

Distribution of Plants Differing in Attitude toward Thermal Conditions in Communities of the Timberline Ecotone on Mount Iremel', the Southern Urals

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Received May 23, 2005

Abstract—Specific features in the distribution of plant species differing in their attitude toward thermal conditions have been studied in communities of the present-day timberline ecotone on Mount Iremel' in the Southern Urals. It has been shown that the distribution of such species is characterized by significant spatial nonuniformity. Elevation above sea level, local conditions in habitats located at the same altitudinal level, and specific features of mountain slopes account for 13–84, 5–30, and 0.4–14% of the total variance of test parameters, respectively. The abundance of plants changes nonlinearly along the altitudinal gradient, whereas changes in the species diversity of different plant groups have an almost linear pattern. Marked differences between plant communities with respect to the proportions of species differently responding to changes in thermal conditions have been revealed on all slopes in the upper part of the timberline ecotone, upon transition from the slopes proper to the plateau-like areas of intermontane depressions.

DOI: 10.1134/S1067413606050031

Key words: high-mountain communities, dynamics, ecotone, timberline, altitudinal gradient, vascular plants, thermal conditions.

In the 20th century, high-mountain forests increased in area and their boundaries changed in different regions of the world (Jakubos and Romme, 1993; Shiyatov, 1993; Woodward et al., 1995; Holtmeier, 2003; Peñuelas and Boada, 2003), including the Southern Urals (Shiyatov, 1983; Moiseev et al., 2004). This phenomenon is usually attributed to global warming. Direct observations on the vegetation of high-mountain regions also provide evidence for an increase in the species diversity of plants at high elevations (Grabherr et al., 1994) and changes in the composition of alpine communities, in which the frequency of thermophilic plant species increases and that of cryophilic species decreases (Keller et al., 2000). However, the expansion of plants to higher elevations and changes in the species composition of plant communities take place at a much lower rate than could be expected upon the observed rise of temperature.

The distribution of species in high mountains is mainly limited by thermal, edaphic, and wind conditions in habitats (Gorchakovskii, 1975; Gorchakovskii and Shiyatov, 1985; Holtmeier, 2003). Upon climate warming, unfavorable edaphic conditions (e.g., on steep slopes) and winds (e.g., in plateau-like intermontane depressions) may retard the invasion of thermophilic species and contribute to the survival of cryo-

philic species in high-mountain plant communities. Moreover, as environmental conditions in high-mountain areas are extremely diverse, the rates of transformation of high-mountain communities upon long-term climate changes may markedly vary even within the same range of elevations

To check these assumptions, the distribution of vascular plant species responding differently to changes in thermal conditions was studied in high-mountain communities on slopes differing in steepness and exposure and in plateau-like areas of intermontane depressions. Studies were performed in the present-day timberline ecotone on Mount Iremel'.

STUDY REGION, OBJECT, AND METHODS

The Iremel' Mountain Range, one of the highest in the Southern Urals, is part of the Iremel'sko-Avalyaksii natural region, characterized by considerable elevations (1200–1600 m a.s.l.), a complex geological structure, the prevalence of dark taiga forests, and distinct altitudinal zonality (Tsvetaev, 1964). According to data from the nearest weather station on Mount Dal'nii Taganai (1146 m a.s.l.), the sum of above-zero temperatures in the region varies from 1100 to 1850°C; the monthly average air temperatures are $10.4 \pm 1.9^\circ\text{C}$ in

June, $12.3 \pm 1.8^\circ\text{C}$ in July, and $10.6 \pm 1.9^\circ\text{C}$ in August; and the annual amount of precipitation ranges from 600 to 1300 mm.

The mountain forest, subgoltzy (subalpine) and mountain tundra belts are distinguished in the plant cover (Gorchakovskii, 1975). The subgoltzy belt covers the slopes of the range at elevations of 1100–1150 to 1350–1400 m a.s.l. Park-type open spruce and spruce–birch forests and tall-herb meadows dominated by Alpine knotweed (*Polygonum alpinum*) and snakeweed (*P. bistorta*) are characteristic of its lower part, while spruce and birch scrub forests with small-herb meadows prevail in its upper part (Nikonova et al., 1992). The range of elevations occupied by the mountain tundra belt is about 200 m. The herb–moss tundras prevail, but there are also stony, lichen, dwarf shrub–moss, and complex tundra types (Sharafutdinov, 1983). Siberian spruce *Picea obovata* and birch *Betula pendula* spp. *tortuosa* are the main tree species forming the timberline.

The Iremel' Mountain Range has two summits, Bol'shoi Iremel' and Malyi Iremel, rising 1582 and 1450 m a.s.l., respectively. Vertical transects were established in the timberline ecotone on the southwestern and southern slopes of Malyi Iremel' and on the northeastern slope of Bol'shoi Iremel' ($54^\circ 31'–33' \text{ N}$, $58^\circ 50'–53' \text{ E}$). The southwestern slope of Malyi Iremel' and the northeastern slope of Bol'shoi Iremel' are not steep (15 and 10 degrees, respectively), with shallow mountain-meadow humus soils in the upper and middle parts and imperfectly developed mountain-forest brown acid soils in the lower parts (T.A. Goryacheva, personal communication). The southern slope of Malyi Iremel' is steeper (20–25 degrees), with mountain-tundra subbrown soils in the upper part and imperfectly developed mountain-forest brown acid soils in the middle and lower parts (in the lower part of the slope, these soils may also be well developed).

Studies were performed in June 2002 and 2003 at six altitudinal levels (elevations) on the southwestern slope of Malyi Iremel', three levels on the southern slope of Malyi Iremel', and three levels on the northeastern slope of Bol'shoi Iremel'. The upper levels corresponded to plateau-like areas in intermontane depressions. At each level, three 20×20 -m plots (below, referred to as macroplots) were established. Horizontal distances between their centers ranged from 50 to 70 m. Macroplots were divided into 10×10 -m squares (mesoplots), and three to eight microplots (1×1 m) were established within each mesoplot. Descriptions of the vegetation involving the assessment of species composition and coverage (%) of all its individual components were made in mesoplots (a total of 132 descriptions) and microplots (396 descriptions). Plant communities and species dominating at different levels are briefly characterized in Table 1.

On the basis of Tsyganov's (1983) scales and other published data, all species recorded on the plots (except

woody plants) were classified into subarctic, boreal, nemoral–boreal, and nemoral groups. Endemic high-mountain species characteristic of mountain tundras (*Festuca igoschiniae* Tzvel., *Lagotis uralensis* Schischk., etc.) were included into the subarctic group, and endemics typical of the subgoltzy belt (*Anemonastrum biarmiense* (Juz.) Holub, *Calamagrostis uralensis* Litv., etc.) were included into the boreal group. The nemoral–boreal and nemoral species were subsequently pooled into one group because of low diversity and abundance of the latter (one to three species with coverage below 0.01% per slope).

Species richness per 100 m² (SR) and average values of total coverage per 100 m² (TC) were used as parameters characterizing the diversity and abundance of plants, respectively. To estimate the influence of conditions in local habitats (on the same slope) on these parameters of species differently responding to changes in the thermal regime, mixed-effects two-way ANOVA was used, with elevation and macroplot taken as a constant (fixed) factor and a random factor, respectively. To estimate the influence of slope, absolute elevation, and local habitat conditions at the same altitudinal level, mixed-effects three-way ANOVA was used, with the first two parameters taken as fixed factors and macroplot taken as a random factor. In both cases, the average values of test parameters in mesoplots were used as replications. For each slope, data on levels 1, 3, and 5 were included in the analysis. ANOVA was performed with values obtained after arcsine transformation that showed the contribution of a certain group of plants to the total species richness or coverage of all species in a given local habitat.

RESULTS

In test plots established at three different levels, 78 species were recorded on the southern slope and 50 were recorded on the northeastern slope. On the southwestern slope, 67 species were recorded at three corresponding levels and 81 species were recorded at all six levels. Boreal species prevailed in plant communities located along all transects (Table 2). The proportions of subarctic and boreal species were comparable only at the highest altitudinal levels; at lower elevations, SR and TC of subarctic species markedly decreased, whereas those of nemoral–boreal species increased. The SR of boreal species reached the highest values at intermediate levels. In general, however, parameters of this group change only slightly along the altitudinal gradient.

The subarctic group was represented on the southwestern, southern, and northeastern slopes by 12, 13, and 9 species, respectively. Changes in the SR of these species along the altitudinal gradient were adequately described by a linear regression equation (Fig. 1a). The respective determination coefficients (R^2) for the southwestern, southern, and northeastern slopes were 0.74,

Table 1. Characteristics of plant communities at different altitudinal levels

Slope	Characteristics
Southwestern	Level 1 (1360 m a.s.l.). Herb–dwarf shrub–moss–lichen tundra. Tree species (T): coverage 5%, height 4 m. Shrubs (S): <i>Salix glauca</i> , <i>Betula humilis</i> , and <i>Juniperus sibirica</i> ; coverage 10%, height 12 cm. Herbs and dwarf shrubs (HDS): <i>Vaccinium uliginosum</i> , <i>Carex vaginata</i> , <i>Festuca igoschiniae</i> , <i>Vaccinium vitis-idaea</i> , etc.; coverage 64%, height 15 cm. Mosses (M): <i>Dicranum scoparium</i> , <i>Hylocomium splendens</i> , etc.; coverage 37%; height 5 cm. Epigeous lichens (L): <i>Cladina arbuscula</i> , <i>C. rangiferina</i> , <i>Cladonia amaurocraea</i> , etc.; coverage 38%, height 6 cm. Proportion of stony area (Stones) 2%
	Level 2 (1345 m a.s.l.). Birch–spruce scrub forest. T: coverage 9%, height 7 m. S: <i>Juniperus sibirica</i> and <i>Salix glauca</i> ; coverage 23%, height 16 cm. HDS: <i>Polygonum bistorta</i> , <i>Vaccinium uliginosum</i> , <i>Carex vaginata</i> , <i>Anemonastrum biarmiense</i> , etc.; coverage 68%, height 20 cm. M: <i>Hylocomium splendens</i> , <i>Polytrichum commune</i> , etc.; coverage 67%, height 4 cm. L: <i>Cladina arbuscula</i> , <i>Cladonia amaurocraea</i> , etc.; coverage 1%, height 4 cm. Stones 3%
	Level 3 (1310 m a.s.l.). Open birch–spruce forest. T: coverage 30%, height 9 m. S: <i>Juniperus sibirica</i> ; coverage 2.5%, height 35 cm. HDS: <i>Polygonum bistorta</i> , <i>P. alpinum</i> , <i>Calamagrostis uralensis</i> , <i>Anemonastrum biarmiense</i> , <i>Sanguisorba officinalis</i> , etc.; coverage 75%, height 50 cm. M: <i>Polytrichum commune</i> , <i>Dicranum scoparium</i> , etc.; coverage 12%, height 1.5 cm. Stones 3.5%
	Level 4 (1280 m a.s.l.). Open birch–spruce forest. T: coverage 38%, height 9.5 m. S: <i>Juniperus sibirica</i> and <i>Salix</i> sp.; coverage 1.7%, height 45 cm. HDS: <i>Polygonum bistorta</i> , <i>P. alpinum</i> , <i>Calamagrostis uralensis</i> , <i>Sanguisorba officinalis</i> , <i>Anemonastrum biarmiense</i> , etc.; coverage 75%, height 50 cm. M: <i>Polytrichum commune</i> , <i>Dicranum scoparium</i> , etc.; coverage 24%, height 1.8 cm. Stones 6.5%
	Level 5 (1260 m a.s.l.). Spruce forest with fragments of meadow communities. T: coverage 50%, height up to 13 m. S: <i>Rubus idaeus</i> ; coverage 1%, height 50 cm. HDS: <i>Polygonum bistorta</i> , <i>P. alpinum</i> , <i>Calamagrostis uralensis</i> , <i>Sanguisorba officinalis</i> , <i>Oxalis acetosella</i> , <i>Stellaria nemorum</i> , etc.; coverage 67%, height 45 cm. M: <i>Polytrichum commune</i> , etc.; coverage 30%, height 1.5 cm. Stones 1%
	Level 6 (1205 m a.s.l.). Spruce forest with fragments of meadow communities. T: coverage 55%, height 17 m. S: <i>Rubus idaeus</i> ; coverage 9%, height 60 cm. HDS: <i>Stellaria nemorum</i> , <i>Polygonum bistorta</i> , <i>P. alpinum</i> , <i>Oxalis acetosella</i> , etc.; coverage 77%, height 44 cm. M: <i>Brachythecium</i> sp., <i>Plagiothecium</i> sp., etc.; coverage 53%, height 1.5 cm. Stones 0.2%
Southern	Level 1 (1355 m a.s.l.). Dwarf shrub–moss–herb tundra. T: coverage 9%, height 5 m. S: <i>Juniperus sibirica</i> and <i>Salix glauca</i> ; coverage 20%, height 30 cm. HDS: <i>Polygonum bistorta</i> , <i>Carex bigelovii</i> , <i>N. vaginata</i> , <i>Vaccinium uliginosum</i> , etc.; coverage 73%, height 20 cm. M: <i>Polytrichum commune</i> , <i>Hylocomium splendens</i> , etc.; coverage 43%, height 4 cm. L: <i>Cladina arbuscula</i> , <i>C. rangiferina</i> , etc.; coverage 3%, height 5 cm. Stones 3%
	Level 3 (1315 m a.s.l.). Open birch–spruce forest. T: coverage 21%, height 8 m. S: <i>Salix glauca</i> and <i>Rubus idaeus</i> ; coverage 13%, height 35 cm. HDS: <i>Polygonum bistorta</i> , <i>P. alpinum</i> , <i>Vaccinium uliginosum</i> , <i>Anemonastrum biarmiense</i> , etc.; coverage 60%, height 30 cm. M: <i>Polytrichum commune</i> , <i>Dicranum</i> sp., <i>Brachythecium</i> sp., etc.; coverage 46%, height 2 cm. L: <i>Cladina arbuscula</i> , etc.; coverage 1%, height 2 cm. Stones 12%
	Level 5 (1260 m a.s.l.). Spruce forest with fragments of meadow communities. T: coverage 52%, height 15 m. S: <i>Rubus idaeus</i> ; coverage 9%, height 30 cm. HDS: <i>Polygonum alpinum</i> , <i>P. bistorta</i> , <i>Calamagrostis uralensis</i> , <i>Vaccinium myrtillus</i> , etc.; coverage 62%, height 40 cm. M: <i>Dicranum</i> sp., <i>Brachythecium</i> sp., etc.; coverage 46%, height 1.5 cm. Stones 3%
Northeastern	Level 1 (1365 m a.s.l.) Dwarf shrub–herb–moss tundra. T: coverage 10%, height 5 m. S: <i>Juniperus sibirica</i> and <i>Salix glauca</i> ; coverage 14%, height 30 cm. HDS: <i>Vaccinium uliginosum</i> , <i>V. myrtillus</i> , <i>Carex vaginata</i> , <i>N. bigelovii</i> , <i>Festuca igoschiniae</i> , <i>Empetrum hermaphroditum</i> , etc.; coverage 70%, height 18 cm. M: <i>Hylocomium splendens</i> , <i>Dicranum scoparium</i> , etc.; coverage 71%, height 5 cm. L: <i>Cladina arbuscula</i> , <i>C. rangiferina</i> , etc.; coverage 3%, height 5 cm. Stones 8%
	Level 3 (1335 m a.s.l.) Open spruce forest with birch. T: coverage 25%. S: <i>Rubus idaeus</i> and <i>Salix glauca</i> ; coverage 3%, height 40 cm. HDS: <i>Anemonastrum biarmiense</i> , <i>Polygonum bistorta</i> , <i>P. alpinum</i> , <i>Vaccinium myrtillus</i> , <i>Deschampsia cespitosa</i> , etc.; coverage 72%, height 40 cm. M: <i>Polytrichum commune</i> , <i>Plagiothecium</i> sp., <i>Dicranum</i> sp., etc.; coverage 57%, height 3 cm. Stones 1.5%
	Level 5 (1290 m a.s.l.). Spruce forest with fragments of meadow communities. T: coverage 48%, height 12 m. S: <i>Rubus idaeus</i> ; coverage 5%, height 20 cm. HDS: <i>Polygonum alpinum</i> , <i>P. bistorta</i> , <i>Vaccinium myrtillus</i> , <i>Calamagrostis uralensis</i> , <i>Oxalis acetosella</i> , etc.; coverage 63%, height 45 cm. M: <i>Brachythecium</i> sp., <i>Polytrichum commune</i> , etc.; coverage 64%, height 2 cm. Stones 1%

Table 2. Average values ($M \pm m$) of species richness (SR) and total coverage (TC) per 100 m² for species groups differing in attitude toward thermal conditions on different slopes of the Iremel' Mountain Range at different altitudinal levels

Altitudinal level	Subarctic		Boreal		Nemoral-boreal	
	SR	TC	SR	TC	SR	TC
Southwestern slope of Mount Malyi Iremel'						
1	7.2 ± 0.3a	41.3 ± 2.3a	10.0 ± 0.4a	41.9 ± 3.8a	3.0 ± 0.3a	7.3 ± 1.5a
2	7.1 ± 0.5a	21.7 ± 1.9b	12.7 ± 0.3b	58.4 ± 4.0b	4.9 ± 0.2b	17.9 ± 4.2b
3	1.6 ± 0.4b	1.6 ± 0.7c	13.3 ± 0.4b	72.6 ± 4.2c	6.7 ± 0.6c	17.4 ± 3.3b
4	1.8 ± 0.4b	1.5 ± 0.8c	14.8 ± 0.6c	61.9 ± 6.2b	8.3 ± 0.7d	14.5 ± 2.2b
5	0.4 ± 0.2c	0.2 ± 0.1d	12.1 ± 0.4b	65.2 ± 6.4b	9.3 ± 0.9d	16.4 ± 3.7b
6	0.2 ± 0.2c	0.01 ± 0.01d	5.8 ± 0.3d	56.0 ± 9.6a, b	6.8 ± 0.6c, d	44.7 ± 6.9c
Southern slope of Mount Malyi Iremel'						
1	8.9 ± 0.4a	43.3 ± 4.9a	11.9 ± 0.6a	56.9 ± 10.2a	4.3 ± 0.4a	2.9 ± 0.7a
3	4.3 ± 0.6b	20.2 ± 5.4b	12.0 ± 0.2a	50.3 ± 7.4a	7.0 ± 1.0b	13.6 ± 3.0b
5	1.0 ± 0.1c	0.4 ± 0.1c	11.2 ± 0.5a	54.6 ± 8.1a	10.3 ± 0.8c	18.6 ± 1.5c
Northeastern slope of Mount Bol'shoi Iremel'						
1	6.4 ± 0.4a	34.7 ± 5.2a	9.6 ± 0.7a	46.8 ± 6.2a	1.9 ± 0.3a	3.7 ± 1.3a
3	3.6 ± 0.4b	2.0 ± 0.4b	11.6 ± 0.4b	58.9 ± 5.2a, b	6.2 ± 0.2b	18.0 ± 2.5b
5	0.4 ± 0.2c	0.5 ± 0.2c	9.2 ± 0.3a	69.3 ± 6.6b	5.6 ± 0.6b	11.7 ± 2.2c

Note: Alphabetical indices (a–d) indicate the existence of significant differences between average values of test parameters recorded at different altitudinal levels on the same slope (Mann-Whitney U test, $P < 0.05$).

0.83, and 0.84 (in all cases, $P < 0.001$). In contrast to the situation with species richness, the abundance of subarctic species abruptly decreased within a relatively narrow interval of the altitudinal gradient. As a consequence, the plots for this parameter were distinctly non-linear (Fig. 1b) and could be adequately described by an exponential regression equation ($R^2 = 0.61, 0.60,$ and 0.64 for the southwestern, southern, and northeastern slopes, respectively; $P < 0.001$). Although the decrease in average values of test parameters between levels 1 and 2 of the southern transect was relatively small, the rates of elevation-dependent change in these values along the three transects differed insignificantly, which follows from similar slope angles of regression lines.

On all slopes, the values of parameters recorded at the same altitudinal level manifested considerable scattering (Fig. 1). Differences between mesoplots were, as a rule, statistically significant, but differences between macroplots located at the same levels on the southwestern and northeastern slopes were insignificant, with elevation being the main factor accounting for variation in the SR (Table 3) and TC (Table 4) of subarctic species along the corresponding transects. On the southern slope, the SR and TC of these species largely depended on the position of a macroplot in the area located at a certain level.

The highest absolute values of SR for subarctic species at all altitudinal levels were recorded on the southern slope. The SR values recorded at the corresponding

altitudinal levels on the southwestern and northeastern slopes, except for level 3, were closely similar to each other. The TC of subarctic species on the southern slope was high at level 3, and that on the northeastern slope had the lowest value for the group at level 1. Relative SR and TC values for subarctic species were generally higher on the southern slope, but the influence of slope exposure on these parameters (if any) lacked statistical significance (Table 5). The contribution of subarctic species to the SR of plant communities decreased from 35.6 to 1.4% on the southwestern slope, from 35.5 to 4.4% on the southern slope, and from 36.6 to 2.8% on the northeastern slope; the contribution to TC decreased from 45.9 to 0.01%, from 45.1 to 0.6% and from 41.4 to 0.6%, respectively.

The total numbers of boreal species recorded in areas of the same size on the southern, southwestern, and northeastern slopes reached 32, 26, and 22 species, respectively. The absolute SR values on the southern and northeastern slopes remained virtually unchanged along the altitudinal gradient (Fig. 2a). In the same segment of the gradient on the southwestern slope, SR initially increased ($R^2 = 0.19, P < 0.001$) but, at still lower elevations, decreased again. Its dependence on elevation in this segment was nonlinear and could be described by a second-degree polynomial ($R^2 = 0.19; P < 0.001$).

Along all transects, the variance of SR was explained for the most part by random factors. The absolute SR values for boreal species at similar altitu-

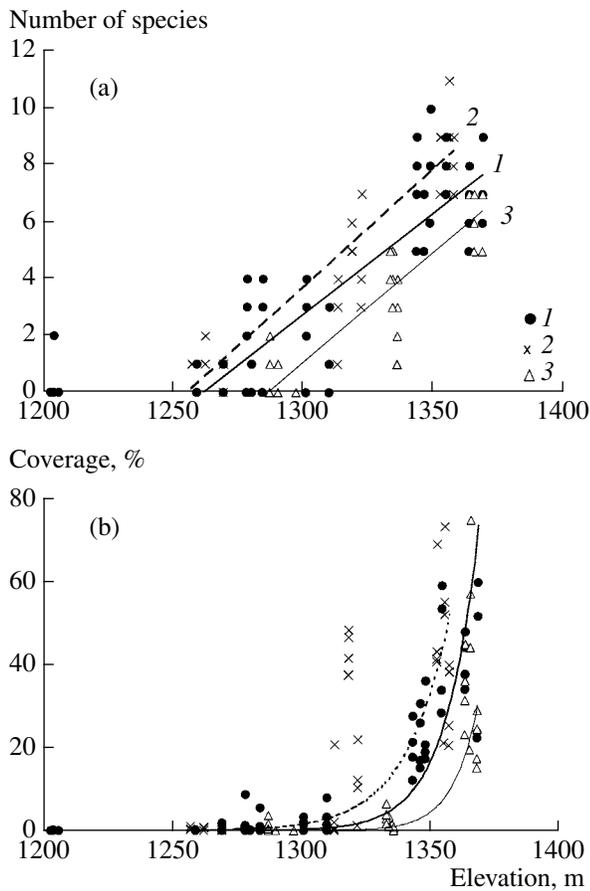


Fig. 1. Changes in (a) species richness and (b) total coverage of subarctic species (per 100 m²) along altitudinal gradient in plant communities of (1) southwestern, (2) southern, and (3) northeastern slopes of Mount Iremel'.

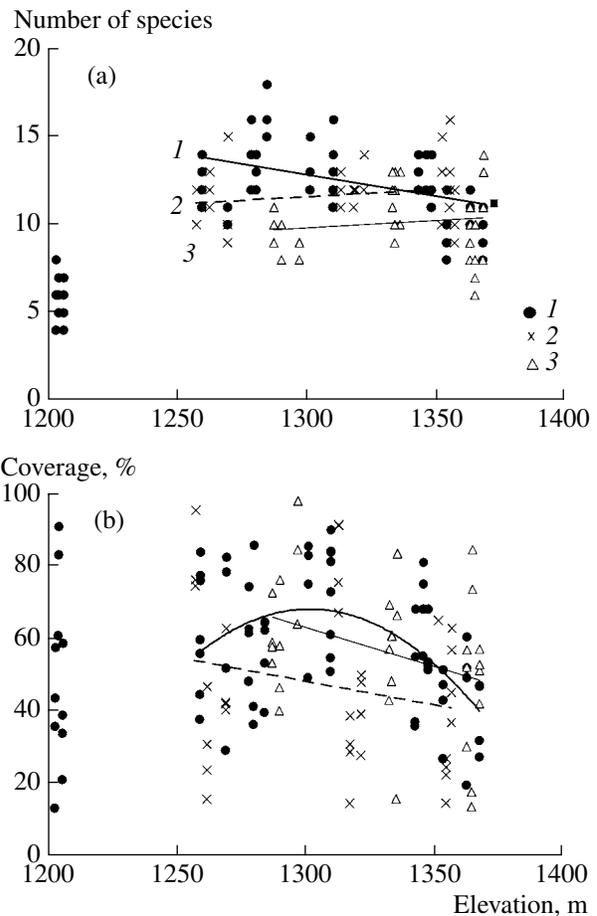


Fig. 2. Changes in (a) species richness and (b) total coverage of boreal species (per 100 m²) along altitudinal gradient in plant communities of (1) southwestern, (2) southern, and (3) northeastern slopes of Mount Iremel'.

dinal levels of the southern and southwestern slopes were almost the same, and the lowest values of these parameters were recorded in communities of the northeastern slope. The lowest relative values of SR were generally characteristic of communities growing on the southern slope (0.49 vs. 0.56 and 0.55 on the northeastern and southwestern slopes, respectively), and differences between the slopes were statistically significant (Table 5).

In the same segment of the altitudinal gradient, the absolute and relative TC of boreal species increased with a decrease in elevation, but this change on the southern slope was very slight (Fig. 2a). On the southwestern slope, TC sharply increased at 1350 m a.s.l., remained approximately the same in a certain range of lower elevations, and decreased at still lower elevations. On the whole, nonlinear dependence of this parameter on elevation was described by a second-degree polynomial ($R^2 = 0.23$; $P < 0.001$).

The variance of TC of boreal species on the southwestern and northeastern slopes was accounted for

mainly by absolute elevation. On the southern slope, the position of a macroplot within the test area on a certain altitudinal level was the main factor responsible for this variance. The relative TC values for boreal species were also lower on the southern slope (0.60 vs. 0.71 and 0.69 on the northeastern and southwestern slopes, respectively). However, differences in this parameter between the slopes lacked statistical significance, which was explained by very strong variation in the abundance of boreal species at the same altitudinal level.

The nemoral-boreal group was represented on the southern, southwestern, and northeastern slopes by 33, 29, and 19 species, respectively. The absolute SR values on the southern slope increased at lower elevations (Fig. 3a); on the southwestern and northeastern slopes, they initially increased and then decreased again. On the other hand, the relative values of this parameter on all slopes increased along the entire gradient. Upon transition from the uppermost to the lowermost level, the contribution of nemoral-boreal species to the total SR increased from 14.7 to 52.6% on the southwestern

Table 3. Results of two-way ANOVA for changes in relative values of species richness along the same slope for species groups differing in attitude toward thermal conditions (*D* refers to the proportion of total variance, %; *F* refers to values of the *F* test)

Factor accounting for variance (number of degrees of freedom)	Slope exposure					
	southwestern		southern		northeastern	
	<i>D</i>	<i>F</i>	<i>D</i>	<i>F</i>	<i>D</i>	<i>F</i>
Subarctic species						
Elevation a.s.l. (2)	94.9	164.30***	85.1	23.48**	88.5	49.60***
Macroplot (6)	0.3	1.22	10.2	9.67***	3.4	2.69*
Residual (27)	4.8		4.7		8.1	
Boreal species						
Elevation a.s.l. (2)	26.6	2.73	1.9	1.12	18.9	2.31
Macroplot (6)	37.1	5.09***	31.4	2.88*	30.4	3.39*
Residual (27)	36.3		66.7		50.7	
Nemoral–boreal species						
Elevation a.s.l. (2)	72.8	12.7**	63.7	7.72*	68.8	9.45*
Macroplot (6)	16.0	6.69***	25.8	10.89***	22.2	10.88***
Residual (27)	11.2		10.5		9.0	

Note: Asterisks indicate that the effect of a factor is significant at * $P < 0.05$, ** $P < 0.01$, or *** $P < 0.001$.

Table 4. Results of two-way ANOVA for changes in relative values of abundance along the same slope for species groups differing in attitude toward thermal conditions (*D* refers to the proportion of total variance, %; *F* refers to values of the *F* test)

Factor accounting for variance (number of degrees of freedom)	Slope exposure					
	southwestern		southern		northeastern	
	<i>D</i>	<i>F</i>	<i>D</i>	<i>F</i>	<i>D</i>	<i>F</i>
Subarctic species						
Elevation a.s.l. (2)	77.6	363.30***	43.6	3.67 [†]	71.0	19.30**
Macroplot (6)	0	0.11	46.5	19.81***	5.8	2.01 [†]
Residual (27)	22.4		9.9		23.2	
Boreal species						
Elevation a.s.l. (2)	85.9	32.20***	0	0.82	55.8	15.12**
Macroplot (6)	6.3	4.09**	68.7	9.78***	1.1	1.10
Residual (27)	7.8		31.3		43.1	
Nemoral–boreal species						
Elevation a.s.l. (2)	19.5	2.12	43.3	4.27 [†]	51.1	8.58*
Macroplot (6)	42.3	5.29***	34.0	6.99***	10.7	2.12 [†]
Residual (27)	38.2		22.7		38.2	

Note: Dagger and asterisks indicate that the effect of a factor is significant at [†] $P < 0.10$, * $P < 0.05$, ** $P < 0.01$, or *** $P < 0.001$.

slope, from 17.3 to 45.5% on the southern slope, and from 10.4 to 36.3% on the northeastern slope. In the same segment of the gradient, dependence of this parameter on elevation were adequately described by linear regression equations ($R^2 = 0.52, 0.49$ and 0.29 for the southwestern, southern, and northeastern slopes, respectively; $P < 0.001$), and slope angles of the regres-

sion lines were similar. Absolute elevation was the main factor accounting for the variance of SR in this group on all slopes, but the position of a macroplot within the area at a certain level also played a considerable role. Relative proportions of nemoral–boreal species in communities growing on different slopes did not differ significantly.

Table 5. Results of three-way ANOVA for changes in relative values of species richness and abundance within the present-day timberline ecotone for species groups differing in attitude toward thermal conditions (*D* refers to the proportion of total variance, %; *F* refers to values of the *F* test)

Factor accounting for variance (number of degrees of freedom)	Species groups					
	subarctic		boreal		nemoral-boreal	
	<i>D</i>	<i>F</i>	<i>D</i>	<i>F</i>	<i>D</i>	<i>F</i>
Species richness						
Slope (2)	1.9	3.20 [†]	13.6	4.13*	2.7	1.16
Elevation (2)	83.7	138.98***	12.7	3.85*	64.9	27.81***
Macroplot (18)	5.4	3.71***	29.7	4.01***	21.0	9.44***
Slope–elevation interaction (4)	2.3	1.94	10.5	1.59	1.3	0.29
Residual (81)	6.6		33.4		10.0	
Exposure						
Slope (2)	2.8	1.30	6.1	2.14	0.4	0.12
Elevation (2)	61.2	28.87***	36.1	12.60***	32.2	9.62***
Macroplot (18)	19.1	7.01***	25.8	4.44***	30.1	4.75***
Slope–elevation interaction (4)	4.7	1.11	5.8	1.02	8.8	1.31
Residual (81)	12.2		26.2		28.7	

Note: Dagger and asterisks indicate that the effect of a factor is significant at [†] $P < 0.10$, * $P < 0.05$, ** $P < 0.01$, or *** $P < 0.001$.

Changes in the TC of nemoral–boreal species along the descending altitudinal gradient had different patterns (Fig. 3b): on the southern slope, this parameter progressively increased ($R^2 = 0.42$; $P < 0.001$); on the northeastern slope, the initial increase was followed by a slight decrease ($R^2 = 0.09$; $P < 0.069$); and on the southwestern slope, TC sharply increased at approximately 1350 m a.s.l., stabilized below this level, and sharply increased again at still lower elevations, beyond the common segment of the gradient. Changes in relative TC values corresponded to those in the absolute values. The proportion of nemoral–boreal species in communities (estimated from TC values) increased at lower elevations from 7.3 to 46.7% on the southwestern slope, from 2.9 to 28.8% on the southern slope, and from 4.6 to 15.3% on the northeastern slope, with a peak (23.1%) at the third altitudinal level.

Random factors accounted for the greater part of the variance of TC of nemoral–boreal species on the southern and southwestern slopes, where absolute elevation proved to have no significant effect on this parameter. However, the effect of elevation was almost significant on the southern slope and really significant on the southwestern slope ($F_{5,12} = 4.3$; $P < 0.017$), being manifested throughout the descending altitudinal gradient. On the southern slope, the abundance of boreal–nemoral species tended to increase more rapidly along this gradient, but corresponding differences between the slopes lacked statistical significance. On the whole, the TC of nemoral–boreal species changed in a stepwise manner, with a sharp increase followed by stabilization of this parameter below 1350 m a.s.l. and a subsequent

repeated increase below 1250 m a.s.l. (data on the southwestern slope).

DISCUSSION

The lower boundary of the mountain tundra belt on Mount Iremel' was located at 1250–1300 m in the mid-20th century (Igoshina, 1964; Gorchakovskii, 1975) and at 1350–1400 m a.s.l. in the 1990s (Nikonova et al., 1992). Until the last quarter of the 19th century, woody species at elevations above 1250 m a.s.l. were represented by single dwarf individuals. They invaded this altitudinal zone in the period from 1915 to the 1990s, and the timberline has ascended above 1350–1400 m a.s.l. since then (Shiyatov, 1983; Moiseev et al., 2004). These data indicate that high-mountain communities in the region under study have undergone significant transformations during this period.

In plant communities of the present-day timberline ecotone on Mount Iremel', boreal species prevail at all altitudinal levels. This feature of the communities of Mount Iremel' and other mountain ranges of the Southern Urals was noted in previous studies (Igoshina, 1964; Gorchakovskii, 1975), but their authors provided no relevant quantitative data. Hence, it is impossible to reliably estimate the extent of changes in the composition and structure of communities during recent decades.

Within the former limits of the mountain tundra belt, the abundance and diversity of subarctic species reach the highest values in the uppermost parts of the transects (above 1350 m a.s.l.) and sharply decrease at

lower elevations. Conversely, the abundance and diversity of the other two species groups increase at these elevations (see Table 2, Figs. 1–3). The boundary at which the structure of communities (with respect to the ratio of these “thermal” groups) undergoes significant rearrangements coincides with the lower limit of the mountain tundra vegetation belt recorded in the 1990s (Nikonova et al., 1991). One more region of significant structural changes (revealed on the southwestern slope alone) is in the lower part of the altitudinal gradient (below 1250 m a.s.l.) and coincides with the former boundary of mountain tundras.

Many authors have shown that parameters of the plant component of natural ecosystems manifest non-linearity of responses in gradients of natural or anthropogenic factors (Noy-Meir, 1975; Walker et al., 1981; *Ekosistemy...*, 1989; *Kompleksnaya ekologicheskaya...*, 1992; Vorobeichik et al., 1994; Trubina and Makhnev, 1997; Scheffer et al., 2000; Trubina, 2002). The existence of zones in which quantitative parameters change more rapidly—i.e., some spatial discreteness of the community structure—indicates that the intensity of action of certain factors sharply changes in certain areas of the study region (Aleksandrova, 1966; Notsenko, 1973). The upper parts of all transects were laid in plateau-like areas of intermontane depressions. In such areas, as on mountaintops, high winds considerably worsen conditions in habitats and make the forest boundary (timberline) more distinct than does the temperature gradient alone (Gorchakovskii, 1975; Gorchakovskii and Shiyatov, 1985; Holtmeier, 2003). Wind conditions are probably the main factors responsible for lower rates of tundra community transformation in these areas during the 20th century. Relatively sharp changes in the structure of communities in the lower part of the transect on the southwestern slope might be associated with the modifying influence of tree species, but the role of biotic relationships was not considered in this study.

The almost linear pattern of elevation-dependent change in the species richness of different plant groups is indicative of similar rates of species invasion/elimination in different segments of the altitudinal gradient. This may be attributed to high small-scale nonuniformity of thermal conditions in high-mountain areas (Minyaev, 1963; Gorchakovskii and Shiyatov, 1975; Holtmeier, 2003) and a broad reaction norm of individual representatives of plant species. According to the results of this study, absolute elevation was usually the main factor accounting for the variance of species diversity and abundance in different thermal groups of plants. On the other hand, differences in these parameters between the fragments of communities located at the same altitudinal level at distances not exceeding several tens of meters were often comparable to differences between communities of different altitudinal levels located hundreds of meters apart or even exceeded them (see Figs. 1–3). Moreover, these differences were even more distinct than those between slopes of differ-

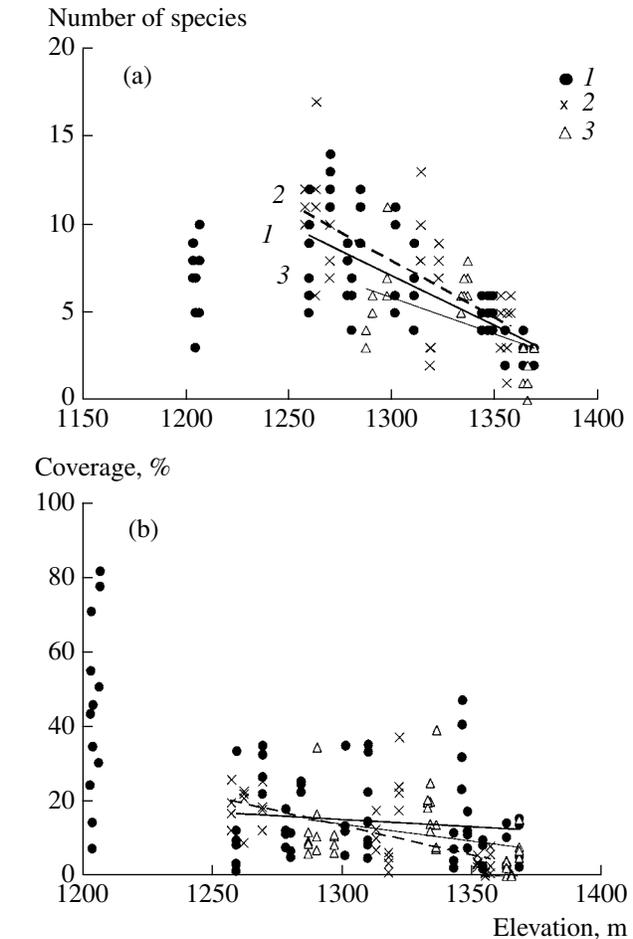


Fig. 3. Changes in (a) species richness and (b) total coverage of nemoral–boreal species (per 100 m²) along altitudinal gradient in plant communities of (1) southwestern, (2) southern, and (3) northeastern slopes of Mount Iremel’.

ent exposures, and conditions in local habitats at the same altitudinal level sometimes explained up to 68% of the total variance. Such a nonuniform distribution of species and individuals at the same altitudinal level provides indirect evidence for considerable small-scale heterogeneity of thermal conditions in high mountains. This factor is important for the survival of individuals representing plant species of different thermal groups under conditions of long-term climatic changes.

Taking into account more favorable thermal conditions on slopes of southern exposure, it could be expected that the rates of invasion of thermophilic species and elimination of cryophilic species in the corresponding plant communities would be higher. The species richness of nemoral–boreal species and the total number of species proved to be really greater on the southern slope, with the minimum values being recorded on the northeastern slope. However, plant communities growing on different slopes were similar with respect to relative indices such as the proportions of subarctic and nemoral–boreal species. This could be

due to different edaphic conditions on mountain slopes: irrespective of favorable thermal regime, adverse edaphic conditions on the southern slope (see above) could retard the invasion of thermophilic plants.

In general, specific features of the distribution of species differing in their attitude to thermal conditions within the former and present-day mountain tundra belt of Mount Iremel' provide evidence that transformations of high-mountain plant communities upon climate warming are extremely nonuniform in time and space. The pattern of change in the abundance of species belonging to different thermal groups is distinctly non-linear, and a mosaic effect of disturbing factors is observed (the distribution of these species at the same altitudinal level is highly nonuniform). Structural differences between plant communities growing on mountain slopes and plateau-like intermontane depressions in the present-day timberline ecotone and specific distribution patterns of different thermal groups of plant species on mountain slopes descending at different angles indicate that winds and edaphic conditions in habitats can significantly modify the rates of transformations taking place in high-mountain communities upon climate warming. The existence of the second zone of relatively sharp changes in the abundance of nemoral-boreal and boreal species at the former boundary of the mountain tundra belt confirms the role of biotic interactions in these transformations, but this problem deserves special investigation.

ACKNOWLEDGMENTS

This study was supported by INTAS, project no. 01-0052.

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