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Dynamics of the Alpine Treeline Ecotone under Global Warming: A Review

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Abstract: The alpine treeline ecotone is defined as a forest-grassland or forest-tundra transition boundary either between subalpine forest and treeless grassland, or between subalpine forest and treeless tundra. The alpine treeline ecotone serves irreplaceable ecological functions and provides various ecosystem services. There are three lines associated with the alpine treeline ecotone, the tree species line (i.e., the highest elevational limit of individual tree establishment and growth), the treeline (i.e., the transition line between tree islands and isolated individual trees) and the timber line (i.e., the upper boundary of the closed subalpine forest). The alpine treeline ecotone is the belt region between the tree species line and the timber line of the closed forest. The treeline is very sensitive to climate change and is often used as an indicator for the response of vegetation to global warming. However, there is currently no comprehensive review in the field of alpine treeline advance under global warming. Therefore, this review summarizes the literature and discusses the theoretical bases and challenges in the study of alpine treeline dynamics from the following four aspects: (1) Ecological functions and issues of treeline dynamics; (2) Methodology for monitoring treeline dynamics; (3) Treeline shifts in different climate zones; (4) Driving factors for treeline upward shifting.

Key words: alpine treeline; treeline ecotone; treeline dynamics; treeline upward shifting

1 Introduction

The alpine treeline ecotone refers to a forest-tundra or forest-grassland ecotone, which is a transition either between subalpine forest and tundra, or between subalpine forest and tree-less grassland (Bader and Ruijten, 2008; Aakala et al., 2014). Three lines are associated with the alpine treeline ecotone: the tree species line, the treeline, and the timber line. The tree species line is the upper boundary of the alpine treeline ecotone, which represents the highest elevational limits of individual trees due to the low temperature limitation for tree growth in the high-altitude regions (Batllori and Gutiérrez, 2008). The timber line is the lower boundary of the alpine treeline ecotone, also referring to the upper boundary of the closed subalpine forest (Jacob et al., 2015a). The treeline is defined as the transition between the elevational region of isolated tree islands and the region of individual trees (Jacob et al., 2015a). The alpine treeline ecotone is the belt region between the tree species line and timber line of the closed forest, and the treeline separates the regions of isolated tree islands and individual trees (Fig. 1).

In the treeline ecotone, tree height and biomass decrease strongly as elevation increases (Hertel and Schöling, 2011). The alpine treeline ecotone serves irreplaceable ecological functions (Balestrini et al., 2013), including serving as

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hotspots of biodiversity (Barros et al., 2017), high quality water sources for downstream areas (Jacob et al., 2015a), and the source of nutrient input and carbon sequestration for ecosystems in the lower elevations (Balestrini et al., 2013). The alpine treeline ecotone reflects the interactions among climate, species ecology, physiography and physiology (Binney et al., 2011). It is one of the most sensitive ecotones to global warming (Hicks, 2001; Batllori and Gutierrez, 2008; Dawes et al., 2015), because it occupies regions at the extremes of tree species temperature tolerance limits (Brown, 2010; McIntire et al., 2016). Therefore, more and more research is focusing on the long-term temporal dynamics of the treeline ecotone (Batllori and Gutierrez, 2008; Wallentin et al., 2008; Mamet and Kershaw, 2012; Trant and Hermanutz, 2014; Jacob et al., 2015a; Jacob et al., 2015b) because treeline dynamics have the potential for use in monitoring global warming effects on ecosystems (Barros et al., 2017).

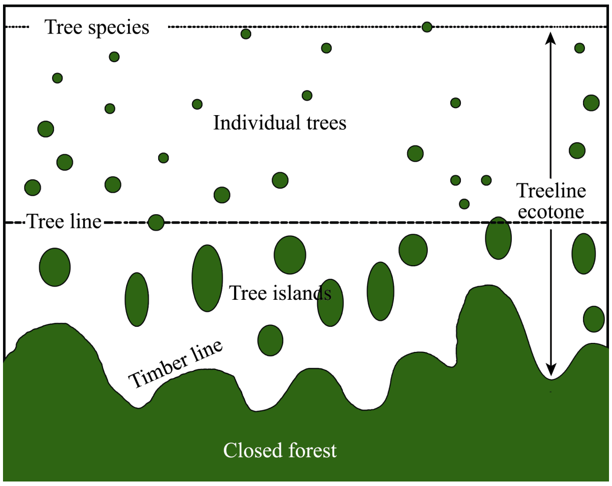

Fig. 1 The ecological concept of the treeline ecotone
Note: Sources from: Jacob et al., 2015a.

Previous research in the field of treeline shifts indicated that in some cases the alpine treeline shifts upwards, while in others the alpine treeline is stable or may shift downward along with altitude. Therefore, the mechanisms involved in treeline shifting according to the increasing temperature are still unclear. In addition, many studies indicate that temperature might not be the primary factor for the upward shifting of the alpine treeline. However, a comprehensive review in the field of alpine treeline advance according to global warming is not available. Therefore, this review will summarize the literature published between 2001–2020 regarding treeline shifting in different climate zones globally, and discuss the theoretical bases and challenges in studying alpine treeline dynamics from the following four aspects: 1) Ecological functions and issues of treeline dynamics; 2) Methodology for monitoring treeline dynamics; 3) Treeline shifts in different climate zones; 4) Driving factors for treeline upward shifting.

2 Ecological functions and issues of treeline dynamics

Along with increasing temperatures in the alpine regions, the upper limitation of tree species will reach higher altitudes and the treeline ecotone will gradually replace areas that were previously alpine grassland or tundra (Batllori and Gutierrez, 2008). During this ecological process of treeline ecotone dynamics under global warming, tree expansion first occurs in tree-favorable microsites, thus the treeline upward shifting is very patchy at the beginning (the same as “tree islands”) (Schwörer et al., 2017; Johnson and Yeakley, 2019). The long-term succession pattern of the treeline ecotone under the condition of increasing temperature includes tree patches (the same as “tree islands”) upward movement in the lower region of the treeline ecotone, in addition to individual tree (the same isolated “individual trees”) encroachment exceeding the original upper elevational limits in the upper region of the treeline ecotone (Peringer and Rosenthal, 2011; Greenwood et al., 2016; Astudillo-Sanchez et al., 2017).

Treeline upward shifting brings more biomass and productivity into the sparsely covered alpine treeline ecotone, and might lead to more carbon sequestration, compensating for the carbon emissions from human activities (Franke et al., 2017). However, treeline advance due to global warming would cause many ecological issues. The replacement of alpine grassland by the migration of subalpine forest because of treeline shifting decreases the albedo in high altitude regions, increases the absorption of solar radiation and causes more evapotranspiration, and eventually leads to future global warming (Franke et al., 2017). Rapid alpine treeline advance would influence future biodiversity in high elevational regions (Binney et al., 2011) and increase the risk of losing biodiversity (Barros et al., 2017), especially the loss of species richness for alpine grassland species (Batllori and Gutierrez, 2008) and changing forest community composition (Greenwood et al., 2016). Increasing forest fragmentation (tree islands and isolated individual trees), generated by alpine treeline upward shifts, cause unexpectedly strong genetic isolation of subalpine tree species and alpine herb species, even for the wind-pollinated species (Hensen et al., 2011). In addition, treeline advance causes more allochthonous organic matter and nutrients to occur in the head water streams of the alpine region (Bo et al., 2014).

3 Methodology for monitoring treeline dynamics

Research methods for monitoring the treeline ecotone align along two directions. One direction focuses on using tree seedlings (Batllori et al., 2009), natality and mortality (Mazepa, 2005; Kullman, 2007; Elliott, 2011; Mamet and

Kershaw, 2012), recruitment (Trant and Hermanutz, 2014; Astudillo-Sanchez et al., 2017), establishment (Danby and Hik, 2007; Dang et al., 2009), radial growth (Cullen et al., 2001a; Berninger et al., 2004; Lara et al., 2005; Asselin and Payette, 2006; Trant et al., 2011; Franke et al., 2017; Shi et al., 2019), age structure (Batllori and Gutierrez, 2008; Fang et al., 2009; Gou et al., 2012; Aakala et al., 2014; Astudillo-Sanchez et al., 2017), population density (Rundqvist et al., 2011; Gou et al., 2012) and tree islands (Alftine and Malanson, 2004) as indicators for the temporal dynamics of treeline ecotones. Another direction emphasizes the positional changes of the treeline. This method either compares current field observations and historical documentation to measure treeline advance (Van Bogaert et al., 2011; Pennisi, 2013), or uses pollen and vegetation remains analysis to construct the past treeline pattern (Bjune, 2005; Birks and Bjune, 2010; Colombaroli et al., 2010; Binney et al., 2011; Bjune, 2014).

Alternatively, remote sensing approaches can be used to capture long-term spatial variations of treeline positions for analyzing treeline upward advancement. First, the classification of forest and non-forest areas from moderate-resolution imagery (Gehrig-Fasel et al., 2007; Bader and Ruijten, 2008; Carlson et al., 2014; Jacob et al., 2015b; Ameztegui et al., 2016) were reported for measuring the treeline position and temporal dynamics. Second, such studies also detect individual trees and tree islands from high-resolution imagery (Paulsen and Korner, 2001; Rosén and Persson, 2006; Groen et al., 2012; Mathisen et al., 2014; Zong et al., 2014), aerial photos or Lidar data (Wallentin et al., 2008; Luo and Dai, 2013) to determine the treeline position. Third, researchers have defined new indicators for detecting the treeline position globally (Wei et al., 2020). However, the classification results of remote sensing images (i.e., forest/non-forest pixels or segments) are not consistent with the precise definition of the treeline (i.e., the boundary between isolated tree islands and individual trees). Therefore, it remains challenging for remote sensing applications to precisely track treeline advance along the elevation gradients.

4 Treeline shifts in different climate zones

Most studies on this topic chose features such as tree radial growth (D'Arrigo et al., 2004; Gou et al., 2012; Franke et al., 2017), tree population density (Mazepa, 2005; Kullman, 2007; Fang et al., 2009; Rundqvist et al., 2011; Chen et al., 2015), tree seedling establishment (Elliott, 2011) or tree recruitment as the indicators for the dynamics of the treeline ecotone that were associated with global warming (Batllori and Gutierrez, 2008; Trant and Hermanutz, 2014). Other research focused on the advancement of the treeline position in the past 10 decades. Among those studies, several have observed that the treeline moved upward in mountain regions (Danby and Hik, 2007; Gehrig-Fasel et al., 2007; Payette, 2007; Kharuk et al., 2010; Van Bogaert et al., 2011; Kirdyanov et al., 2012; Mamet and Kershaw, 2012; Aakala et al., 2014; Mathisen et al., 2014; Jacob et al., 2015b; Ameztegui et al., 2016), while some others did not observe any clear upward (Cullen et al., 2001a; Liang et al., 2012) or downward (Lara et al., 2005; Fajardo and McIntire, 2012; Jacob et al., 2015a) movement of the treeline location. Studies which did not observe a clear change in the treeline position indicated the increasing of population density (Liang et al., 2011) and seedling establishment in the treeline ecotone. The reason for the absence of an obvious change in the treeline might be the relatively short time period examined in the research, as Lloyd (2005) indicated that the mean time lag between initial tree recruitment and forest development is 200 years. A few studies observed downward movement of the treeline or a tree population density decline in the treeline ecotone, such as in Montana, USA, a mid-latitude semiarid steppe climate region (Fajardo and McIntire, 2012); tropical African highlands, a highland climate region (Jacob et al., 2015a); and the Chilean Andes, a highland climate region (Lara et al., 2005), which imply that temperature might not have been a dominant driving factor for treeline advance under long-term global warming until now. The intensity of treeline advance varies among different climate types. In a tundra climate region, Mathisen et al. (2014) showed that the treeline advanced nearly 30 meters within 55 years in Khibiny Mountain, northwest Russia. In subarctic climate regions, Kirdyanov et al. (2012) observed a treeline shift upslope of 30 to 50 meters (Putorana mountain, northern Siberia) in the past century; Van Bogaert et al. (2011) indicated a treeline shift upward by about 24 meters in Tornetrask, northern Sweden, during 1912 to 2016; and Danby and Hik (2007) found that the treeline had a south-facing rise of 65 to 85 meters in elevation (Yukon, Canada) during early to middle 20th century. In humid continental climate regions, the treeline showed an upward shifting by 0.5 meter per year during 1960 to 1985 in Finland (Aakala et al., 2014); Kharuk et al. (2010) found a 0.8-meter upward movement of the current treeline per year during the last century; and Mohapatra et al. (2019) observed an 11.3 meter upward shifting of the treeline per year over the past 33 years in Arunachal Pradesh Himalaya. In addition, large upward shifts of the treeline happened in sites with heavy anthropogenic disturbance in the tropical highland climate region (Jacob et al., 2015b) and the Mediterranean climate region (Ameztegui et al., 2016), but the upslope shifted treelines still did not reach their potential treeline positions associated with climatic factors (Gehrig-Fasel et al., 2007). However, our knowledge of treeline dynamics under global warming in the tropical or subtropical climatic region is fragmentary, thus this information is needed to compare the intensity of treeline advance across the different climate zones.

There are four possible reasons for the inconsistency in the intensity of treeline upward shifts among different climate types. First, the uneven distribution of climate change (i.e., the increasing temperature is not uniform globally) (IPCC, 2013) has the potential to cause different intensities of treeline advance upwards. Second, the temperature is no longer a primary factor dominating the treeline upward advancement under long-term global warming until now (Fajardo and McIntire, 2012). Third, the dominant species or vegetation communities in different climate zones are significantly different, and the dominant environmental factors for different species or vegetation communities are also significantly different (Schrag et al., 2008). Fourth, heavy anthropogenic disturbance, especially in tropical or subtropical climate regions, introduce great challenges for the treeline upslope advancement response to climate change (Jacob et al., 2015a).

5 Driving factors for treeline upward shifting

Temperature has been proven as the primary factor for treeline upward shifting in many previous studies. Previous research indicates that the elevational position of the treeline follows a mean growing season temperature of around 6 ℃ under natural climate controls without any anthropogenic effects (Hoch and Koerner, 2009). In the Southern Hemisphere, the mean growing season temperature in the treeline position is a little higher but still within the normal range, at around 7–8 ℃ (Cieraad et al., 2014). Other studies have found that the elevation position of the treeline is at 5–8 ℃ of mean growing season surface temperature (Kirdyanov et al., 2012). However, some studies indicate that temperature may no longer be the dominant factor for treeline upward shifting. Research opinions regarding the dominant factors of treeline upward shifting align in two directions. One is that the annual mean temperature can no longer be used as the indicator temperature for treeline shifting studies; while the other is that local variations of treeline advance in the same region indicate that other factors besides temperature might be the dominant driving factors for treeline upward shifting.

5.1 Climate indicators of temperature for treeline upward shifting

Most researchers have begun to embrace the idea that annual mean temperature can no longer be used as the climate indicator for treeline studies because seasonal changes in temperature are very important for vegetation growth (Koerner, 2016), however, the results are not consistent among different studies. Some research shows that the winter temperature is the main control factor for treeline dynamics (Bi et al., 2017), because short freezes might enhance seedling survival for some species along the alpine treeline (Pennisi, 2013; Maher et al., 2020); while some studies indicate that the spring temperature (Shennongjia Mountains, central China) (Dang et al., 2009) or the fall temperature (Switzerland) (Coops et al., 2013) is the major climate factor for tree growth in alpine treeline; meanwhile, some other studies prove that the summer temperature controls tree growth within the treeline ecotone (New Zealand) (Cullen et al., 2001b) and treeline upward advancement (Schwörer et al., 2017). More specifically, a few studies have implied that leaf and root biomass is related to temperature in different seasons (Aakala et al., 2014). On the other hand, some researchers propose that the temperature measured from weather stations is no longer appropriate for describing the treeline response to climate change because air temperature is not always consistent with the temperature of the vegetation community, and weather station temperature data do not represent any spatial heterogeneity (Koerner, 2016). Therefore, some studies have explored the relationship between soil temperature and treeline dynamics, and the results show positive feedback of soil temperature (Alftine and Malanson, 2004; Aakala et al., 2014; Dawes et al., 2015).

5.2 Local variations for treeline upward shifting

The relationships between vegetation responses and environmental factors are also related to spatial scales (Alftine and Malanson, 2004). On the global scale, climatic factors are the dominant factors that control vegetation distribution (i.e., vegetation gradients by latitude or altitude) (Elliott, 2011). On the regional scale, environmental factors which influence the treeline position and dynamics are more complex, however, because the dominant environmental factors related to treeline position vary from site to site and from species to species (Batllori et al., 2009), or due to interactions between climatic factors and local environmental factors (Ameztegui et al., 2016; Astudillo-Sanchez et al., 2017). Many studies observed local variations in the treeline upward shifting (Danby and Hik, 2007; Aakala et al., 2014; Trant et al., 2015; Schworer et al., 2017), even in the same study area (Mamet and Kershaw, 2012). The phenomena of local variation in treeline position and upward shifting also indicate that temperature is not the only environmental parameter which promotes treeline upward advancement.

5.3 Driving factors other than temperature for treeline upward shifting

Besides temperature, the dominant drivers for treeline upward shifting on the regional scale which have been proven by previous researches are: aspect (Danby, 2003; Bader and Ruijten, 2008; Dearborn and Danby, 2020), soil moisture (Liang et al., 2012; Astudillo-Sanchez et al., 2017), soil fertilization (Rousi et al., 2018), wind exposure issues and wind speed (Alftine and Malanson, 2004; Payette, 2007; Peringer and Rosenthal, 2011; Wagemann et al., 2015), N deficiency (Wang and Godbold, 2017), radiation stress (McIntire et al., 2016), biotic interactions (Tingstad et al., 2015), species composition (Aakala et al., 2014), surrounding vegetation that shields tree seedlings (Mazepa, 2005), drought (Barros et al., 2017; Gavilán and Callaway, 2017), volcanic eruptions (Gervais and MacDonald, 2001), fire

(Lloyd et al., 2005; Cierjacks et al., 2007; Brown, 2010; Colombaroli et al., 2010), grazing (Grace et al., 2002; Sarmiento and Frolich, 2002; Cairns and Moen, 2004; Ducic et al., 2011), land use changes (Bader and Ruijten, 2008; Wallentin et al., 2008; Kirdyanov et al., 2012; Ameztegui et al., 2016) and land management (Milligan et al., 2004; Pennisi, 2013). Understanding which environmental factors control the position and dynamics of alpine treelines is very important for linking ecological process and spatial patterns, as well as ecosystem responses to climate change (Elliott, 2011; Coops et al., 2013). However, there are no consistent research results about the drivers of treeline advance in the literature, and some results are even contradictory in different climate zones. Therefore, it is important to study the driving factors related to treeline dynamics at the local scale, especially in tropical and subtropical climate zones where a variety of human activities might aggravate the influences of climate change on treeline advance (Barros et al., 2017).

6 Conclusions

Recent studies on alpine treeline shifting show inconsistent results in different regions. However, the mechanism behind the inconsistent intensity of treeline advance in different locations remains unknown under global warming. Therefore, research on the alpine treeline advance globally, according to increasing temperature, will be the future direction. Moreover, current research indicates local variation in the alpine treeline advance, which also implies the existence of other driving factors of treeline upward shifting. However, it still remains unclear which factors (besides temperature) are the dominant factors for the local variations in treeline advance. To explore the local variations of alpine treeline advance and its dominant driving factors, large scale mapping techniques (e.g., remote sensing approaches) for alpine treeline location need to be studied and further developed in the future. In addition, studies comparing alpine treeline shifting in different climate zones will also be the future direction, in order to analyze the general mechanism of treeline shifting according to increasing temperature and the driving factors of local variation in treeline advance.

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全球变暖背景下高山林线交错带的动态综述

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摘　要：高山林线交错带是亚高山森林与苔原之间、亚高山森林与无树草原之间的过渡带状区域，是生物多样性热点区域，具有营养物质输入源和低海拔生态系统的碳固存等不可替代的生态功能，提供着各种生态系统服务。与高山林线交错带相关的三种树线是树种线、林线和木材线。由于高山林线交错带占据了树种耐受温度极限的极端区域，对气候变化非常敏感，经常被用作植被对全球变暖响应的指标。随着全球气候变暖的加剧和不同气候区海拔梯度的变化，高山林线交错带中的树高和生物量也会发生显著变化。同时分布在全球不同气候带上的林线变化也表现出不同的规律，其中的原因包括温度升高程度的不一致、优势种和植物群落的不同、人为干扰程度的不同等。另外，关于林线推进的驱动因素也无一致的研究结果，不同气候区之间的研究结果可能会相互矛盾。然而，目前在气候变化下的高山林线发展领域，缺乏全面的综述。因此，本文从以下四个方面对此前的研究进行了总结，并探讨了高山林线动态变化的理论基础和挑战：（1）高山林线动态变化的生态功能和生态问题；（2）监测高山林线动态变化的研究方法；（3）全球不同气候区的林线迁移；（4）林线向上迁移的驱动因素。

关键词：高山林线；林线交错带；林线动态变化；林线向上迁移