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Consequences of treeline shifts for the diversity and function of high altitude ecosystems

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Abstract

Treeline expansion is reported as a widespread response to rising temperatures, yet few studies have considered the impact of treeline advance on the diversity and function of high altitude systems. Evidence suggests that climate change is already having a negative impact on alpine diversity and is modifying functions such as carbon sequestration and nutrient cycling. Treeline advance is likely to further affect diversity and function, yet our understanding of the processes involved is limited. Here we review and synthesize literature that assesses the impact of treeline advance into treeless ecosystems. Using published literature, we explore to what extent treeline advance will lead to the displacement of alpine species and the fragmentation of alpine habitats. While large changes will be observed in the ecosystems above the current treeline as trees migrate, it is likely that these newly forested areas will deviate substantially from the established forests from which they have developed. Consequently, at the forest community level we investigate the potential for differential response speeds of typical forest plant species, and the potential for treeline advance to lead to community disassembly. Given that changes in species presence and abundance can alter the functional composition of plant communities, we explore the potential for shifts in tree distribution to lead to changes in carbon storage, nutrient cycling, and hydrological properties of ecosystems. Despite typically being intensively studied regions, the likely impact of forest expansion above the current mountain treeline has received relatively little attention and so we identify key knowledge gaps that should act as priorities for future research in mountain systems.

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Introduction

Recent and historical changes in species distributions in response to environmental change are well documented in the scientific literature. In recent decades, investigation of the impact of current changes in climate has been a major focus in biogeographical studies (Parmesan, 2006; Parmesan and Yohe, 2003; Walther, 2003). Climate conditions play an important role in determining the limits to species distributions. Consequently, when climatic conditions change rapidly, it is often observed that species distributions can respond rapidly, for example, by migration to new areas that have only recently become climatically favorable for survival (Pauli et al., 1996; Lenoir et al., 2008) or through range retraction elsewhere (Beckage et al., 2008; Kelly and Goulden, 2008). These changes in distribution will continue into the future as climate continues to warm (IPCC, 2007, 2013).

Upward elevational migration of mountain treelines and latitudinal advance toward the poles (treeline shifts) represent a well-studied and ecologically highly important example of species distributional change occurring across the globe. Many authors have discussed the factors responsible for controlling treeline position and the phenomenon and mechanisms of treeline advance; the majority of alpine and polar latitudinal treelines are showing at least some response to climate change (Harsch et al., 2009). However, despite the widespread nature of this biotic response to changing climate, little attention has been devoted to gaining an understanding of the impacts that this change in species distribution is likely to have in ecosystems occurring at and above the current tree limit. Forest advance into alpine areas will have profound effects on ecosystem structure and function. Trees are a key structural feature of the landscapes in which they occur and determine the soil and light environment and microclimate conditions experienced by the biotic communities associated with them, and also on the wider climate system through their functional roles in ecosystem processes such as carbon sequestration and hydrology.

Treeline position is strongly dependent on temperature (Tranquillini, 1979; Körner, 1998; Jobbágy and Jackson, 2000; MacDonald et al., 2008), although other factors such as precipitation levels and drought (Daniels and Veblen, 2004), nutrient availability (Sveinbjörnsson et al., 1992), and orographic and anthropogenic influences also play a significant role in treeline position (Holtmeier and Broll, 2005; Wieser, 2007). Treelines are, therefore, very sensitive to temperature increases associated with anthropogenic climate change, and they can provide early indications of the responses to be expected elsewhere in forest ecosystems. Climate change scenarios for 2100 predict a mean global temperature increase in the range of 0.3–4.8 °C compared with 1985–2005 mean values (IPCC, 2013).

The response of treelines to warming climate via an upward range expansion is widespread (Suarez et al., 1999; Kullman, 2002; Lloyd and Fastie, 2002, 2003; Moiseev and Shiyatov, 2003; Peñuelas and Boada, 2003; Shiyatov et al., 2005, 2007; Baker and Moseley, 2007; Devi et al., 2008; Beckage et al., 2008; Kharuk et al., 2009, 2010). A recent global meta-analysis by Harsch et al. (2009) found evidence for a treeline advance at 52% of studied sites, and in cases where no actual advance has been documented (e.g., Masek, 2001) treelines are often still responding to climate through changes in growth (Villalba and Veblen, 1997), growth form (Lescop-Sinclair and Payette, 1995), or density (Lescop-Sinclair and Payette, 1995; Sziecz and MacDonald, 1995; Camarero and Gutiérrez, 2004; Liang et al., 2011).

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However, rising temperatures at the regional scale will not necessarily lead to treeline expansion. Steep slopes and lack of suitable substrate can be important limiting factors for treeline advance at high altitudes (Batllori et al., 2009a; Macias-Fauria and Johnson, 2013). Where appropriate substrates occur, microsite factors determining temperature and soil moisture conditions are extremely important in allowing for the successful establishment of tree seedlings (Cui and Smith, 1991; Gobbi and Schlichter, 1998; Lee et al., 2004; Catorci et al., 2012). Establishment success can also be dependent on the degree of shelter due to microtopographic variation (Resler et al., 2005), surrounding ground-level vegetation (Germino et al., 2002; Smith et al., 2003; Bader et al., 2008; Mamet and Kershaw, 2012), and the presence of krummholz (Hättenschwiler and Smith, 1999; Germino and Smith, 2001; Batllori et al., 2009b), rocks, and boulders (Resler et al., 2005). This sheltering effect can result in positive feedback (Bader et al., 2008), whereby establishment of tree seedlings above the treeline promotes further establishment by creating more favorable microclimate conditions (Smith et al., 2003; Bekker, 2005; Resler et al., 2005).

Consequently, there will be considerable variability in the response of treelines to changes in climate at both the local and regional scale (Hofgaard et al., 2013), with some treelines remaining stable and lagging climate changes while others advance (Lloyd, 2005). This variability has important consequences for the diversity and function of ecosystems above the treeline, since rising temperatures in alpine regions will not always be associated with treeline advance. While experimental work assessing impacts of elevated temperatures on alpine and tundra vegetation have been conducted (Chapin et al., 1995; Walker et al., 2006) relatively few studies have looked directly at the impact of treeline advance on the invaded ecosystems. In the following sections of this review, we discuss the consequences of treeline expansion for the structure and function of ecosystems, using evidence from direct assessments of changes occurring in advancing treeline ecotones, experimental manipulation of ecosystems beyond the treeline, predictions from modeling studies, and indirect evidence from other ecosystems. We conclude by outlining important gaps in our knowledge in this area. Specifically, we discuss impacts on biodiversity through an investigation of the displacement of alpine communities, alterations to microclimate associated with changes in tree cover, and the influence of individualistic responses on community structure. We then move on to explore impacts on ecosystem function, specifically carbon and nitrogen dynamics, hydrology, and slope stabilization (see Fig. 1 for a visual summary). We aim for a global discussion of these topics, although most of the literature cited comes from studies of temperate and arctic regions, as this has been where most relevant research has been focused. While we explore the likely impacts of treeline shifts on biodiversity and ecosystem function, it is not our aim to exhaustively review the literature on treeline advance, which has been done previously. For detailed reviews on treeline positions, shifts, and their causes see Rochefort et al. (1994), Körner (1998), Harsch et al. (2009), Grace et al. (2002), Körner and Paulsen (2004), and Holtmeier and Broll (2005).

Biodiversity Impacts

High altitude areas can be disproportionately important for their biodiversity; high levels of habitat heterogeneity and isolation allow for the development of high levels of species endemism, species richness, and the retention of many rare species (Essl et al., 2009; Körner, 2003). However, mountainous areas are very sensitive to the effects of climate change and are also predicted to experience higher than average increases in temperature (Pauli et al., 1996; Dirnböck et al., 2011; IPCC, 2007).

Climate change will have diverse effects on plant communities, for example, advancing phenological events, extending growing season length, and altering plant productivity (Peñuelas et al., 2002; Walther et al., 2002; Parmesan and Yohe, 2003; Parmesan, 2006). Changes in climate affect plant distribution (Walther, 2003; Lenoir et al., 2008) and competitive dynamics (Callaway et al., 2002). Changes to plant communities may be particularly evident in mountainous or high latitude regions where the presence or absence of species is often determined by relatively low threshold temperatures (Körner, 2003; Kullman, 2007). The upslope migration of forests can be a threat for many plant species due to outcompetition for space or substrate (Grabherr et al., 1994). It is, therefore, probable that the upward migration of vegetation zones will eventually lead to species loss and a reduction in diversity through the removal of specialized species with small niche tolerances and an increase in more widespread species from lower altitudes (Jump et al., 2012).

Displacement of Alpine Communities

Treeline advance leads to a reduction in the area available for alpine and nival species and can cause the fragmentation of remaining habitat. Forest expansion in the Urals has already reduced the area of alpine grassland and heath by around 10%–30% (Moiseev and Shiyatov, 2003), and in the Mediterranean advancing shrub and broom have displaced nival vegetation (García-Romero et al., 2010). In Glacier National Park, Arizona forest encroachment has led to a reduction in diversity; open areas have four to five times higher diversity than areas with high tree cover but are much reduced in size as tree regeneration increases (Moore and Huffman, 2004).

A number of predictive modelling studies have come to similar conclusions; general circulation model scenarios coupled with ordinal regression models of alpine vegetation responses in Austria show that expansion of *Pinus mugo* is likely to occur at the expense of alpine habitat (Dirnböck et al., 2003). Moen et al. (2004) simulated treeline advance on Swedish mountains using climate predictions and a digital elevation model and found that the predicted degree of treeline advance led to a severe reduction in alpine areas: even a conservative estimate of a 100 m rise in treeline position would reduce the occurrence of alpine heath by 41%, and the majority of alpine areas remaining would be on scree slopes and boulder areas. Cliffs and rocky areas act as refugia for alpine species during periods of tree expansion, allowing alpine species to persist in areas with forest cover (Bruun and Moen, 2003); such areas could become increasingly important as treelines advance and further reduce alpine habitat. However, open refuges in newly expanding forest that are unsuitable for forest development will be inadequate to maintain the full range of species currently found in alpine areas since they will be dramatically different in terms of area, microclimate, and substrate quality compared with the range of existing alpine habitats.

Accordingly, alpine plant extinctions have been predicted. In New Zealand, substantial loss of species is expected under a scenario of a 3 °C rise in temperature and an associated 500 m rise in treeline, because the already fragmented alpine habitat will be disturbed by treeline advance and 93% of alpine habitat

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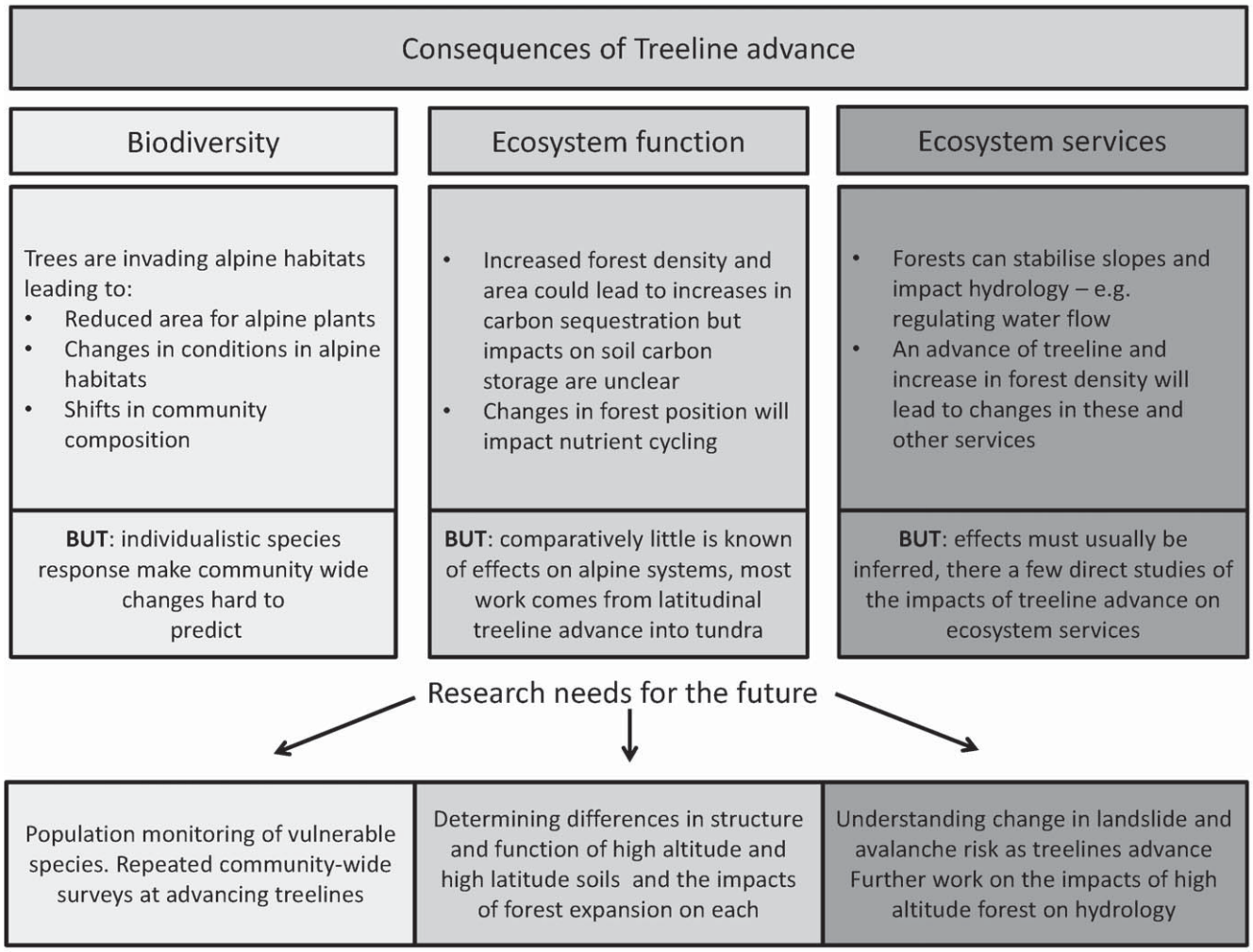


FIGURE 1. Summary of key points and research needs.

islands will likely be lost (Halloy and Mark, 2003). Dirnböck et al. (2011), combining the distribution of endemic species in the Austrian Alps with a model projecting forest expansion under different climate scenarios, found that, even with conservative estimations of climate change, the area of alpine habitat lost to forest was very high and that areas of high endemism suffered disproportionately.

Ground-level non-vascular plants such as bryophytes and lichenized fungi occurring beyond the treeline may be especially at risk from forest encroachment. They will face increased competition for light resources where elevated temperatures result in increased plant growth and/or the establishment of more competitive species from lower altitudes (Trivedi et al., 2008). For alpine communities dominated by non-vascular plants, such as *Racomitrium* heath, this is likely to result in their out-competition and replacement by faster growing plant species. This effect has already been reported for *Racomitrium* heath in response to changes associated with nitrogen deposition in Scotland (van der Wal et al., 2005). *Sphagnum* spp. occurring above treeline in peat-lands in both mountain and boreal areas could also be at risk from forest advance, as can be seen from their response to afforestation by modern management and to past changes in treeline position (Dudova et al., 2012). However, direct out-competition of such communities by forest species is unlikely since they typically occur well beyond the treeline under current conditions.

Trees substantially modify their surrounding environment (Holtmeier and Broll, 2005) and play a critical role in determining the identity of co-occurring plant species. Soil temperatures are lower during summer and higher during winter under tree canopies compared with open sites (Jennings et al., 1999; Körner, 1998; Kammer et al., 2009), and dense canopies can almost completely prevent the penetration of photosynthetically active radiation to understory level (Canham and Burbank, 1994). The transmission of light through the forest canopy is the most important factor limiting understory plant diversity and productivity (Hart and Chen, 2006), such that a positive relationship is often found between understory light levels and plant cover and diversity and a negative one with canopy density (e.g., Grytnes, 2000; Doležal and Šrutek, 2002; Coop et al., 2010). Forest development also modifies factors including soil, nutrient content, pH, and soil moisture (Augusto et al., 2002), all of which can impact the presence and abundance of understory species. The environmental modifications associated with tree establishment will, therefore, substantially modify plant communities as forest cover expands at high latitudes and altitudes. The influence of tree establishment extends well beyond the forest edge; Hofgaard (1997) found a high turnover of species across

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the treeline ecotone, and both Hofgaard and Wilmann (2002) and Camarero and Gutiérrez (2002) found a positive relationship between field layer diversity and distance from the treeline, and a negative relationship with tree cover. The commonality of evidence showing that alpine species are unable to survive below forest cover has important implications for diversity changes associated with treeline shifts, and displacement of alpine and nival species is therefore largely inevitable as treelines migrate upward.

Increased density in high elevation forest below and at treeline will also lead to changes in microclimate that are likely to drive changes in the composition of existing forest understory communities, as seen in experimental work manipulating the density of managed stands (Thomas et al., 1999; Ares et al., 2010). A higher density of trees throughout the treeline ecotone will reduce light levels and increase sheltering effects, reducing the probability of persistence of alpine species co-occurring in the woodland/grassland mosaics that often occur at high altitudes. However, many treelines were higher during the early Holocene, and Hofgaard and Wilmann (2002) found that some species occurring in plant communities above the treeline were indicative of past treeline position. An advance of the treeline was, therefore, less likely to dramatically change the field layer composition in such areas as it was pre-adapted to a higher forest position. Consequently, increased treeline elevation should not be viewed as an indication of the definite loss of species that currently exist in unforested areas at higher altitudes, though greater ecological information is needed for species in such areas in order to better predict those most likely to be displaced.

Differential Migration Rates and Community Disassembly

Species display individualistic responses to climatic change (Huntley, 1991; Pauli et al., 1996; Hansen et al., 2001) and will, therefore, migrate at different rates with climate warming. Such differential responses are detected both within and between plant functional types. Tree species co-occurring in the same forests can show different responses to change (Rasaba et al., 2013); for example, in southern Siberia (Kharuk et al., 2009) and the Alps (Motta and Nola, 2001), pine species show a greater response of growth and regeneration to temperature and are beginning to replace larch species as dominant. Similarly, proportions of tree species have been altered in the Northern Urals due to birch showing higher responses than pine or larch (Kapralov et al., 2006) and in Vermont where northern hardwood species are replacing boreal species that are suffering from high mortality rates as the climate warms (Beckage et al., 2008).

Upslope expansion of species on the sub-Antarctic Marion Island led to community changes because more than half of the species studied were unable to move upslope in pace with climatic changes, whereas the remainder demonstrated high migration rates; an average of 1.8 m yr^{-1} change in altitudinal limit (le Roux and McGeoch, 2008). Species responded individualistically to warming and nutrient addition treatments in alpine sites in Norway (Klanderud, 2008); grass species generally responded positively, whereas many forb species, mosses, sedges, and lichens had negative responses (species of large stature responded well, but small species showed a decline with treatment), leading to changes in community composition. As Pigott and Huntley (1978) identified, this interspecific variation in sensitivity to temperature can alter the competitive balance of communities, potentially leading to greater changes in species composition than would be expected based solely on individual species responses.

The migration rate of forest herbs is very different from that of tree species; migration rates of common European forest herbs are around 0.3–0.5 m yr^{-1} (Brunet and Von Oheimb, 1998). This contrasts sharply with the much higher rates of around 100 m yr^{-1} suggested for tree species (McLachlan et al., 2005). Understory plants tend to produce fewer seeds and have slower migration rates than tree species (Roberts, 1989) and are often dispersal limited (Matlack, 1994; Cain et al., 1998), so it is likely that understory species will not be able to respond quickly to changes in treeline position where advance is occurring rapidly. Epiphytic lichens and non-vascular plants such as bryophytes are also likely to have different migration and colonization rates from trees. Forest lichens and bryophytes have been shown to be very sensitive to forest disturbance (Johansson, 2008) and to have low growth and establishment rates. The negative impact of disturbance could be due to dispersal limitations (Sillett et al., 2000), establishment limitation (Kuusinen and Siitonen, 1998), or because of high sensitivity to microclimate (Sillett et al., 1994). Dispersal ranges and colonization rates are very variable among lichen species, and those with low colonization rates require more stand continuity (Ruete et al., 2014). Studies suggest that epiphytic lichens can be slow to respond to changes in forest conditions (Johansson et al., 2013), with current lichen distributions often reflecting past, rather than current forest conditions (Ellis and Coppins, 2007, 2009).

The logical consequence of individualistic species responses is that community composition will change, and new assemblages will form. There is evidence of this from Quaternary migration rates, inferred from isochrones (Huntley, 1991) and isopoll maps (Huntley, 1990) showing that past compositional changes in forests led to the formation of communities with no modern analogue. Edwards et al. (2005) also provided evidence from early Holocene (13,000–10,000 yr B.P.) fossil pollen, showing that during this time, the structure and functioning of communities was very different from that of assemblages found in the same areas today. Studies of fossilized packrat middens in the southwestern United States (Van Devender and Spaulding, 1979), together with macrofossil investigations of the tree flora of the Swedish Scandes (Kullman, 1998) and forest composition in the Pacific Northwest (Sea and Whitlock, 1995) during the early Holocene, confirm the generality of these findings of community breakup and change in response to past warming periods.

Consequences of Response Lags for Biodiversity

Both modelling (Chapin and Starfield, 1997; Bugmann and Pfister, 2000) and dendro-ecological studies have suggested that a lag of at least several hundred years is likely to occur between a change in climatic conditions and the subsequent development of forests at higher altitudes or latitudes. This lag is thought to be due to limitations in seed availability and establishment probability, disturbance events, and variations in tree growth rates. Furthermore, this lag varies both spatially and temporally due to local site conditions such as the presence of permafrost, krummholz, or high wind exposure (Lloyd, 2005). The critical factor that will determine how a lag in the response of vegetation to climate will affect biodiversity and community composition is the difference in response rate between different species and vegetation types. If, due to greater seed production and higher dispersal distances, trees respond more rapidly to increased temperatures than alpine plants, the likelihood of survival of many alpine species will be

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low. However, evidence exists that forests may be less responsive to interannual changes in climate because of the buffering effect of the canopy (Lenoir et al., 2008) and are often more influenced by long-term climate trends rather than interannual variation. In contrast, alpine vegetation is responsive to these short-term changes (Kullman, 2007) and is therefore likely to be able to respond faster, although more variably, to climatic change. The lag in treeline response to climate is likely to have positive implications for the survival of alpine communities, at least in the short term, as they might show increased response rates compared with forest understory communities and be able to migrate to areas of suitable habitat before they are displaced by advancing treelines.

Ecosystem Function and Services

High altitude ecosystems also play crucial roles in many ecosystem functions that will be impacted directly as temperatures rise, but also indirectly as plant species and life-forms from lower altitudes migrate upward and increase in abundance. High altitude forests provide important ecosystem services, including carbon sequestration and storage (Peng et al., 2009; White et al., 2000), slope stabilization, and erosion prevention (Stoffel et al., 2006; Schönenberger et al., 2005), and they play key roles in water and nutrient cycling (Dirnböck and Grabherr, 2000). There is already a large body of evidence to suggest that the response of forests to climatic change will have an impact on associated ecosystem functions (Saxe et al., 2001), although relatively little research has been conducted on the specific impacts of treeline advance in alpine systems. In the following sections, we discuss the likely consequences of treeline advance for some of the fundamental processes in which forests are involved.

Carbon Sequestration and Storage

Given the fundamental dependence of processes such as photosynthesis, respiration, and soil decomposition rates on temperature and CO_2 concentrations (Saxe et al., 2001; Xu et al., 2012), climate change will modify plant photosynthetic assimilation rates, and hence growth and production, as CO_2 concentration and temperature continue to rise (Griffis et al., 2003; Kallarackal and Roby, 2012). However, indefinite increases in productivity are not expected since studies show that the response of plant productivity to rising CO_2 saturates (Nabuurs et al., 2013). Forests are major carbon stores both in plant biomass and in soils (Hyvönen et al., 2007), and rising temperatures in high altitude forests could result in increased CO_2 sequestration, growth, and plant biomass (Devi et al., 2008; Fan et al., 2009). In a recent meta-analysis, Lin et al (2010) reported that biomass increased in all plant types with warming but that woody species showed the greatest response. As rising temperatures drive tree range expansion and increases in woody biomass at and above the current the treeline, carbon accumulation at treeline will increase, although such increases may be accompanied by carbon release from low altitude forests and the overall balance remains unclear (Zierl and Bugmann, 2007). There is, however, considerable evidence that increased growth and biomass at many treelines is increasing their ability to act as carbon sinks—for example, Lopatin et al (2006) in Russia, Tømmervik et al. (2009) in Norway, and from the many recent studies of increased tree growth, density, and forest expansion (Devi et al., 2008; Kharuk et al., 2009; Kullman, 2002; Villalba and Veblen, 1997). Modelled changes in vegetation and net primary productivity (NPP) in China under various climate warming scenarios show that a replacement of alpine vegetation by forest trees and shrubs occurs alongside overall increases in net photosynthesis (Wang, 2013), although such changes are expected to be highly spatially variable.

Increased growing season temperatures can combine with an increase in growing season length due to warmer spring and/or milder winter temperatures to increase net ecosystem production (NEP) (Griffis et al., 2003; Barr et al., 2007). However, the relationship between growing season and NEP can be complicated at high altitude. For example, there was a negative correlation between growing season length and NEP in subalpine forests in the Western United States due to a decrease in water availability because of decreased snowfall and earlier snowmelt (Hu et al., 2010). Similar results have been reported by other authors, including transitory increases in productivity that are then offset by higher temperatures and/or low water availability later in the season (Monson et al., 2002; Angert et al., 2005; Delpierre et al., 2009). The impact of growing season and temperature changes on carbon sequestration at the treeline will therefore be influenced by other factors and is likely to vary between regions.

Increased temperature is also likely to elevate soil respiration, which represents a major component of the carbon cycle. A meta-analysis by Rustad et al. (2001) found that an increase of temperature in the range 0.3–6 °C would increase soil respiration by as much as 20%, with the largest increases occurring in forested systems. This has major implications for carbon sequestration and ecosystem carbon balance (Sjögersten and Wookey, 2002). Soils in colder regions, such as treeline and alpine areas are especially sensitive to warming (Sjögersten et al., 2011). The response can be due to the direct effect of temperature on microbial activity; experimental warming of alpine soils in Switzerland led to a greater microbial use of older soil organic carbon, potentially reducing long-term C storage (Streit et al., 2014). Indirect effects of changes in ecosystem properties and functions can also be important; such as the change across the forest ecotone when treelines advance with subsequent changes in microenvironment and litter inputs.

Changes in vegetation cover at the treeline have been shown to have an impact on soil carbon storage and on the quality of soil organic matter (SOM). Kammer et al. (2009) found that tundra soils contained significantly more carbon in organic layers, but less in the mineral horizon compared with forest soils. Total stocks of carbon did not vary significantly, so treeline advance was likely to have little impact on soil carbon pools. Soil respiration rates were found to vary across the mountain birch forest-tundra ecotone in Abisko, Sweden (Sjögersten and Wookey, 2002), with higher rates occurring in forest soils, and in tundra soils transplanted to forest sites, than in tundra sites. Consequently, an expansion of forest into tundra in response to warming could lead to increased soil respiration, at least initially (Rustad et al., 2001), potentially reducing the impact of higher carbon storage in plant biomass.

Evidence of this offsetting of carbon sequestration exists from a study of forest expansion into tundra in northwest Alaska (Wilmking et al., 2006) where it was found that conversion of tundra into forest led to a net loss of ecosystem carbon; increases in soil respiration completely offset the increase in above ground biomass. This effect was also reported by Hartley et al. (2012), who found that soil carbon stocks were lower in mountain birch forest than in nearby tundra sites, by an amount that offset the increase in aboveground biomass, and that the establishment of birch led to a loss of soil carbon in tundra.

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These studies are in agreement with simulations conducted by Peng et al. (2009), who modelled the effects of climate change on forest C dynamics in northeastern China. However, Steltzer (2004) proposed that expansion of spruce into tundra would lead to increases in the carbon storage of the system due to the higher NPP values of forest compared with tundra and because of the possibly lower decomposition values, given the lower litter quality of trees and the cooling effect of shading. This study found that soil carbon accumulated under spruce trees as the trees aged. Although in contrast with the findings of the studies above, the work of Steltzer (2004) suggests the need for observational and experimental timescales that are long enough to fully capture the range of processes that can occur during natural stand development.

The relationship between tree cover and soil carbon storage may be very different depending on whether altitudinal or latitudinal treeline advance is considered; in the case of latitudinal expansion, trees are invading tundra sites with a high proportion of carbon contained within soils (Tarnocai et al., 2009), conversely, in altitudinal treelines the soils of the invaded alpine areas tend to be thinner with lower carbon content (Michaelson et al., 1996; Körner, 1998) and, because trees tend to preferentially regenerate on mineral soils in these areas, it is probable that tree expansion into alpine zones will increase the carbon content. Due to the importance of carbon storage in high latitude tundra sites, the majority of studies investigating the impacts of treeline advance on carbon dynamics have been concentrated in these systems; more studies in alpine ecosystems are needed to explore the impact of treeline advance on soil carbon properties and the balance between carbon sequestration and emissions. Increased focus on mountain systems will allow us to better identify how altitudinal and latitudinal treelines differ in this respect.

Nitrogen Content and Availability

Soil decomposition rates, and the amount of SOM, affect nitrogen availability (Spargo et al., 2011), and because nitrogen is frequently limiting to plant growth in high latitude/altitude areas (Rustad et al., 2001), it is important to consider how its availability may be affected both by climate change and by treeline advance. It is clear that increasing temperatures can directly alter nutrient cycling and potentially increase availability (Butler et al., 2012; Rustad et al., 2001), but the effects of climate warming on N cycling are likely to be complex. For example, recent evidence suggests that warming leads to increases in the amount of N fixed by cryptogams in arctic areas (Lett and Michelsen, 2014) but that reduced snow cover could reduce rates of decomposition and release of N from plant litter (Wu et al., 2014). It is also possible that an advance of treeline could have more impact than warming on N availability (Sjögersten and Wookey, 2005).

Forest soils at the mountain birch-tundra treeline in Fennoscandia had significantly higher ammonification and mineralization rates, and higher N availability than did tundra soils, so the expansion of birch forest in the study areas could have significant impacts on N cycling (Sjögersten and Wookey, 2005). Similar results have been obtained by Davis et al. (1991) in Fennoscandia and Sveinbjörnsson et al. (1995) in Alaska, where ammonium concentrations were found to be higher within the forest areas than at the treeline and krummholz zones, though Hartley et al. (2012) provided a counter-example.

Plants from lower altitudes tend to have lower N contents (Reich and Oleksyn, 2004) so the upslope migration of lower altitude plants as temperatures rise could decrease the N inputs from plant litter. However, the concentration of N in shrubs growing within a forest was found to be higher than those from tundra sites (Kaarlejärvi et al., 2012), so the converse could be true, with treeline advance leading to an increase in plant N levels. Lower N levels in needles and soil have been found at Arctic treeline sites and attributed to lower microbial activity at low temperatures (McNown and Sullivan, 2013). N availability reduced with elevation at Patagonian treelines and there was a change in microbial communities from bacteria to fungal dominated. Changes in forest cover and composition influence both microbial communities and N availability through litter inputs (Thébault et al., 2014).

Lower nutrient availabilities at the approach to and beyond treeline have been hypothesized to account for the increase in fine root biomass that has been observed at treeline compared with lower elevation forest (Hertel and Scholing, 2011), such that increased N availability through vegetation and temperature change at the treeline would likely lead to alterations in biomass partitioning. A positive feedback mechanism whereby warming increased tree establishment, which then increases nitrogen content and subsequent tree establishment, is possible (Sjögersten and Wookey, 2005; Sundqvist et al., 2011).

Evidence is mixed on the likely effects of treeline advance for N cycling and availability. As with C dynamics, most research has focused on latitudinal treelines; current evidence suggests that for N similar patterns of change will be observed at advancing altitudinal and latitudinal treelines, and N tends to be limiting at both (Rustad et al., 2001; Thébault et al., 2014). However, there is little direct evidence of the effect of altitudinal treeline advance, and since C and N are closely linked, because N is stored in soil organic matter (Thébault et al., 2014), more research is required to fully understand the impacts of altitudinal treeline advance on N availability and mineralization.

Hydrology

Mountain areas are extremely important in terms of controlling the volume and quality of water provision; plant cover and associated soil properties have a major influence on this service (Dirnböck and Grabherr, 2000). Plant cover can reduce flood flow but also increases infiltration into the soil and water table and hence will augment low flow and provide water supply throughout the dry season (Dirnböck et al., 2003). Treeline advance into previously treeless areas has the potential to significantly impact downslope hydrology since the development of krummholz and montane forest in grasslands increases the water absorption and retention capacities of soils (Dirnböck and Grabherr, 2000). Furthermore, the impacts of forests on hydrological properties can have implications for human societies because the degree of forest cover has been shown to affect sediment load and therefore water quality (Douglas et al., 1992). However, afforestation may lead to reductions in stream flow due to reduced runoff and reduced but more predictable water availability downstream (McVicar et al., 2007). In areas where water supply is already limited this could produce major problems, yet our current understanding of the impact of treeline advance on hydrology, especially in mountain areas, is limited by lack of direct research.

Slope Stabilization and Avalanche/Rockfall Prevention

Mountain forests also play a highly important role in slope stabilization and the prevention of landslides and avalanches (Bebi et al., 2001), and the anthropogenic lowering of the treeline due to land use in regions such as the European Alps is believed to have

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led to increased avalanche risk (Li and Yang, 2004). Modelling of avalanche risk based on forest cover found that the risk of extreme events depends on degree of forest cover and forest structural features (Teich and Bebi, 2009), with avalanche risk being significantly reduced by the presence and high cover of structurally complex undisturbed forest. Wehrli et al. (2006) combined a forest dynamic model (ForClim) with a model of rockfall risk (RockFor) in order to investigate the role of forests in preventing rockfall, and the degree to which this was affected by forest dynamics. It was found that high stand density, as well as high regeneration, improved the ability of forests to protect against small rocks but that forests were limited in their ability to prevent the damage caused by large rock displacement. Model simulations by Dorren et al. (2005) produced similar results; an absence of forest would lead to a greater impact of rockfall events, whereas an increase in tree density improved the protective function of forested areas.

Conclusion

Treelines are advancing upward and toward the poles in response to rising temperatures worldwide (Harsch et al., 2009). Although these changes in distribution and the reasons for them are relatively well investigated, much less attention has been focused on the impacts of treeline advance for ecosystems beyond the current treeline. Research discussed herein suggests that the upward migration of forests will have major consequences for biodiversity (Fig. 1), eventually leading to reductions in alpine diversity (Moore and Huffman, 2004; Halloy and Mark, 2003). However, this process is highly unlikely to occur as a simple replacement of one ecosystem by another. Rather, newly formed communities are likely to lack historical precedent, retaining some components of former vegetation types due to differential migration rates of individual species and variation in their tolerance of shading in the forest understory. Evidence from assessments of responses to past periods of temperature change indicates that species have responded to environmental fluctuations in the past in a similar way, with the breakdown of communities and formation of novel assemblages (Edwards et al., 2005; Van Devender and Spaulding, 1979). Such changes, and the possible impacts that they will have on the surrounding communities, represent a natural continuous process because treeline position and vegetation composition are dynamic. However, the current rate of climatic warming is unprecedented (IPCC, 2013) and is therefore likely to drive larger and more variable impacts on species migration and community response compared to that which has occurred in the past. In addition to impacts on diversity across the treeline ecotone and in the alpine zone above, ecosystem functions will be affected in a multitude of ways (Fig. 1) such as alterations to net ecosystem productivity and carbon storage (Griffis et al., 2003; Rustad et al., 2001), nutrient cycling (Sjögersten and Wookey, 2005), and hydrology (Dirnböck and Grabherr, 2000). However, at present there is insufficient information available, particularly from mountain regions to make reliable predictions on the direction and magnitude of effects in most cases. Mountain regions present a particular challenge in this respect as their varied topography can result in ecosystems showing a wide diversity of responses in a relatively small area.

Future Research

From a biodiversity perspective, knowledge is particularly lacking in the diversity of recently colonized areas of high altitude forest compared to long established areas and in the migration rates of forest understory and epiphytic species. Given the importance of alpine areas for biodiversity, and because of the high endemism rates, more field-based research on the impacts of treeline expansion on alpine species' survival and migration is required. An important aspect of such research should be the determination of the balance between competition and abiotic factors such as habitat availability and climate in determining the presence or absence of key species. Given the highly heterogeneous landscapes of mountain regions, such knowledge would allow us to substantially improve local scale modelling of species distributions to better forecast species loss or retention.

In terms of ecosystem function, research is required to assess the spatial heterogeneity of impacts of treeline advance for carbon and nutrient cycling. The imbalance in our understanding of tree invasion into arctic and alpine areas is particularly important to redress given feedbacks of such changes in vegetation and soil properties to the global climate system. Furthermore, in order to better predict the effects of forest expansion on ecosystem carbon storage, a better understanding of the relationship between above- and belowground processes is required across the alpine treeline ecotone.

Treeline inertia in response to climate could modify the degree of feedback that occurs with climate, and this phenomenon produces significant uncertainties in models attempting to simulate the consequence of treeline advance for climate feedbacks. Further field research on rates and time courses of treeline advance in arctic and alpine areas will contribute vital information that can reduce this uncertainty.

The advance of treelines into previously treeless ecosystems will continue as the climate continues to warm. The consequences of such advance for biodiversity and ecosystem function will be felt over ever-greater areas. To date, the majority of investigations of the consequences of treeline advance have been focused on northern tundra ecosystems, which seems intuitively sensible given both the expanse of tundra and boreal forest, with a consequently large potential to influence climate, and the far larger predicted rate of treeline advance (distances of kilometers rather than tens of meters) compared with alpine sites. However, given that mountain ecosystems cover a major proportion of the Earth's surface (somewhere between 20%–24% of total land surface) (IPCC, 2007), it is essential to ensure that data availability on ecosystem response to change in high altitude and high latitude regions is comparable. On the broadest scale, an assessment of the comparability of such data from altitudinal and latitudinal systems is lacking, and is necessary if we are to fully understand the interactions between spatial scale and heterogeneity and ecological processes over altitudinal and latitudinal gradients (Jump et al., 2009). A clear understanding of the potential for data transferability between these systems would be highly advantageous for more accurate modelling of ecosystem responses to current and future environmental changes.

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