

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

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25 **Abstract:**

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

45

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

48

49 **Introduction**

50 Arctic and subarctic vegetation including the forest-tundra ecotone (FTE; i.e. the transition
51 zone from boreal forest to treeless tundra) has undergone large changes over past post-glacial
52 millennia and over recent centuries and decades with further and more pronounced changes
53 predicted for the current century (ACIA 2005). An increasing number of studies from the
54 circumarctic have shown evidence of changing arctic ecosystems in response to recent climate
55 change (ACIA 2005; IPCC 2007; CAFF 2010; Callaghan et al. 2011). A consistent major
56 concern regarding threats to arctic terrestrial biodiversity, as stated in both individual
57 scientific papers and assessments, is tree and shrub encroachment of the tundra (e.g. ACIA
58 2005; Chapin et al. 2005; Tape et al. 2006). Some models project that the FTE will advance
59 north by as much as 200-600 km by the end of current century, resulting in a mean loss of 40-
60 50% of the current tundra habitats at the circumarctic scale (ACIA 2005; Callaghan et al.
61 2005; Kaplan and New 2006). Although these rates are not supported by empirical data
62 (Lloyd 2005; Van Bogaert et al. 2011; Hofgaard et al. 2012), tundra habitats and biodiversity
63 are being affected by local, regional and global pressures including tree and shrub
64 encroachment.

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

74

75 **Diversity across the forest-tundra ecotone**

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

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

99 the FTE and the tundra to search for food and occasionally for breeding, and animals
100 associated with tundra such as lemmings and caribou/reindeer periodically or annually forage
101 in the FTE (Post et al. 2009; Killengreen et al. 2011).

102 Ecotones are known for their relatively high diversity (Harris 1988) since they contain
103 potential habitat for species from both adjacent ecosystems. However, the concept is highly
104 scale dependent and evidence for this general pattern of greater diversity at transitions
105 between species communities can be weak (Walker et al. 2003; Shrestha and Vetaas 2009).
106 Studies of species diversity across or within the FTE are scarce and most are from the alpine
107 environment in temperate regions rather than the arctic. The general trend with decreasing
108 species diversity towards high latitudes or altitudes (Young 1993; Kernaghan and Harper
109 2001; Callaghan et al. 2004; Vittoz et al. 2010) makes the FTE an indistinct species boundary.
110 A general decrease in species diversity across the FTE and into the Arctic for many terrestrial
111 fauna groups (Chervov 1995) is accompanied by a strong nutrient and productivity gradient
112 (Callaghan et al. 2004). However, there is lack of evidence for a causal connection between
113 latitudinal decrease in species diversity and productivity (Rohde 1992). Indeed some species
114 groups with high frequency in the FTE show a reversed latitudinal trend, such as willows,
115 wasps, sawflies, aphids and peatland birds, which has been related to habitat heterogeneity
116 (Kouki 1999).

117 Generally the species diversity and turnover at FTE displays evidence of a broad
118 transition zone (Hofgaard 1997a; Weckström and Korhola 2001) corresponding to landscape
119 heterogeneity caused by the gradual change in tree cover (Doležal and Šrůtek 2002; Camarero
120 and Gutiérrez 2002; Hofgaard and Wilmann 2002; Camarero et al. 2006; Bowden and Buddle
121 2010) but without strong correlation with any specific altitude or structural limit within the
122 zone (e.g. forest line, tree line or krummholz line) (Hofgaard 1997a; Batllori et al. 2009).
123 There are several reasons for the lack of correspondence between biodiversity and particular

124 physical structures including the dynamic character of FTE, longevity of its characteristic
125 species, and inertia processes (Holtmeier 2003; Payette and Delwaide 2003). Although there
126 is restricted direct evidence of greater diversity within the FTE, the importance of the FTE to
127 arctic biodiversity can be inferred from large scale vegetation patterns in terms of both species
128 and habitat diversity. As a gradient of decreasing tree and shrub density as well as a mosaic of
129 patches of forest, trees, shrubs and tundra at different scales (Payette et al. 2001; Humphries
130 et al. 2007; Harper et al. 2011), the FTE provides a variety of microhabitats with the potential
131 of high biodiversity at a landscape scale.

132

133 **Drivers of change**

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

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

149 Mathisen and Hofgaard 2011) and biotic interactions such as herbivory (Cairns and Moen
150 2004; Olofsson et al. 2009). Wind and snow distribution constitutes a main structuring force
151 to subarctic vegetation distribution, including trees and shrubs (Kullman 1986, 1998; Lavoie
152 and Payette 1992; Schaefer and Messier 1995; Camarero et al. 2000; Alftine and Malanson
153 2004; Dalen and Hofgaard 2005; Holtmeier and Broll 2010; Harper et al. 2011) along with
154 chronic and episodic abiotic and biotic disturbance regimes (Tenow and Bylund 1989; Payette
155 and Delwaide 2003; Boudreau and Payette 2004; Jepsen et al. 2008; Aune et al. 2011;
156 Trindade et al. 2011). If released from current pressures (abiotic or biotic) the current tundra
157 dominated part of the FTE may change to patch forest (through increased growth and/or new
158 recruitment) and subsequently change to forest if enhanced environmental conditions prevail
159 (Kullman 1986; Weisberg and Baker 1995; Hofgaard 1997b). However, the responses are
160 likely highly scale dependent and site specific (Harper et al. 2011).

161

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

163 On-going global change with warming temperatures at high latitudes is predicted to result in
164 northward forest expansion within the current FTE and northward movement of the FTE
165 (Epstein et al. 2004; Chapin et al. 2005; ACIA 2005; IPCC 2007). Implications for these
166 shifts in forest cover throughout the circumpolar north include altered biodiversity in the FTE
167 and current Low Arctic as well as climatic and socioeconomic consequences (Callaghan et al.
168 2002a; Vlassova 2002). The climate sensitive FTE vegetation provides essential feedbacks to
169 the regional and global climate through energy partitioning, carbon storage, and carbon
170 sequestration (Betts 2000; Harding et al. 2002; Hyvönen et al. 2007; McGuire et al. 2009;
171 Tarnocai et al. 2009; Swann et al. 2010). In particular increased tree cover by non-deciduous
172 species can decrease regional albedo of currently tundra-dominated areas and thus offset
173 expected negative radiative forcings (Hyvönen et al. 2007; IPCC 2007). Accordingly, changes

174 in this zone will have profound environmental effects beyond its own region with both direct
175 and indirect effects on Arctic biodiversity (Harding et al. 2002; Callaghan et al. 2004; Chapin
176 et al., 2005).

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

188 Current biodiversity monitoring within the FTE is largely species-based with limited
189 inclusion of recorded variables related to change of the FTE itself. In the ‘Arctic Species
190 Trend Index’, developed to provide trends in arctic vertebrates, a majority of the species and
191 data sites representing the terrestrial environment are from the FTE (CAFF 2010). However,
192 inclusion of the FTE in recommendations for monitoring efforts has focused almost
193 exclusively on northernmost tundra-dominated part of FTE. South of the FTE boreal forest
194 research focuses on the merchantable portion of the boreal forest. As a consequence the
195 southern tree-dominated part of FTE makes up a ‘no man’s land’ regarding field-based
196 monitoring. This is unfortunate as change of this part of the ecotone, composed of scattered
197 forest patches and tree aggregations, will likely have the most pronounced effect on
198 biodiversity and the global climate through vanishing habitats (infilling processes, Harper et

199 al. 2011) and feedback mechanisms (Harding et al. 2002). This treed part of the zone serves as
200 habitat for arctic wildlife and a source of seeds for new seedlings and saplings in the tundra-
201 dominated part.

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

215

216 **Need for site-based monitoring**

217 Much of the circumpolar FTE is remote with difficult or low accessibility. Remote sensing
218 from air- and space-borne platforms can, therefore, be a significant tool in monitoring changes
219 in FTE structural diversity. At a regional to circumpolar scale a resolution between 30 and
220 100 m is most commonly used due feasibility when large geographical areas are covered
221 (Ranson et al. 2011). At this low resolution, individual trees cannot be recognized. Thus,
222 resolution and classification problems can create unrealistic map- and model products
223 regarding both current tree or forest distribution and the rate of change. Deviation between

224 low resolution map products and ground-based products can be large, and if translated to a
225 temporal scale in the order of predicted decadal to century scale changes. For example the
226 circumarctic FTE tree cover mapping by Ranson et al. (2011) plots dense forests in current
227 tree island regions (e.g. the northern Mackenzie region in Canada) and no forest in forested
228 regions (e.g. northern Scandinavia). Data from ground-based studies provide a different story
229 for tree cover in these regions (Walker et al. 2012; Hofgaard et al. 2012). This calls for site
230 based monitoring in combination with remote sensing based monitoring (Mathisen et al.
231 2012). Site-based knowledge is fundamental to understanding intra- and inter-regional
232 variation in causes of the current characteristics and dynamics of FTE. This site-based
233 knowledge of diversity-driving processes across and along the FTE is needed both for
234 enhanced understanding of its current status as well as for the development of better
235 predictions of FTE responses to global changes and subsequent implications for arctic
236 biodiversity. Successful site-based monitoring of the circumarctic FTE needs to address the
237 present location, characteristics and complexity of the boundary in a systematic manner,
238 which requires approved definitions and concepts, as well as consistent techniques for
239 measurements and experiments (Callaghan et al. 2002a).

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

249 www.iasc.com) and provides circumarctic coverage for global change impact studies. The
250 endorsed principles are funded in conceptual models (Hofgaard 1997b; Callaghan et al.
251 2002a, 2002b; Holtmeier 2003; Payette 2007) specifying links between drivers of change,
252 functional processes and focal ecosystem components.

253

254 **Concluding remarks**

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

269

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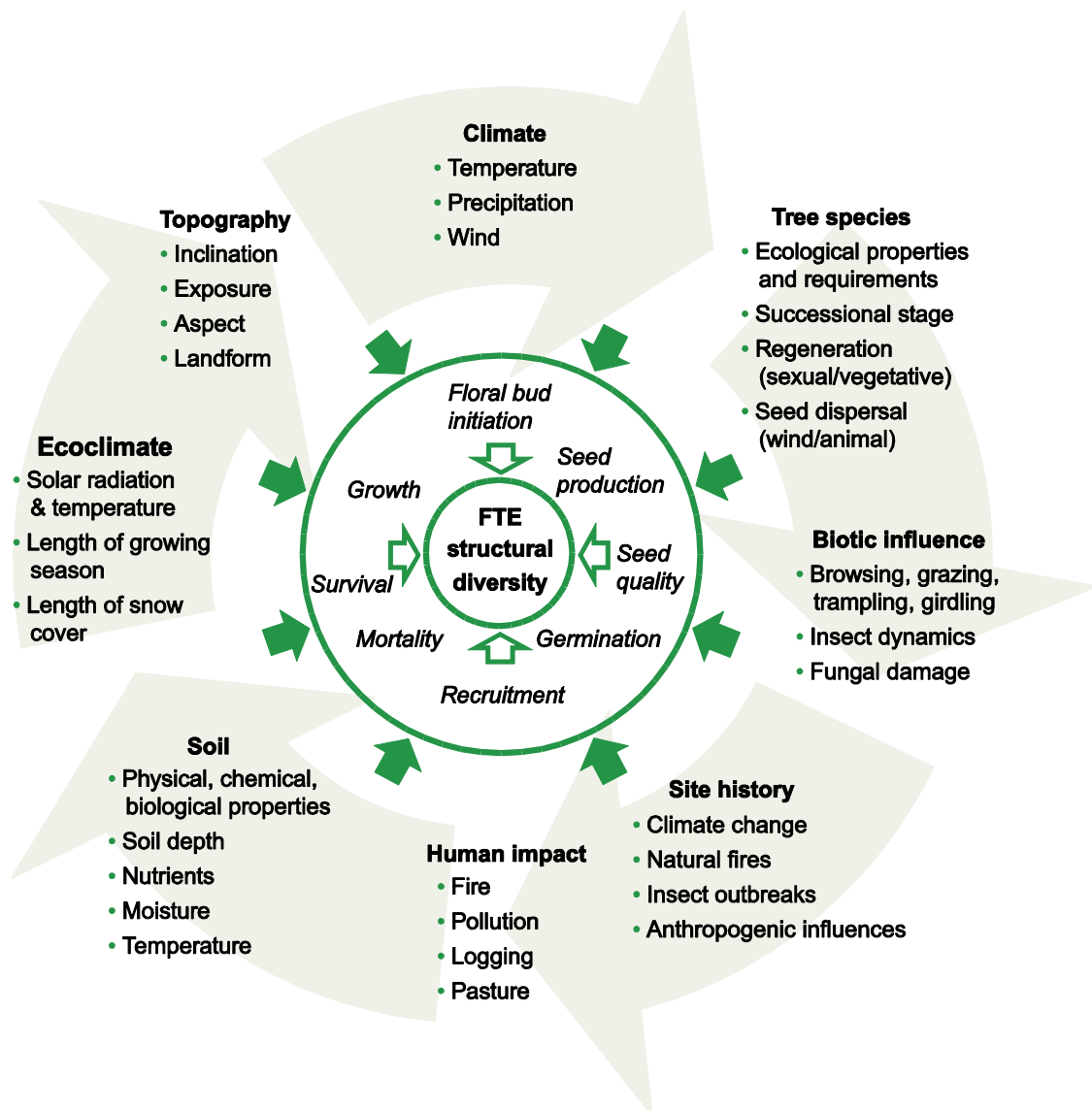
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495 **Figures:**

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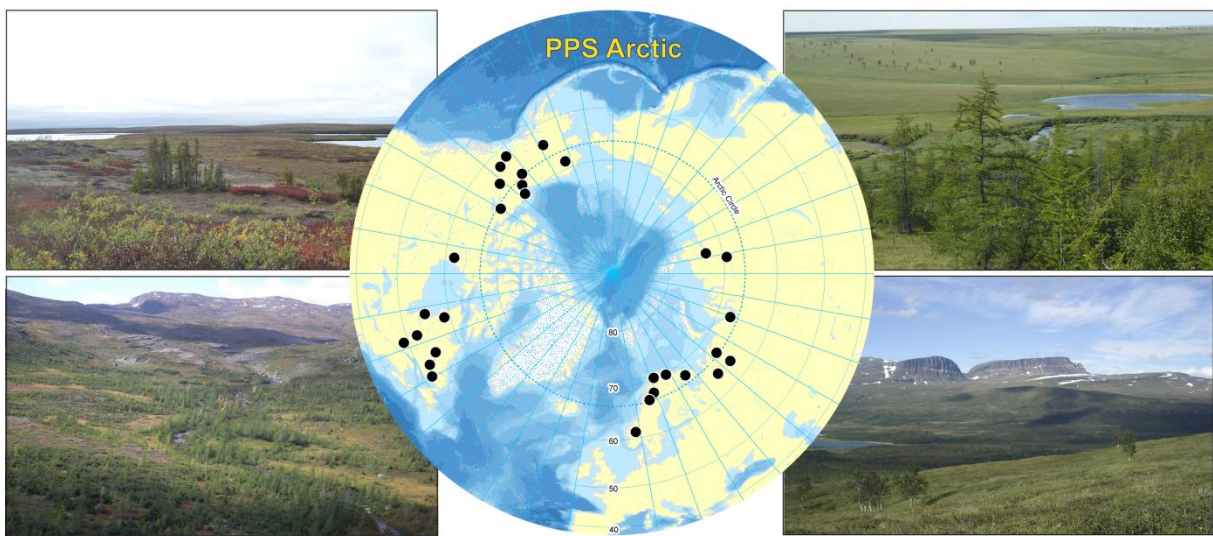
497 Figure 1. Main impact factors and ecological processes driving the forest-tundra ecotone
 498 (FTE) structural diversity. Impact of life history processes (in italic) is shown by open arrows,
 499 and filled arrows illustrate the impact of abiotic and biotic environmental factors on these
 500 processes.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



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