub vegetation, which can inhibit the establishment of trees and subsequent expansion of treelines, even if temperatures become more favorable for tree growth (Spatz 1980; Motta et al. 2006). A recent re-assessment of a 40 year old survey of treeline trees in the Dischmatal in the Swiss Alps has shown that treeline expansion occurred mainly during time periods after the cessation of intensive grazing pressure and before the establishment of dense dwarf-shrub vegetation (Erdle 2013). Legacies of extreme anthropogenic air pollution including sulfur, nitrogen (causing acid rain) and dimming or brightening of the atmosphere (Stanhill

& Cohen 2001; Wild et al. 2005) can likewise interact with climate to affect pathways of tree establishment near treeline. One of the striking examples of this is at the border of Poland and the Czech Republic, where forest dieback due to pollution was especially extensive (Mazurski 1986; Schulze 1989; Renner 2002; Treml & Migoń 2015).

Understanding present-day treelines across spatial and temporal scales

Recent data from monitoring networks, including National Forest Inventories, remotely sensed data from satellite images or airborne light detection and ranging (LIDAR) cover large areas and facilitate monitoring and studying treeline dynamics. However, most of these data sets currently cover a relatively short duration. Where they are available, historical data, including dendro-ecological approaches, repeated aerial photographs, or historical maps (Coop & Givinish 2007; Ameztegui et al. 2010; Kulakowski et al. 2011; Mathisen et al. 2014; Kaczka et al. 2015b) can be combined with recent data sets to shed light on treeline dynamics over the past decades or centuries. Landscape models can then leverage these spatiotemporal data to predict potential future changes in treeline position.

Conclusions

Important advances are being made in understanding how non-climatic variables interact with climatic ones to shape treelines across

Europe. Taken together, this literature indicates that to more completely understand changes in treeline over time, it is important to consider not only individual drivers of change, but also the interacting effects of multiple drivers, including ecological, physiographic, and human ones (Fig. 1). It is likely that future treeline dynamics will be shaped not only by the direct effects of climate change, but also by the indirect effects of climate change, including altered disturbance regimes. The importantly, the relative importance of individual driving factors, as well as the nature of their interactions, should be expected to vary over space and time.

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Editors’ note:

Unless otherwise stated, the sources of tables and figures are the authors’, on the basis of their own research.

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