The role of the circumarctic forest-tundra ecotone for arctic biodiversity

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Abstract:

The arctic forest-tundra ecotone, which links species communities of the boreal forest with those of the arctic tundra, is expected to respond swiftly to climate change with a profound reduction of tundra as the dominating scenario. With its circumarctic expanse and up to several hundred kilometres in width, the zone occupies a large part of the vegetated surface at high latitudes. Relocation and structural changes of the ecotone vegetation will affect not only plant but also animal and other biological diversity. A large number of arctic species are dependent on the forest-tundra ecotone in terms of food and habitat during parts of their life cycle or annual migration. In the 'Arctic Species Trend Index', developed to provide trends in arctic vertebrates, more than half of the species and data are from the forest-tundra ecotone. However, in assessments of arctic biodiversity, only the northernmost tundra-dominated areas of the ecotone are included. This is unfortunate and somewhat problematic since the treed part that serves as a source of seeds for new seedlings and saplings in the tundra-dominated part is excluded. This inconsistency hampers monitoring efficiency and biodiversity conservation efforts. During the International Polar Year, a large international research project on the forest-tundra ecotone established numerous sites around the circumpolar north where causes and consequences of vegetation change were analysed. This network of sites and data forms an excellent basis for necessary monitoring of the spatial and temporal complexity of forest encroachment into tundra and its relation to arctic biodiversity.

Keywords: arctic biodiversity; circumarctic vegetation; climate change; forest-tundra ecotone; monitoring; tree and shrub encroachment

Introduction

Arctic and subarctic vegetation including the forest-tundra ecotone (FTE; i.e. the transition zone from boreal forest to treeless tundra) has undergone large changes over past post-glacial millennia and over recent centuries and decades with further and more pronounced changes predicted for the current century (ACIA 2005). An increasing number of studies from the circumarctic have shown evidence of changing arctic ecosystems in response to recent climate change (ACIA 2005; IPCC 2007; CAFF 2010; Callaghan et al. 2011. A consistent major concern regarding threats to arctic terrestrial biodiversity, as stated in both individual scientific papers and assessments, is tree and shrub encroachment of the tundra (e.g. ACIA 2005; Chapin et al. 2005; Tape et al. 2006). Some models project that the FTE will advance north by as much as 200-600 km by the end of current century, resulting in a mean loss of 40-50% of the current tundra habitats at the circumarctic scale (ACIA 2005; Callaghan et al. 2005; Kaplan and New 2006). Although these rates are not supported by empirical data (Lloyd 2005; Van Bogaert et al. 2011; Hofgaard et al. 2012), tundra habitats and biodiversity are being affected by local, regional and global pressures including tree and shrub encroachment.

The current and potential vegetation change of the FTE will impact many arctic species within and north of the FTE including non-resident animals that are dependent on the FTE for food and habitat during parts of their life cycle or annual migration. Although more than half of the arctic vertebrate species in the ‘Arctic Species Trend Index’ (CAFF 2010) inhabit the forest-tundra ecotone, assessments of arctic biodiversity exclude most of the FTE. This inconsistency hampers monitoring efficiency and biodiversity conservation efforts. In this paper we outline the role of the circumarctic FTE for arctic terrestrial biodiversity, and discuss implications of FTE change and the need for site-based FTE monitoring at the circumarctic scale.

Diversity across the forest-tundra ecotone

The circumarctic FTE is a complex region-wide boundary where latitudinal and altitudinal gradients in environment, land use, vegetation, and biodiversity undergo major changes (Blüthgen 1970; Callaghan et al. 2002a). With its circumarctic expanse and up to several hundred kilometres in width, the FTE not only occupies a large part of the vegetated surface at high latitudes, but also encompasses a large variety of abiotic and biotic environments (Callaghan et al. 2002a). This environmental diversity provides living space for a diverse assemblage of organisms adapted to alternating arctic and boreal conditions characterizing the ecotone. Accordingly, relocation and/or structural changes of the FTE vegetation will most likely affect not only resident plant diversity but also animal and other biological diversity utilising the zone in a resident, migrational or episodic manner.

In general the FTE is characterised, from south to north, by a decrease in temperature, vegetation cover, soil organic matter, and nutrient stock as well as an increase in unoccupied space and periglacial processes (Holtmeier 2003). However, geologic, topographic, anthropogenic, ecological and climatic factors cross-cutting at local or regional scales have produced the structural diversity seen along the circumarctic FTE (Holtmeier 2003). This diversity is characterized by differences in both the dominant tree and shrub species, and the vegetation structure across the transition from forest to treeless tundra. Structural characteristics include diffuse and abrupt transitions, and the presence or absence of tree islands and krummholz (Holtmeier 2003; Harsch and Bader 2011). The heterogeneity of the FTE provides different macro and microhabitats which support a variety of organisms from soil microorganisms that specialize in particular habitats to animals with large ranges that require different habitats for forage and shelter. For example, animals typically associated with forested areas such as corvids, golden eagle, lynx, wolverine and red fox frequently use the FTE and the tundra to search for food and occasionally for breeding, and animals associated with tundra such as lemmings and caribou/reindeer periodically or annually forage in the FTE (Post et al. 2009; Killengreen et al. 2011).

Ecotones are known for their relatively high diversity (Harris 1988) since they contain potential habitat for species from both adjacent ecosystems. However, the concept is highly scale dependent and evidence for this general pattern of greater diversity at transitions between species communities can be weak (Walker et al. 2003; Shrestha and Vetaas 2009). Studies of species diversity across or within the FTE are scarce and most are from the alpine environment in temperate regions rather than the arctic. The general trend with decreasing species diversity towards high latitudes or altitudes (Young 1993; Kernaghan and Harper 2001; Callaghan et al. 2004; Vittoz et al. 2010) makes the FTE an indistinct species boundary. A general decrease in species diversity across the FTE and into the Arctic for many terrestrial fauna groups (Chervov 1995) is accompanied by a strong nutrient and productivity gradient (Callaghan et al. 2004). However, there is lack of evidence for a causal connection between latitudinal decrease in species diversity and productivity (Rohde 1992). Indeed some species groups with high frequency in the FTE show a reversed latitudinal trend, such as willows, wasps, sawflies, aphids and peatland birds, which has been related to habitat heterogeneity (Kouki 1999).

Generally the species diversity and turnover at FTE displays evidence of a broad transition zone (Hofgaard 1997a; Weckström and Korhola 2001) corresponding to landscape heterogeneity caused by the gradual change in tree cover (Doležal and Šrůtek 2002; Camarero and Gutiérrez 2002; Hofgaard and Wilmann 2002; Camarero et al. 2006; Bowden and Buddle 2010) but without strong correlation with any specific altitude or structural limit within the zone (e.g. forest line, tree line or krummholz line) (Hofgaard 1997a; Batllori et al. 2009). There are several reasons for the lack of correspondence between biodiversity and particular physical structures including the dynamic character of FTE, longevity of its characteristic species, and inertia processes (Holtmeier 2003; Payette and Delwaide 2003). Although there is restricted direct evidence of greater diversity within the FTE, the importance of the FTE to actic biodiversity can be inferred from large scale vegetation patterns in terms of both species and habitat diversity. As a gradient of decreasing tree and shrub density as well as a mosaic of patches of forest, trees, shrubs and tundra at different scales (Payette et al. 2001; Humphries et al. 2007; Harper et al. 2011), the FTE provides a variety of microhabitats with the potential of high biodiversity at a landscape scale.

Drivers of change

The forest-tundra ecotone is never in equilibrium with its abiotic environment due to the stochastic nature of natural and anthropogenic disturbance regimes and a recovery to pre-disturbance conditions cannot be expected (Hofgaard 1997b; Payette 2007). The gradual biodiversity change seen at a large scale FTE perspective might as a consequence be obscured when studied at smaller scales. This obscurity is also enhanced by the multitude of abiotic and biotic FTE drivers acting at a large number of temporal and spatial scales (Figure 1).

Temperature is generally considered the main driver of FTE recruitment and growth processes (Körner 1998; Grace et al. 2002; Holtmeier 2003), but this perspective is too simplistic in the context of ecotonal change (Sveinbjörnsson et al. 2002). Temperature changes may have immediate impacts on plant growth, yet responses in recruitment and establishment are site-specific and often not immediately responsive to increased temperature (Sveinbjörnsson et al. 2002; Aune et al. 2011; Holtmeier and Broll 2011; Walker et al. 2012). The structural diversity and pattern of the zone mediated through recruitment, growth and mortality is to a large extent driven by winter climate conditions other than temperature (Lavoie and Payette 1992; Harsch et al. 2009; Harsch and Bader 2011; Harper et al. 2011;

Mathisen and Hofgaard 2011) and biotic interactions such as herbivory (Cairns and Moen 2004; Olofsson et al. 2009). Wind and snow distribution constitutes a main structuring force to subarctic vegetation distribution, including trees and shrubs (Kullman 1986, 1998; Lavoie and Payette 1992; Schaefer and Messier 1995; Camarero et al. 2000; Alftine and Malanson 2004; Dalen and Hofgaard 2005; Holtmeier and Broll 2010; Harper et al. 2011) along with chronic and episodic abiotic and biotic disturbance regimes (Tenow and Bylund 1989; Payette and Delwaide 2003; Boudreau and Payette 2004; Jepsen et al. 2008; Aune et al. 2011; Trindade et al. 2011). If released from current pressures (abiotic or biotic) the current tundra dominated part of the FTE may change to patch forest (through increased growth and/or new recruitment) and subsequently change to forest if enhanced environmental conditions prevail (Kullman 1986; Weisberg and Baker 1995; Hofgaard 1997b). However, the responses are likely highly scale dependent and site specific (Harper et al. 2011).

Implications of change in the forest-tundra ecotone and the need for monitoring

On-going global change with warming temperatures at high latitudes is predicted to result in northward forest expansion within the current FTE and northward movement of the FTE (Epstein et al. 2004; Chapin et al. 2005; ACIA 2005; IPCC 2007). Implications for these shifts in forest cover throughout the circumpolar north include altered biodiversity in the FTE and current Low Arctic as well as climatic and socioeconomic consequences (Callaghan et al. 2002a; Vlassova 2002). The climate sensitive FTE vegetation provides essential feedbacks to the regional and global climate through energy partitioning, carbon storage, and carbon sequestration (Betts 2000; Harding et al. 2002; Hyvönen et al. 2007; McGuire et al. 2009; Tarnocai et al. 2009; Swann et al. 2010). In particular increased tree cover by non-deciduous species can decrease regional albedo of currently tundra-dominated areas and thus offset expected negative radiative forcings (Hyvönen et al. 2007; IPCC 2007). Accordingly, changes in this zone will have profound environmental effects beyond its own region with both direct and indirect effects on Arctic biodiversity (Harding et al. 2002; Callaghan et al. 2004; Chapin et al., 2005).

The lack of distinct separation between Arctic and sub-Arctic species assemblages and their dependence on the FTE for food and/or habitat calls for consideration of effectual monitoring of the FTE at relevant scales that allow for regional variation in dominating drivers and processes. In general, ecotones are considered sensitive to global climate change (Risser 1993). The projected swift response of the FTE and subsequent implications has repeatedly been quoted in the scientific, management, and political literature over the last decades including assessment reports (ACIA 2005; IPCC 2007). Despite its relevance to both the global climate and arctic biodiversity comprehensive coordinated monitoring strategies are lacking for the FTE. Monitoring of biogeographical and structural changes in the FTE is essential for biodiversity in general and for providing empirical-based estimated rates of change.

Current biodiversity monitoring within the FTE is largely species-based with limited inclusion of recorded variables related to change of the FTE itself. In the ‘Arctic Species Trend Index’, developed to provide trends in arctic vertebrates, a majority of the species and data sites representing the terrestrial environment are from the FTE (CAFF 2010). However, inclusion of the FTE in recommendations for monitoring efforts has focused almost exclusively on northernmost tundra-dominated part of FTE. South of the FTE boreal forest research focuses on the merchantable portion of the boreal forest. As a consequence the southern tree-dominated part of FTE makes up a ‘no man’s land’ regarding field-based monitoring. This is unfortunate as change of this part of the ecotone, composed of scattered forest patches and tree aggregations, will likely have the most pronounced effect on biodiversity and the global climate through vanishing habitats (infilling processes, Harper et al. 2011) and feedback mechanisms (Harding et al. 2002). This treed part of the zone serves as habitat for arctic wildlife and a source of seeds for new seedlings and saplings in the tundra-dominated part.

Central to the prediction of forest expansion is an increase in the reproductive capacity and establishment of new trees throughout the forest-tundra ecotone (Sirois 2000; Hofgaard et al. 2009; Tremblay and Boudreau 2011). However, the reproduction capacity naturally decreases northward from the subarctic forest towards the Arctic tundra due to a shorter and cooler growing season (Black and Bliss 1980; Hadley and Smith 1986; Sirois 2000; Sveinbjörnsson et al. 2002), and thus emphasizes the importance of the southern part of FTE. Consequently, a geographically widened monitoring approach incorporating both the latitudinal and longitudinal expanse and response variation of FTE would be desirable. Without this approach the relevance of, for example, the 'Arctic Species Trend Index' will be limited, since the trends provided by the index are closely related to changes in the southern treed zone of FTE. The dependence of arctic biodiversity on conditions outside the Arctic and the interplay between a multitude of drivers in shaping arctic biodiversity has been emphasized (CBMP 2008), but a holistic view of the role of the FTE is lacking.

Need for site-based monitoring

Much of the circumpolar FTE is remote with difficult or low accessibility. Remote sensing from air- and space-borne platforms can, therefore, be a significant tool in monitoring changes in FTE structural diversity. At a regional to circumpolar scale a resolution between 30 and 100 m is most commonly used due feasibility when large geographical areas are covered (Ranson et al. 2011). At this low resolution, individual trees cannot be recognized. Thus, resolution and classification problems can create unrealistic map- and model products regarding both current tree or forest distribution and the rate of change. Deviation between low resolution map products and ground-based products can be large, and if translated to a temporal scale in the order of predicted decadal to century scale changes. For example the circumarctic FTE tree cover mapping by Ranson et al. (2011) plots dense forests in current tree island regions (e.g. the northern Mackenzie region in Canada) and no forest in forested regions (e.g. northern Scandinavia). Data from ground-based studies provide a different story for tree cover in these regions (Walker et al. 2012; Hofgaard et al. 2012). This calls for site based monitoring in combination with remote sensing based monitoring (Mathisen et al. 2012). Site-based knowledge is fundamental to understanding intra- and inter-regional variation in causes of the current characteristics and dynamics of FTE. This site-based knowledge of diversity-driving processes across and along the FTE is needed both for enhanced understanding of its current status as well as for the development of better predictions of FTE responses to global changes and subsequent implications for arctic biodiversity. Successful site-based monitoring of the circumactic FTE needs to address the present location, characteristics and complexity of the boundary in a systematic manner, which requires approved definitions and concepts, as well as consistent techniques for measurements and experiments (Callaghan et al. 2002a).

During the International Polar Year (IPY; www.ipy.org), the last decade’s largest internationally coordinated research activity, attention was directed to the Earth’s polar regions. Under the auspices of IPY the project PPS Arctic (http://ppsarctic.nina.no), a multidisciplinary international research network, explored processes, changes, and spatiotemporal variability of biotic and abiotic drivers of change in the FTE with numerous sites around the circumpolar north (Figure 2). This network of sites and aggregated data forms an excellent basis for necessary monitoring of the spatial and temporal complexity of forest encroachment of tundra and its relation to arctic biodiversity. PPS Arctic uses common protocols based on principles endorsed by the International Arctic Science Committee (IASC;

www.iasc.com) and provides circumarctic coverage for global change impact studies. The endorsed principles are funded in conceptual models (Hofgaard 1997b; Callaghan et al. 2002a, 2002b; Holtmeier 2003; Payette 2007) specifying links between drivers of change, functional processes and focal ecosystem components.

Concluding remarks

The expectation of a swift response of FTE to climate warming is based on fairly simple global vegetation models that relate the position of the ecotone to the local climate. However, nature responds in a complex manner to climatic or other environmental changes. The multitude of abiotic and biotic drivers all interact in region-or site-specific ways causing a multitude of responses collectively offsetting modelled predictions. As a consequence, existing models need to be expanded to include more complex parameterized empirical data from a variety of sites representing a diversity of geographical and climatic sections of the circumarctic FTE. The traditional geographical separation between tundra and non-tundra using a ‘line’ is unfortunate and ecologically inconsistent. This inconsistency hampers goal-oriented monitoring with focus on cause and consequences of change, and how monitoring targets are mutually linked through ecosystem process relations. A change of the traditional approach to include and acknowledge the importance the entire FTE would be beneficial to biodiversity monitoring efficiency, comprehensive understanding of trends in arctic biodiversity, and biodiversity conservation efforts.

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Figures:

Figure 1. Main impact factors and ecological processes driving the forest-tundra ecotone (FTE) structural diversity. Impact of life history processes (in italic) is shown by open arrows, and filled arrows illustrate the impact of abiotic and biotic environmental factors on these processes. The effectual role of individual processes and factors is highly variable through time and space (shaded arrows). Some of the text in the figure is adapted from Holtmeier and Broll (2005).

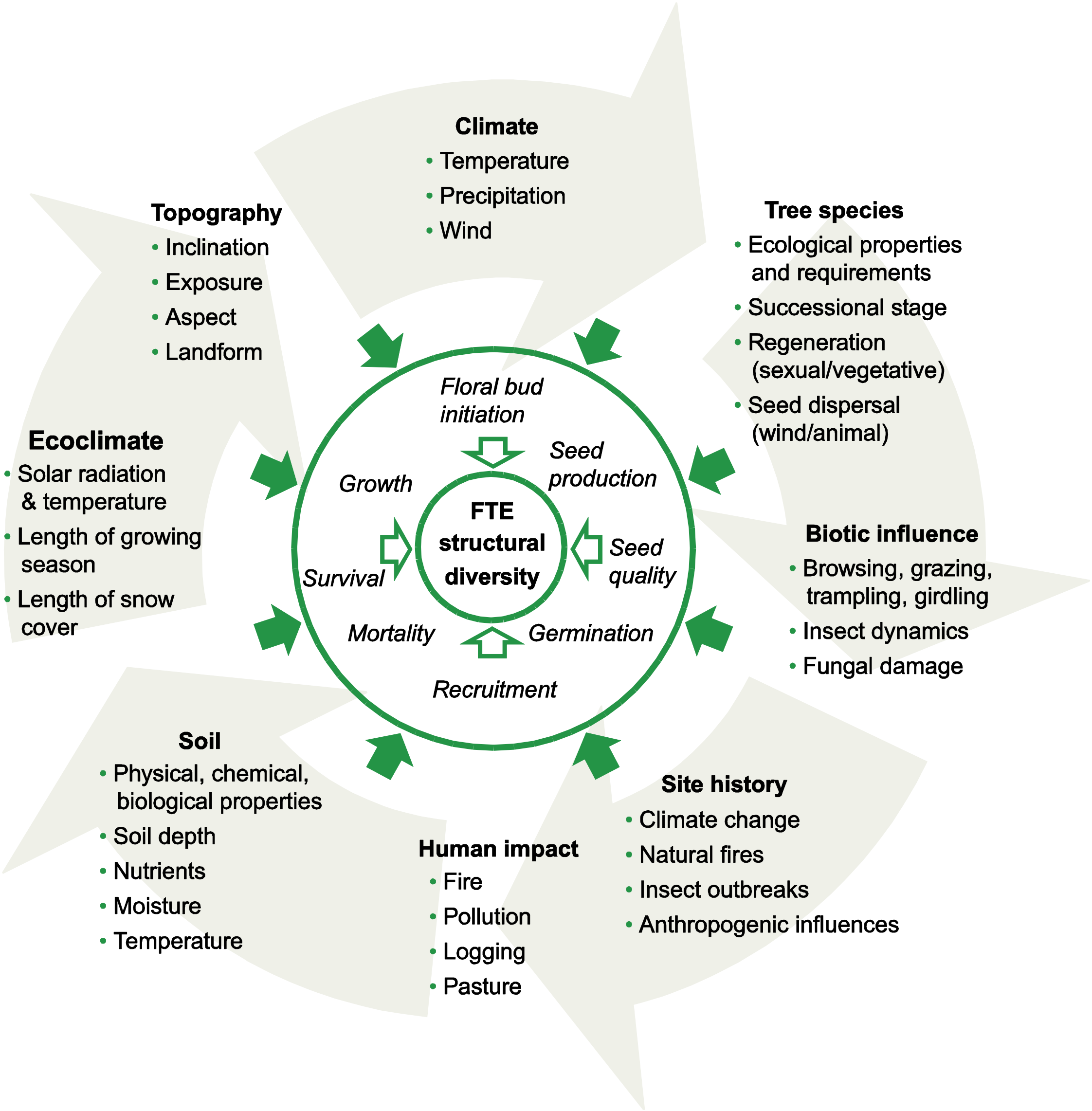

Figure 2. Distribution of PPS Arctic sites. Each dot represents one to several sub-sites (e.g. across latitude, longitude, altitude and aspect). The upper left photo signify northern Mackenzie region, Canada (X. Walker); lower left Mealy Mountains, southern Labrador, Canada (B. Starzomski); upper right Taymyr, Russia (N. Kolupanov) and lower right southern Troms, Norway (S. Aune).