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Landscape structure and forest dynamics in subcontinental Russian European taiga

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The landscape structure and dynamics of NE-European forests were analysed using data from Landsat TM in combination with systematic surveys in the field. The frontier of intensive forestry meets forests undergoing natural dynamics in the image's area. In exploited areas the structural heterogeneity of the vegetation is pronounced, but the most prominent differences between the landscapes in exploited and natural areas were detected in the sizes and surroundings of stands of climax coniferous forests. The distance to the nearest vegetation edge, as measured around random points, decreases by 95% and the former landscape matrix turns to islands surrounded by deciduous vegetation. In natural areas the dynamic processes controlling the landscape structure include fires, windstorms and fluvial dynamics. Vegetation and the processes affecting it vary according to site qualities. In dry sites frequent low-intensity wildfires create small scale vegetation mosaics. In mesic sites post-fire successional stands of deciduous trees are present close to river valleys. In mature *Picea abies* dominated forests birches also remain essential components of the canopy layer, and forest regeneration occurs in windstorm gaps along with tree mortality through pathogen stress. These steady state boreal forests represent the climatic climax in the study area. The study suggests that some frequently cited generalizations about fire dominated boreal forest dynamics may be over-simplified.

1. Introduction

Boreal forests form a continuous circumpolar vegetation zone, the taiga, which is the largest terrestrial biome on Earth. Coniferous trees prevail in all sites from dry to mesic, even wet, and the environmental factors that determine the vegetation pattern tend to be more or less alike throughout the region. The most important natural disturbance is forest fire, while the other processes maintaining ecological succession in disturbance gaps include windstorms, snowbreaks, flooding, paludification, insect outbreaks and fungal diseases. The local details in vegetation development depend on site conditions and the timing and intensity of different disturbances

(Berg 1950, White 1979, Turner 1989, Kuusela 1990).

Forest succession in the Russian European taiga, i.e. the boreal forests between Fennoscandia and the Ural mountains, usually starts by the invasion of the broad-leaved pioneer trees of white birch (*Betula pendula*), downy birch (*Betula pubescens*) and aspen (*Populus tremula*). Scots pine (*Pinus sylvestris*) is also a typical pioneer tree of bare and treeless sites though it has an ambiguous nature including climax qualities (Kuusela 1990). In time the pioneer stands become occupied by the true climax trees of Norway spruce (*Picea abies*) and Siberian fir (*Abies sibirica*), and these forests are considered steady-state climatic climax (Tseplyaev 1965). While still being internally dynamic, they maintain their general nature until a new major external disturbance (fire) re-initiates the recovery process.

The average cycle between successive forest fires varies in European and American forests between 50 and 200 years, and the extremes in humid refuges may reach 500–800 years (Zackrisson 1977, Bonan & Shugart 1989). Fire intensity and severity also vary by terrain and by site conditions. Dry sites tend to present shorter cycles than the moister ones, and usually it is believed that the flammability increases with the age of the stand due to accumulation of unburned biomass (fuel) (Romme & Despair 1989). Again, differences between years can be distinctive. In normal years fires are few and only affect small areas, whereas destructive fires can affect large taiga areas in certain years (Engelmark 1984). Consequently fire-intensive years may be responsible for the creation of a major proportion of the successional stands in the landscape.

Vegetation dynamics promoted by windstorms resembles that of forest fires. In extreme years windstorms can have a great role to play in promoting natural forest regeneration (Foster 1988, Sernander 1936, Fischer 1992). In normal years their impact remains local and in certain sites it can be quite modest (Sirén 1955).

As a consequence of all of these processes, a pristine taiga landscape should comprise a mosaic of climax forests that alternate with stands undergoing succession (cf. Hall et al. 1991). Each forest type is floristically and faunistically distinctive, and the arrangement and relative proportions of different stand types further enhance the distribution and abundance of forest species (Angelstam 1992, Forman & Godron 1986, Haila et al. 1987). In man-dominated areas, by contrast, the construction of the landscape and its species composition reflect such factors as land holding and forestry. Now, when pristine forests and many original forest species are becoming increasingly threatened by contemporary forestry all over northern Europe (Barr & Braden 1988, Dudley 1992), a need has arisen to understand the structure and dynamics of those forest areas that have retained their original character (Hansson 1992).

This study examines boreal forest structure and dynamics in Russian European taiga where the last representative fragments of near-to-natural boreal forests in Europe can be found. Using satellite imagery to detect structurally distinctive forest and other landscape units, and ground-truth data from the most critical forest types, we will investigate the following problems:

1) which are the characteristic landscape-level patterns in natural taiga;
2) which are the external processes that create the observed patterns;
3) which forests represent steady state climatic climax; and
4) how do the forest landscape elements change after intensive harvesting.

The implications of the work's findings in relation to biodiversity management are discussed.

2. Study area and methods

The study area of 8100 km^2 (90 × 90 km) is defined by the limits of the Landsat TM 5 image (path 168, row 17, subquadrat B), which has its centre at 61°48′N, 57°97′E (Fig. 1). It represents the NE corner of forest-covered Europe, approximately 400 km east of the city of Syktyvkar, the capital of the Komi Republic of Russia.

The image presents the headwater zone of the River Pechora adjacent to the East European platform of Mesozoic origin; in addition Paleozoic formations are present near the Ural mountains (Sidorenkova 1984). Some ridges which are locally known as *parma*s (Komi name) are also present in the image's area, although Quaternary sedimentary plains of low elevation (appr. 100–200 m a.s.l.) prevail. The podzolic soils typical of the boreal zone alternate with peatlands. The northern margin of the River Pechora is marked by a sandy terrace occupied by dry *Pinus sylvestris* forest. Deciduous forests are most commonly found in river valleys. Although forest fires have been suppressed in recent decades, marks of fire, and forests in post fire successional stages can easily be found in many places.

The Eurasian taiga can be divided into ecologically distinctive areas along a climatical gradient from oceanic to continental. The monitored area belongs to the subcontinental area of the middle boreal vegetation zone, where summers are cooler, the temperature range lower and winters less severe than in the continental areas east of the Ural mountains (Sector group OC in Tuhkanen 1984). The average annual temperature is 1.6°C and the annual precipitation is 470 mm in the nearby town of Troitsko-Pechorsk (Sidorenkova 1984). Winters are continentally cold but summertime temperatures and the amount of rainfall are quite similar to those in central Fennoscandia.

The study area presents the current frontier of advancing industrial-scale forest exploitation. The Yaksha settlement, which is the local centre of forest harvesting, lies a few kilometres away from the study area. Extensive clear-cutting areas occupied by naturally regenerating vegetation of deciduous trees continue hundreds of kilometres to the west and south. The lowland part of the Pechoro-Ilych Biosphere Reserve preserves a fraction of the original vegetation near Yaksha.

The forests in the central and eastern parts of the image's area are much less affected by man. Although riverine areas and other easily accessible places have traditionally been used as sources of household timber, most forests have presumably never been harvested. Also the peatlands have retained their natural condition except for riverside swamps and flooded meadows, which are used for hay-making. There is thus good reason to believe that in this part of the image's area most vegetation patterns and limits between adjacent forest units are natural.

The Landsat TM image that was used in this survey was recorded on 19th June 1988. It was processed using data recorded in the TM channels 2 (0.52–0.60 μm), 4 (0.76–0.90 μm) and 7 (2.08–2.35 μm) in the National Land Survey of Finland. A transparency was produced with a film scanner to the scale 1:500 000, and further enlarged to 1:100 000 and 1:50 000 for visual interpretations. The acquired image enhancement product is especially sensitive to fine scale variations in boreal forest vegetation (cf. Kalliola & Syrjänen 1991).

The visual interpretation of the TM image was made in two phases. First, image examination combined with small plane flight observations over the most critical areas enabled us to develop a general interpretation key. Thereafter the area covered by the image was divided subjectively into 7 regions or subregions representing human influence, riverine areas, and other general features of the landscape.

A quantitative-qualitative survey of the landscape structure was made at 577 random points. These points we located on the image (scale 1:100 000) with the help of a transparent coordinate plate. For each point, the following characteristics were determined by the same person (K.S.): region or subregion (based on rough visual delimitation of major landscape elements, Fig. 1), ground cover and vegetation type (15 categories, Table 1), structural heterogeneity (the number of colours within a radius of 500 m, i.e. an indication of variations in the ground cover's reflectancy), distance to the closest edge of the nearest neighbour (km), sharpness of the edge (sharp, intermediate, smooth), type of the edge (natural, unknown, man-made), patch outline at 2.1 km (recorded as the number of transections by the same vegetation type at the perimeter of a circle of radius 2.1 km) and patch extension percentage at 2.1 km (recorded as the percentage of the perimeter of a circle of radius 2.1 km around the point, crossed by the same vegetation type).

Data on forest structure was collected in September 1992 along 20 transects near the River Pechora, representing the major forested ground cover types in the natural part of the image's area. The transects were 500 m long and were placed so that they covered only one vegetation type of the satellite image. 1–5 transects of each colour type of the image were studied. The basal area of the tree species was determined by relascope surveys in 10 sites on each transect 50 m apart; in each site, an average individual of the

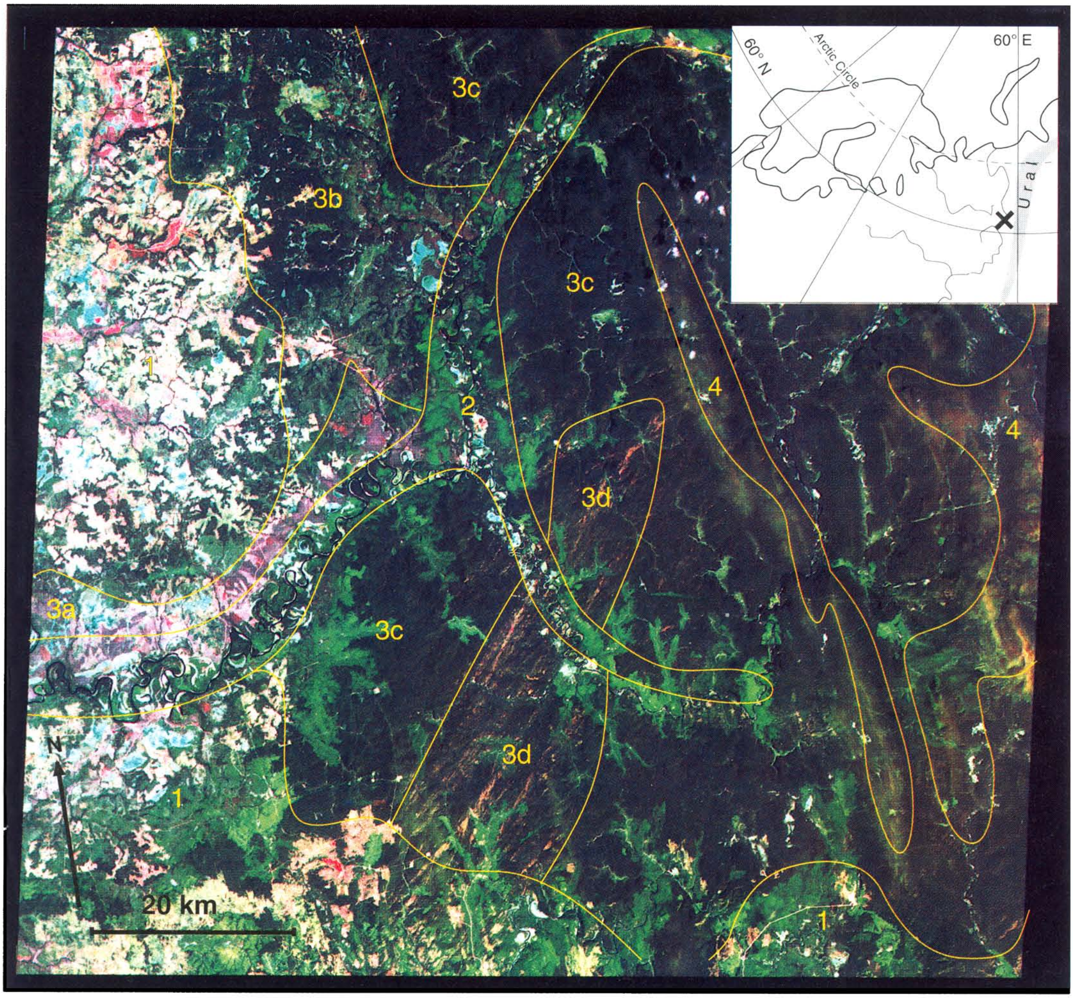

Fig. 1. Landsat TM-image of the Pechora region in the Komi republic, Russia. Dark green = mature *Picea* forest, dull green = mixed coniferous forest, light green = deciduous forest, dull red = dry pine forest, red = burned area, grey = mixed forests and mires, orange-brownish = storm tracks, pinkish – white colours = open areas and regenerating vegetation, blue = wet mires, black = water. (For a key to colours, see also Table 1). ©ESA/1988/EURIMAGE, National Land Survey of Finland, Remote Sensing and Thematic maps. — 1. Exploited plains, 2. Riverine areas, 3. Unexploited plains; 3a. Dry *Pinus* taiga, 3b. Mixed taiga, 3c. Uniform taiga, 3d. Windstorm taiga, 4. Elevated ridges. (see Table 2).

dominant species was selected to serve as an example tree of the stand (Table 1).

The other set of tree data (Table 4) come from a sampling corridor of 2 × 500 m (0.1 ha) along which all the trees and shrubs were identified, the DBH (diameter at breast height) of the trees was measured (tree = DBH over 5 cm), the state of the trees was determined, and decomposing trunks crossing the middle line of the transect were counted. The data were collected separately for each section of 20 × 2 m. In the present article these data are used so far as they relate to the general landscape structure; in a later article they will be used for a finer-grained analysis of internal forest structure and dynamics.

3. Results

3.1. Landscape structure

Natural forests dominated by *Picea abies* comprise half of the image's area (Fig. 1, Table 1) the other half being a mosaic of ten other forest classes, clear-cut areas, mires and some miscellaneous landscape types. *Picea abies* and *Pinus sylvestris* are the most important coniferous trees in most forests; *Abies sibirica* is also very frequent but always remains less abundant. *Betula* spp. form mixed forests together with coniferous trees and/or *Populus tremula*. The other tree

Table 1. Colour-key for the Pechora TM image (Fig. 1) with reconnaissance data of ground cover and vegetation. Relative coverage (RC) gives the percentage of hits out of 577 random points. Data of trees (mean ± *SD*) are based on relascope surveys in 10 sites per transect 50 m apart; in each site, a typical canopy-forming tree was studied and the table gives their average height and diameter at breast height. *N* = number of relascope surveys, – no data available.

Colour	Ground cover			Example tree		Average basal area (m²/ha)								
	Vegetation	*N*	RC	height m	dbh cm	*Abies*	*Larix*	*Picea abies*	*Pinus cembra*	*Pinus sylv.*	*Betula* spp.	*Populus tremula*	*Salix caprea*	Dead trees
Dark green	*Picea* dominated forest	50	48.0	16.7 ±2.1	26.2 ±6.1	3.5 ±3.7	0.2 ±0.6	17.9 ±6.8	1.3 ±1.6	0.9 ±2.8	4.0 ±5.1	0	0	1.9 ±2.5
Dull green	Mixed coniferous forest	20	3.3	16.6 ±2.5	21.8 ±5.4	2.6 ±3.2	0.3 ±0.6	7.1 ±5.7	0.7 ±1.4	6.0 ±7.6	7.5 ±4.0	3.1 ±4.4	0.1 ±0.5	0.9 ±1.1
Green	Mixed deciduous forest	20	10.6	16.6 ±0.1	22.1 ±5.5	3.4 ±3.3	0.5 ±2.3	12.6 ±6.0	0.2 ±0.4	1.2 ±4.5	18.2 ±7.6	0.7 ±1.2	0	0.5 ±0.6
Bright green	Deciduous forest	20	5.5	16.2 ±2.1	21.3 ±0.6	2.0 ±2.0	0.7 ±1.4	7.8 ±2.8	0	1.2 ±1.6	13.5 ±6.1	4.6 ±4.4	0.1 ±0.3	0.7 ±1.1
Grey with green	Coniferous, heterogeneous class	20	5.4	15.5 ±3.1	28.8 ±10.4	1.5 ±2.0	3.2 ±3.2	3.4 ±2.9	0.3 ±0.6	9.8 ±6.9	4.5 ±3.6	0.1 ±0.3	0.1 ±0.2	1.9 ±1.2
Grey	*Pinus* mire	20	0.3	13.1 ±1.3	23.9 ±7.3	0.2 ±0.7	0.1 ±0.3	3.5 ±4.3	1.5 ±2.2	12.9 ±6.7	2.1 ±1.4	0	0	2.1 ±2.3
Dull red	Dry *Pinus* forest	20	1.6	14.9 ±1.8	26.8 ±8.9	0	0	0.1 ±0.2	0	22.0 ±7.0	0.8 ±1.4	0	0	1.3 ±1.5
Red	Dry *Pinus* forest, burned	20	0.2	14.4 ±1.2	27.0 ±5.3	0	0	0	0	20.5 ±4.7	0	0	0	2.0 ±1.6
Whitish pink	Recent clear-cut area		10.0	–	–	–	–	–	–	–	–	–	–	–
Greenish pink	Regenerating vegetation	10	3.6	9.9 ±2.4	15.2 ±5.8	0	0.1 ±0.3	0	0	4.9 ±2.6	4.9 ±3.7	0	0	0.2 ±0.4
Orange brown	Windstorm gap		1.6	–	–	–	–	–	–	–	–	–	–	–
Greyish brown	Sparse coniferous hill forest		6.6	–	–	–	–	–	–	–	–	–	–	–
White & blue	Open mire		2.8	–	–	–	–	–	–	–	–	–	–	–
White	Bare soil		0.2	–	–	–	–	–	–	–	–	–	–	–
Black	Water		0.5	–	–	–	–	–	–	–	–	–	–	–

species are less important components at the level of the total landscape.

The image was visually divided into four major landscape types (regions, for subregions, see Fig. 1B and Table 2):

1) intensively *exploited plains*,
2) *riverine areas*,
3) predominantly *unexploited plains* and
4) *elevated ridges* (*parma*s)

The general appearance of the vegetation and the overall landscape structure are very different between these regions.

The lowland plains are characterized by a dissected relief of repeating river valleys. The exploited and unexploited areas differ drastically from each other in most of the characters measured to describe the landscape.

The intensively *exploited plains* (region 1) present heterogeneous vegetation due to abundant clearcut areas and stands of early succession. Most of the edges between adjacent patches are sharp, many are man-made and the patches display convoluted outlines. The distance to the edge of the nearest neighbour is about 300 m.

The *riverine areas* (region 2) also appear heterogeneous as they display four physiognomically different vegetation types within the radius of 500 m. The distance to the edge of the nearest neighbour stays at 200 m. Most vegetation edges are natural, although some patches have undoubtedly been created by man. Half of the edges are sharp, while about a tenth of the edges changes evenly between adjacent successional stands. Several patches occur as relatively small (1–25 ha) habitat islands of edaphically contrasting site characters. The *Picea*-dominated areas are predominantly minerotrophic mires with solitary individuals of *Pinus cembra* being present. The well-lighted terrace margins often harbour mixed stands of *Pinus sylvestris* and *Larix sibirica;* the undergrowth is formed by shrubs including *Alnus viridis* and *Lonicera caerulea. Picea* and *Abies* form dense patches of young trees, and sometimes also *Populus tremula* is present. Furthermore this region is characterized by small meadows, narrow beaches and riverside thickets of *Salix viminalis* (sensu lato). The typical size of these patches is around one hectare or less, i.e. near or below the resolution limit of the Landsat TM imagery.

In the predominantly *unexploited plains* (region 3), physiognomically uniform vegetation patches are extensive. Distances to the edges of the nearest neighbours are usually long, and most forests represent the state of climatic climax. The

Table 2. Landscape characteristics (mean ± *SE*) in different regions and subregions of the study area. *N* = number of random points studied. Heterogeneity = number of different ground cover types within a radius of 500 m. Distance to nearest neighbour in km. Patch outline = the number of transects by the same patch at a radius of 2.1 km. Patch extension = percent cover of same vegetation type at the perimeter of a circle with 2.1 km radius.

Regions and subregions	*N*	Hetero-geneity	Nearest neighbour	Edge characteristics (%) sharp	smooth	nat.	artif.	Patch outline	extension
1. Exploited plans	178	3.9 ± 0.1	0.3 ± 0.06	71	5	55	26	2.2 ± 0.2	21.1 ± 1.9
2. Riverine areas	66	3.7 ± 0.1	0.2 ± 0.02	51	11	91	5	0.9 ± 0.2	13.2 ± 21.6
3. Unexploited plans									
a. Dry *Pinus* taiga	8	3.6 ± 0.3	0.2 ± 0.05	38	0	88	12	1.8 ± 0.6	16 ± 6.3
b. Mixed taiga	33	2.9 ± 0.1	1.2 ± 0.52	64	3	94	3	2.8 ± 0.5	41.9 ± 7.6
c. Uniform taiga	229	1.9 ± 0.1	3.6 ± 0.40	54	11	94	6	2.2 ± 0.1	73.8 ± 2.2
d. Windstorm taiga	27	2.9 ± 0.1	1.0 ± 0.51	59	7	89	7	5.4 ± 0.7	67.2 ± 7.5
4. Elevated ridges	36	2.4 ± 0.1	0.7 ± 0.27	19	42	97	0	1.9 ± 0.2	54.8 ± 5.1

dynamics of each of these subregions is to a large extent characterized by forest fires of different frequencies and intensities.

The sandy terraces north of the Pechora River present a distinctive belt of lichenous-shrubby *Pinus sylvestris* forests (subregion 3a). This *dry Pinus taiga* subregion occupies a relatively small area but it differs greatly from the surrounding forests on less barren substrates. The heterogeneity of this landscape is pronounced, as in riverine and managed regions. Also, the distance to the edge of the nearest neighbour — only 200 m — is distinctive when compared to other subregions in unexploited plains. The sharpness of the edge was in most cases (60%) characterized as intermediate, which means that no major physiognomical changes were usually observed between adjacent vegetation patches; in the remaining 40% of the cases such edges are however sharp.

In the *mixed taiga subregion* (3b) north of the Pechora River the landscape is a mixture of dryish and mesic forests dominated by *Pinus sylvestris* or *Picea abies*, and of various types of peatlands. The vegetation is structurally heterogeneous and many of these patches are relatively small and intermingled. These characters are tied to the dissected relief of the landscape, and to the varying soil conditions and drainage. The distance to the nearest neighbour (1.2 km) is 6 times greater than in the subregion of dry *Pinus* taiga.

The subregion of *uniform taiga* (3c) comprises most of the unexploited plains. The average distance to the nearest neighbour is as long as 3.6 km, and the same landscape patch on average crosses a circle drawn at 2.1 km around a random point in 74% of the length of the perimeter (patch extension %). About half of the natural limits between adjacent patches of vegetation are sharp, due mainly to abrupt changes in the relative proportion of deciduous trees and the presence of open mires. Differently sized stands of deciduous, mixed deciduous, or mixed coniferous forests follow the river valleys. Such areas are clearly distinguishable patches of vegetation (Figs. 2A, B), and in most cases they represent post-fire succession, where large birches and aspens are undergrown by coniferous saplings. However, the prevailing forest type (78% of the subregion) is *Picea*-dominated forest with *Abies* and *Betula* spp. being present (Figs. 2D, E). The latter forests are taken to represent the climatic climax, though their internal dynamics appears complex: patches of dead or dying trees are common at any location. No marks of recent disturbance by wildfires were detected in these forests.

One of the most eye-catching features in the unexploited plains is the parallel chains of storm tracks (*windstorm taiga*, subregion 3d). It is possible that these were created by a single storm in 1986–1987, and that the fallen trees were turning brown at the time of the image's registration about two years later. In 1992, no signs of forest regeneration by deciduous trees were as yet observed in these gaps (Figs. 2A, C), but due to their sporadic occurrence the closed forest outline in this subregion (3c) appears particularly split. Consequently, compared to all the other regions of the image, the relative patchiness of this landscape type is the highest (patch outline in Table 2).

The *elevated ridges* (region 4) present mossy and sparse *Picea abies* forests which grade smoothly into the surrounding taiga of the lowland plains. The proportion of sharp edges is only 20%, which is the lowest value of all the regions in this image area. When compared to *uniform taiga* wildfires are likely to be even less important, and human impact is lower than in the lowland plains.

3.2. Vegetation type characteristics

Out of the 13 vegetation types recognized in the satellite image the combined class of mature *Picea* forests and mires appears structurally the most uniform: 277 random points were studied in this vegetation type, and on average only 2.2 structurally distinctive vegetation types were discernible within a radius of 500 m (Table 3). Thus, within an area of 80 ha adjacent to any random point of *Picea* forest, usually only one different vegetation type is present, and according to a rough estimation based on the "patch extension" character, 70% of the surrounding 1000 ha at any random point of mature *Picea* forest is formed by the mature *Picea* stand itself.

Mixed forests and those dominated by *Pinus sylvestris* are substantially less uniform and the

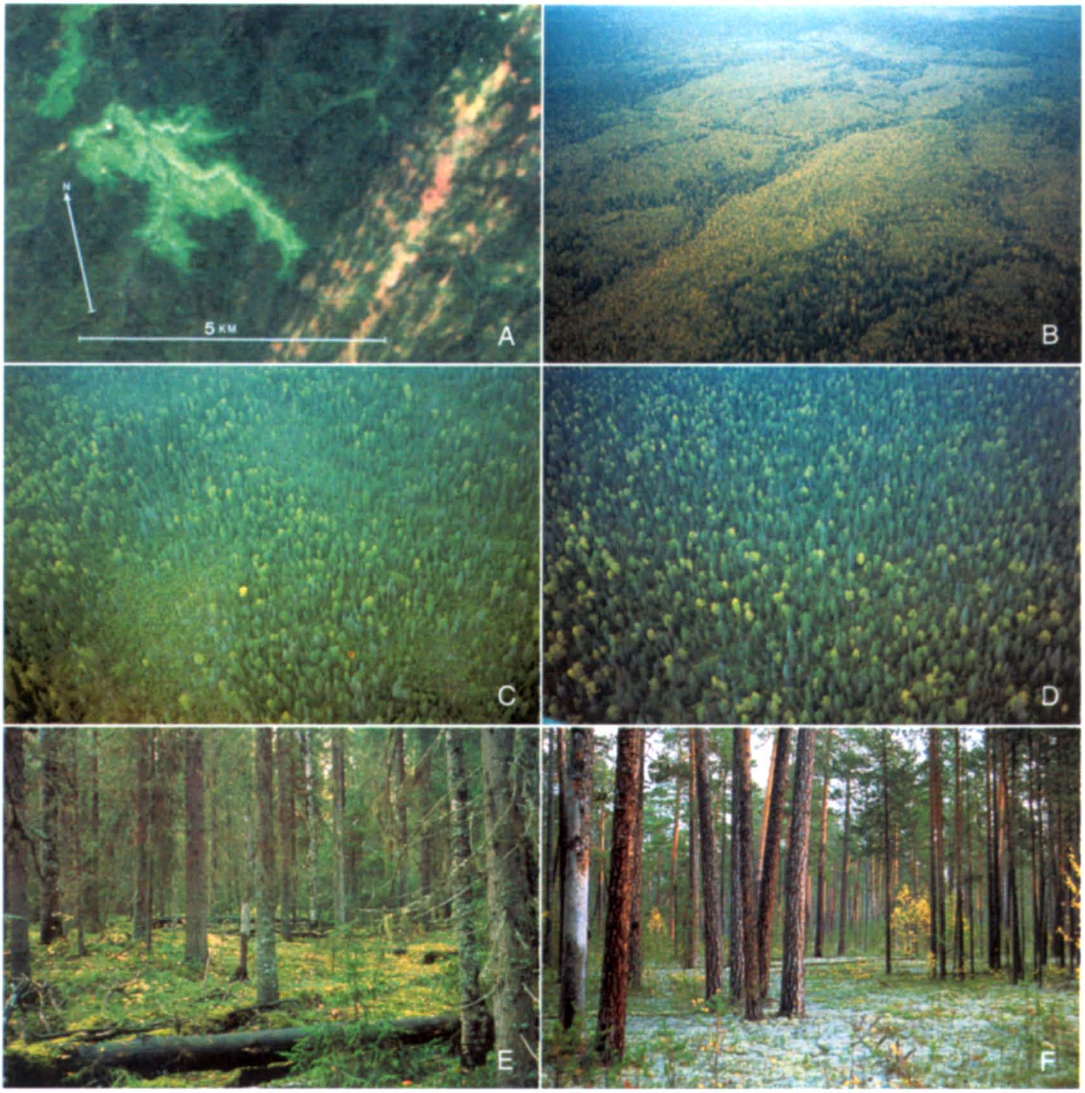

Fig. 2. Photos from the image area. — A enlarged part of Fig. 1 from the region of unexploited plains; light green = post-fire successional patch with *Populus tremula*, light orange brown = windstorm gaps in mature *Picea* forest, dark green = mature *Picea* forest. — B oblique view of a deciduous patch of fire origin (shown in Figs. 1, 2A). — C windstorm tracks in *Picea* dominated forest. — D relatively sparse steady state *Picea* forest, with dead standing spruces and deciduous trees. — E a mature *Picea abies* dominated forest with decaying logs, abundant young trees and occasional birches. — F a mature dry *Pinus sylvestris* forest which has not been burned recently. Note the patchiness of young and old pines, the latter having survived many fires. — Photos: Jorma Mattsson and Risto Kalliola 1992.

unvaried patches remain relatively small in size. The closest vegetation edge can be found at a distance of a few hundred metres. The deciduous, and especially the mixed deciduous stands, often follow river valleys, thus repeating the branching pattern of the river. The windstorm gaps occur as small islands in the spruce forest matrix; these tracks form loose chain-like corridors up to 50 km long. The mires of the study area are structurally heterogeneous, yet they tend to be isolated and small in size.

Man-created vegetation types are responsible for the majority of sharp edges between adjacent vegetation patches. The clearcut areas are very extensive and express particularly convoluted outlines. The latter is due to the administrative rules in Russia which require buffer zones 200 m wide to be left untouched along all rivers and creeks. These remnant corridors of forests do not have correspondences in the pristine landscape.

Fig. 3 examines the anthropogenic influence in the level of vegetation types. Here the random points representing different mesic forest types are divided into two categories, depending on whether the closest border is natural or made by man. Any random point in forests of the *exploited plains* (region 2) is also included in the 'exploited' group in order to demonstrate the differences between natural and harvested forest areas. The most dramatic changes can be observed in the combined class of *Picea* forests and mires (marked as *Picea* forests in Fig. 3) where the heterogeneity of the vegetation within 500 m increases considerably. In natural forests only one other vegetation type is to be found within a radius of 500 m, whereas in the 'exploited' group 2.6 other types of vegetation are present. Moreover the distance to the nearest neighbour decreases from almost 4 km to 250 m, the edge sharpens and the patches become less extensive and show convoluted outlines.

The differences detected in deciduous and mixed deciduous forests are of a less dramatic nature. Within the monitored area, 15% of the forests are deciduous or mixed deciduous occurring in natural and an additional 17% in exploited areas. The exploited areas also comprise open land and regenerating stands which will soon turn to deciduous forests. Intensive forest exploitation makes the successional deciduous patches less outstanding elements of the landscape as compared to natural conditions. It can

Table 3. Landscape characteristics (mean ± *SE*) in the major vegetation (habitat) types of the study area. For explanations, see Table 2.

Type of vegetation	*N*	Hetero-geneity	Nearest neighbour	Edge characteristics (%) sharp	smooth	nat.	artif.	Patch outline	extension
Windblow gap	9	3.9 ± 0.3	0.1 ± 0.01	78	0	77	0	0	0
New clearcut area	10	3.4 ± 0.3	0.2 ± 0.03	100	0	0	100	1.3 ± 0.4	10.5 ± 3.7
Clearcut area	47	4.0 ± 0.1	0.2 ± 0.1	70	9	70	4	2.9 ± 0.4	25.7 ± 3.4
Regenerating vegetation	21	3.9 ± 0.2	0.8 ± 0.47	67	5	76	5	3.9 ± 0.7	42.6 ± 6.5
Deciduous forest	32	3.4 ± 0.2	0.1 ± 0.01	75	3	84	6	0.9 ± 0.3	8.1 ± 4.2
Mixed deciduous forest	61	3.4 ± 0.1	0.3 ± 0.04	39	10	77	16	1.6 ± 0.2	22.6 ± 3.7
Mixed coniferous forest	19	3.5 ± 0.2	0.3 ± 0.04	58	21	58	32	1.3 ± 0.5	23.2 ± 6.8
Dry *Pinus* forest	10	3.5 ± 0.2	0.2 ± 0.04	60	0	80	20	1.4 ± 0.5	8.7 ± 4.5
Mesic *Pinus* forest	31	3.6 ± 0.1	0.2 ± 0.03	52	10	90	10	1.1 ± 0.3	13.7 ± 4.3
Picea forest/mire	277	2.2 ± 0.1	3.2 ± 0.35	59	9	83	13	2.7 ± 0.1	71.9 ± 2.0
Picea forest at ridges	29	2.4 ± 0.1	0.8 ± 0.34	24	48	100	0	1.8 ± 0.3	55.6 ± 5.9
Sparce *Picea* forest at ridges	9	2.7 ± 0.2	0.5 ± 0.06	22	11	89	0	2.4 ± 0.5	48.9 ± 10.7
Mires	18	3.9 ± 0.2	0.1 ± 0.02	61	0	78	17	0.1 ± 0.11	1.9 ± 1.9

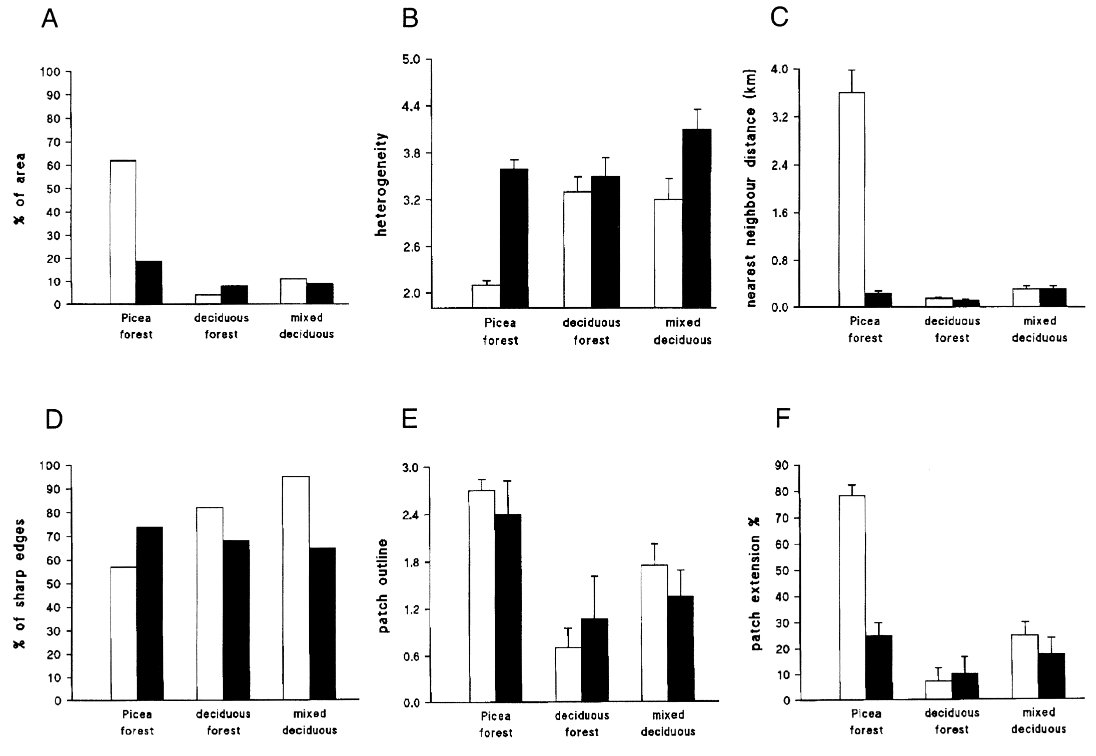

Fig. 3. Comparision of mature *Picea* forests/mires, deciduous forests and mixed deciduous forests in natural (open bars) and exploited (solid bars) conditions. — A: coverage of the vegetation types in the study area, — B: the heterogeneity (number of different ground cover and vegetation types within the radius of 500 m), — C: distance to nearest neighbour (km), — D: percentage of sharp edges, — E: patch outline (the number of transects by the same patch at the radius of 2.1 km), — F: patch extension -% (the % cover of same vegetation type at the perimeter of a circle with 2.1 km radius).

be expected that in the near future the deciduous forests will form 65% of the landscape. In fact the whole landscape matrix is just about turning upside down due to forest exploitation.

3.3. Structure of natural forests

Quantitative surveys of living and dead trees as well as of decaying trunks were made along the transects of 2 × 500 m in different site types (Table 4, Fig. 4). The forests and mires dominated by *Picea abies* are here distinguished although they cannot be differentiated by colour in the satellite image.

Dry *Pinus* forests were studied at five places representing three types of succession history (Fig. 4A). The young stand is recovering from a relatively recent forest fire (approximately 30–50 years ago) and contains 1040 small-sized trees/ha, one third of them birches; the density of saplings is 300/ha. Of the two mature *Pinus* forests, one has been affected by a relatively recent (appr. < 15 years) ground fire, whereas the other has not been disturbed by recent wildfires (Fig. 2F). These forests have 450 and 735 trees/ha, respectively, out of which one third are dead and an additional 2–3% are weak or dying. In undisturbed forests 600 young trees/ha are present. In the mature stands affected by recent ground fires the amount of young trees is relatively low (70 trees/ha). Deciduous trees are rarely present in the canopy level yet they comprise one third of the small tree class. The amount of decaying logs is quite high in all of these forests, but least abundant in burned stands.

Dryish *Pinus-Larix* forests were studied on three ancient terraces of the Pechora River. Two thirds of the standing trees were coniferous, but in the small tree class conifers comprise only 57%. This result is indicative of good light conditions at the terrace slopes and margins, which promotes the development of an exceptionally dense shrub layer (> 3000 individuals/ha), rich in deciduous species. The amount of windfalls is fairly low in these forests, which may result from severe fires or timber harvesting.

The mesic *Picea* dominated forests (Figs. 2D & E, 4B) contain 900–1500 trees/ha, and between 10% and 14% of the standing crop is formed by dead trees; an additional 1–4% of the trees are weak or dying. The number of tree seedlings varies between 900 and 2000. The similar relative proportions of deciduous trees and seedlings (15% and 13%, respectively) suggests that these forest are in dynamic equilibrium, with deciduous species also being essential components of the tree layer. The mixed coniferous forests show only a few marks of slow directional vegetation change. The mixed deciduous forests, on the other hand, seem to be becoming more conifer-rich. The amount of windfalls is high in the later successional mesic forests, almost reaching the frequency of the standing crop in some mature stands.

Table 4. The structure of naturally regenerating forests of the study area as based on transect analyses. The total number of canopy forming standing crop, percentage values of coniferous, deciduous and dead trees in standing crop, amount of windfalls, and amount of young trees, are expressed. All the values are calculated per one hectare area except the amount of windfalls (decomposing trunks crossing the transect).

Type of vegetation	Standing crop					Wind-falls	Young trees			Successional status
	ind/ha	conif	decid	dead	weak		ind/ha	conif	decid	
Mesic sites										
Picea forest	1000	85.5	14.5	11	3	985	1820	87.4	12.6	mature stand "climax"
Pinus mire	1032	87.6	12.4	13	0	423	629	81.6	18.4	mature stand, "climax"
Picea mire	1136	89.2	10.8	10	4	1113	1010	82.5	17.5	mature stand, "climax"
Mixed coniferous forest	900	77.8	22.2	14	1	1065	895	70.9	29.1	later after-fire stage
Mixed deciduous forest	1543	46.7	53.3	10	2	563	1950	71.8	28.2	early after-fire stage
Dryish sites										
Mesic *Pinus* forest	1295	67.7	32.3	4	1	456	3029	57.4	42.6	after fire stage
Dry sites										
Dry *Pinus* forest	735	94.6	5.4	30	3	500	600	76.7	23.3	mature stand, "climax"
Dry *Pinus* forest, with ground fire	450	100	0	27	2	465	70	64.3	35.7	recently disturbed
Mixed young *Pinus* forest, regenerating	1040	64.4	35.6	1	1	340	300	73.3	26.7	early after fire stage

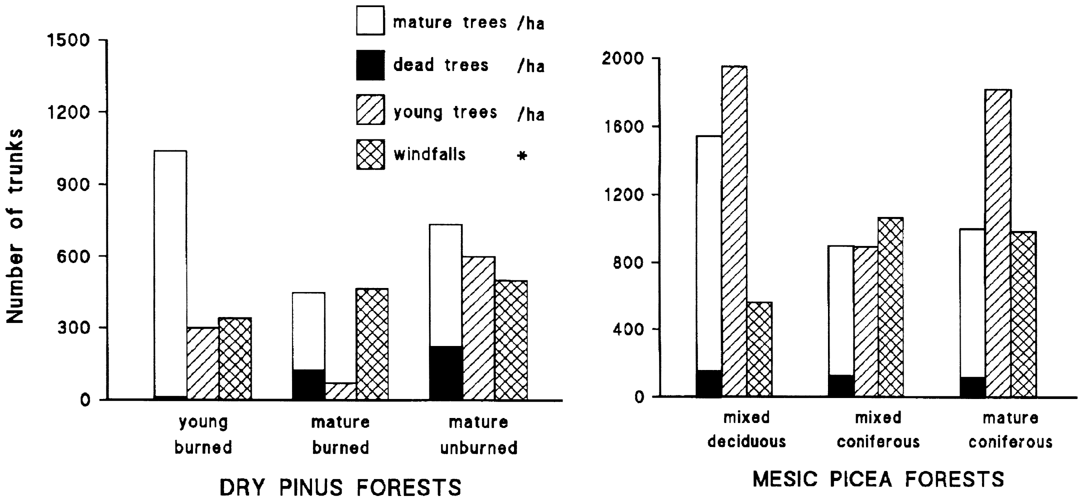

Fig. 4. Structure of dry *Pinus*- and mesic *Picea*- forests. Standing crop/ha together with dead trees/ha is shown in the first bar. The second bar gives the amount of young trees/ha and the third shows the amount of windfalls. * = the amount of windfalls is based on the amount of fallen trees and decaying logs crossing the middle line of the 2 × 500 m study transect (0.1 ha) × 10 (= 1 ha).

Picea mires very much resemble *Picea* forests with regard to their tree species composition and stand dynamics. The frequency of standing trees equals that of fallen logs. The amount of young trees is lower than the number of canopy forming trees. In addition to occasional *Pinus cembra* the most distinctive differences are found in the herbaceous layer. *Pinus* mires are relatively densely covered by low-growing *P. sylvestris* and *P. cembra*. A clear distiction in their structure, as compared to *Picea* mires, is the scarcity of windfalls and young trees. The forest ground layer contains *Sphagnum* mosses and dwarf shrubs typical of peat bogs.

4. Discussion

4.1. Landscape structure and dynamics in dry and dryish sites

Stand structure and dynamics in dry and dryish sites is dominated by repeated forest fires. Especially the regeneration and maintenance of the dry *Pinus* forests are characterized by low-intensity fires which can occur in cycles of only 30 to 50 years (A. Blagovidov, personal communication). Fire cycles in dry sites are greatly enhanced by human activities. The recently burned areas are relatively small in size (0.5–100 ha) — in the satellite image they can be seen as red dots — and often fire passes only through the undergrowth, consuming lichens, shrubs and litter. In northern Sweden the common fire cycle in *Pinus* forests is reported to be 80–90 years (Engelmark 1984), and sometimes in dry sites 50 years (Zackrisson 1977). Due to such frequent fires the density and age distribution of the trees is variable; crown fires may be supressed by the patchiness of the tree layer. Despite the single-species dominance these forests can retain their mosaic structure where the distance to the nearest edge remains low, yet it should be remembered that timber harvesting has enhanced the patchy nature of these forests as well.

In dry sites, *Pinus sylvestris* is the first tree species to occupy the recently burned sites. Having thick bark at the lower half of the trunk, large individuals survive fire and are able to set seeds for the future tree generation(s). Due to frequent fires successional replacement by other trees hardly occurs at all. The result is a rather sparse forest with occasional clearings and clumps of young trees. Due to frequent fires such stands can maintain their general structure for centuries.

In forests where fire has not occurred for several decades, dense groups of young trees or saplings may be found in otherwise sparse forest. With time the impact of pathogens, snowbreaks and wind contribute to the forest regeneration dynamics. The amount of dead standing pines is quite high both in climax and disturbed forests. The most dense *Pinus* forests with relatively large-sized individuals have escaped fires through their occurrence in islands or peninsulas surrounded by mesic forests or mires. It has also been recorded elsewhere that even large *Pinus* forests can avoid wildfires if they are surrounded by open mires (Engelmark 1984).

In dryish sites mixed coniferous forests prevail. *Picea abies* and *Abies sibirica* can invade sites which were earlier colonized by *Pinus sylvestris* with occasional individuals of *Larix sibirica* and *Betula* spp. Wildfires are probably less frequent than in the dry sites, but after the accumulation of flammable material the forests are renewed through intense fires. Large gaps created by wildfires or windstorms may change the level of ground water and thus affect site conditions and the tree species composition even in adjacent plains (cf. Berg 1950).

4.2. Landscape structure and dynamics in mesic sites

The extensive areas characterized by recent windfalls cover thousands of hectares of mesic forests in the image's area, and the length of some tracks exceeds 50 km. Although such destructive winds have probably been enhanced by the enormous clear-cut areas of the Perm region south of Komi, disturbance by windstorms is an essential process in a boreal forest landscape. In the Komi area extremely strong storms are rare compared to the middle Russian plains (Lyakhov 1987). These storms may promote cyclic forest regeneration somewhat comparable to the fire dynamics. In the more humid areas in NE North America (Foster 1988) and Fennoscandia (Sernander 1936) the importance of great devastations caused especially by forest fires is less pronounced than in the continental areas of Siberia and North America. In these more humid areas the role of windfalls is more important at mesic forests.

Over half of the natural landscape in the image's area is covered by mesic *Picea* forests which represent the climatic climax. Mesic deciduous and mixed deciduous forests are common at river margins and in the valleys of small tributaries. This pattern suggests a possible antropogenic influence in the origin of the fires.

The landscape structure in these areas seems to confirm the general scheme of post-fire succession in boreal forests (see Introduction). *Betula* spp. and *Populus tremula* pioneer most burned areas and become replaced by species of the "dark taiga". In the early stages of succession the deciduous forest is dominated by birches and aspen with young coniferous trees and saplings arising from the herb-rich ground. Both the amount of standing crop and the number of young trees are relatively high.

During succession, competition between individuals increases and thinning occurs while the volume of the individual trees increases. In the late stages of succession, giant individuals of *Populus tremula* are typically present in mixed coniferous forests, which are otherwise dominated by *Picea abies* with occasional birches (*Betula* spp). The forest bottom contains more mosses and shrubs than in earlier successional stages, but still the amount of grasses and herbs is high. Decaying logs are common, including deciduous trunks, mainly aspen. The amount of young trees is relatively low, probably due to the dense standing crop and closed forest canopy. Still every third young tree is deciduous.

Mixed coniferous forests are valuable from the point of view of nature conservation because of the presence of old deciduous trees. Many endangered species (bryophytes, lichens, insects, fungi) are dependent on old deciduous trees and decaying logs, especially those of aspen. According to several models of forest growth, these successional stages are slowly replaced by shade tolerant climax trees (Leemans & Prentice 1987).

However, varying small scale disturbances, such as those reported in this study, are not included in many of these models. It seems to us that such causes as pathogens and windfalls, together with waterlogging and uprooting of spruces, can provide disturbance gaps which allow the succesful regeneration of *Populus tremula*, *Salix caprea* and *Betula* spp. during several tree generations, at least by vegetative means. According to Steijlen & Zackrisson (1986) postfire succession will not necessarily lead to a total spruce dominance in fire refugia, while more complex tree species composition is also possible.

A mature *Picea* stand, which is the most typical vegetation type in the unexploited part of the image, is dominated by *Picea abies* and to a lower extent *Abies sibirica*. The forest is relative open and it is characterized by the presence of dead standing trees and scattered birches. Every fourth tree is either deciduous or dead. The abundance of dead standing trees separates these forests in a very clear manner from managed forests. In the natural forests of northern Sweden the amount of dead standing trees (10–12 m^3/ha, in Linder & Östlund 1992) is comparable to our area. These natural *Picea* forests are also quite open (1000 trees/ha) and have at least 20–50% lower volume than the managed forests. This means that tree biomass does not necessarily accumulate and the flammability does not increase with stand age, as has sometimes been presumed (Romme & Despair 1989). Also, the severity of fires may not be at the same level as in the more dense successional stands. Much potential fuel is lost through decaying logs on the forest floor, and these forests are characterized by the number of young trees and saplings exceeding that of the canopy trees. No apparent marks of wildfires are usually visible.

In wet places wildfires obviously have an even minor role to play. Forested mires are typically characterized by scattered varyingly aged individuals of *Pinus cembra*, which are sensitive to fires due to their thin bark. Their presence is thus indicative of the absence of wildfires. The vegetation is probably in a steady state, but the turnover time of successive tree generations can be very long. Tree replacement is mostly based on windfalls and changes in the surrounding landscape.

4.3. Dynamics of climatic climax

It is a common belief that long term spruce-domination causes negative changes in the micro-environment, and that without disturbances climax stands would slowly degrade (Kuusela 1990). Such stands are reported to have regeneration problems at least in thick moss sites throughout the northern parts of the boreal zone (*Picea abies* forests; Sirén 1955, *Picea mariana* forests; Bonan & Shugart 1989), and therefore wildfires provide the only successful natural regeneration mechanism.

Our study suggests that forest fires can be rare in mesic sites, forcing us to presume that there are indeed successful regeneration mechanisms operating even in the steady state climax forests dominated by *Picea abies*. They may be based on small-scale dynamics beyond the resolution limits of the satellite imagery (scale < 1 ha). This observation is in agreement with the idea of a dynamic species composition by Kuusela (1990): ‘On and near the forest border,’ where ‘the incidence of fire is relatively rare’ and ‘the soil is loamy, compact and water retaining, spruce dominates with a mixture of birch over limited areas.’ (see also Jonsson & Esseen 1990). To us it even seems possible that such areas with dynamical species composition indeed cover a great part of the subcontinental taiga in pristine conditions.

Wind is undoubtedly the most important exogeneous disturbance factor in *Picea* stands (Sernander 1936, Delin 1992); here and there in the forest fallen logs and broken trees are common consequences of windfalls, snowbreaks and uprooting. Local windstorm gaps and patches of 0.01–0.5 ha are very common. The formation of such gaps may sometimes cause waterlogging and thus increase the danger of freezing-up (tree uplift through frost activity) and uprooting of spruces (Delin 1992). Other important gap-forming mechanisms in mature *Picea* stands include fungal diseases which occur in synergism with insect pests. In these gaps decaying logs together with uprooted trees form important regeneration niches on the forest floor. The deciduous litter of birch also causes local variation in the soil chemistry (Bonan & Shugart 1989). Thus, the light and soil micro-environment in the forest floor appears temporally and spatially variable and provides sufficient regeneration niches for the canopy-forming trees. The gap dynamics in Russian *Picea* stands seem to have some of the same mechanisms as in pristine forests in Scandinavia, which are usually considered fire refugia (Sernander 1936, Liu Qinghong & Hytteborg 1991, Hytteborg et al. 1987, Steijlen & Zackrisson 1987).

4.4. Biodiversity and the role of man

The most prominent impact of man in the boreal forest landscape of the Russian European taiga is the intensive and systematic exploitation of forests. A landscape that was characterised by old coniferous woods changes into one dominated by deciduous stands. Natural forests are left intact only along mires, rivers and brooks. These sites may serve as dispersal corridors for forest species. They also maintain a store of decaying wood in moist conditions, which is needed by several species of plants and animals. Whether the remnant patches of mature forests indeed remain effective refugia for the threatened forest species is, however, not known.

The question of the steady state boreal landscape is of primary importance in discussions on nature conservation. Most works on fire dynamics predict that the overall forest landscape should represent stages of post-fire succession. Thus, the discovery of large spruce-dominated forests where birches are also present, instead of vegetation mosaics, in the pristine parts of our study area, was unexpected. The distribution of the major deciduous forests along river valleys was suggestive of human-enhanced fire dynamics in the taiga. In research on fire cycles the role of man should not be ignored.

According to our experiences, the plant species richness in the study area is always highest at riverine sites where river processes together with traditional land use have created several habitat types. In dry and dryish sites natural and human-enhanced fire dynamics plays an important role in maintaining forest structure. Probably also the mesic sites adjacent to dry sites suffer from regular fires, whereas in large mesic areas other processes seem to be responsible for the present forest structure and species composition (see also Kuuluvainen 1994).

The Russian European taiga still offers a good opportunity to study those natural processes that affect both the spatial and the temporal aspects of biodiversity in pristine boreal forests. We find it necessary to use this unique opportunity effectively because some widely cited generalizations about boreal forests are based on conditions encountered in North America, and may thus not be applicable to Europe. The massive forest exploitation in northern Russia appears most alarming because the relative proportions of coniferous and deciduous forests are being altered in a short time on a continental scale (Barr & Braden 1988, Dudley 1992). Thus, it is important to strive for international joint efforts with Russian scientists to carry out research in the still existing pristine forest areas. This necessity also reveals the great value of large conservation areas, such as the Pechoro-Ilych Biosphere Reserve.

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