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Variability of plant species diversity during the natural restoration of the subalpine birch forest in the Central Great Caucasus

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Abstract: The northern slopes of the Central Great Caucasus of Georgia were covered by birch (*Betula litwinowii*) forests in the past, but forest degradation resulted in subalpine secondary meadows. Over the past 20 years birch forest natural reforestation processes have taken place. The aim of this study was to determine the changes in plant species diversity during reforestation. Different habitat types were selected to trace the development of birch forests from subalpine meadows. Species richness was determined in 100 research plots (25 m^2 each) of different habitat types. Pioneer succession was distinguished by the highest level of species richness due to the mixture of two habitat types. Degraded forest showed the lowest species richness. At the initial stages of forest restoration we observed several species of subalpine dwarf shrubs. They grow only in open canopy areas and are absent in closed forests. The alpine treeline habitat type and pioneer succession of subalpine meadows revealed close relations in species composition and diversity. These similarities show forest restoration in lower elevations as it is restricted in the treeline ecotone by local climatic conditions. The natural regeneration is apparently in close relation with the global climate change, but the most important factor is the reduction of uncontrolled sheep grazing.

Key words: *Betula litwinowii,* birch forest, pioneer succession, plant diversity, Central Great Caucasus

1. Introduction

The timberline on the northern slope of the Central Greater Caucasus of Georgia consists of broadleaf deciduous birch forests (Dolukhanov, 1978; Nakhustrishvili, 2013). Birch (*Betula litwinowii* Doluch.) is the dominant timberline species in the subalpine zone between 1750 and 2500 m above sea level (m a.s.l.). It is formed at lower elevations as a subalpine forest occurring as monotypic stands, and at higher elevations as an upper timberline with crook-stemmed forests (Akhalkatsi et al., 2006). The highest elevation treeline is mixed with *Rhododendron caucasicum* Pall. shrubs occurring only on the northern slopes at 2100–2900 m a.s.l. (Dolukhanov, 2010). These birch-dominated forests are widespread in the subalpine belt of the Kazbegi district of Georgia (Nakhustrishvili et al., 2006).

Currently, birch forests have significantly decreased in the temperate zone worldwide. They are represented as treelines only in four regions (Dolukhanov, 2010): Mount Etna (Sicily) - *Betula aetnensis* Raf., the Caucasus - *B. litwinowii*, the Himalayan range - *B. utilis* D. Don and *B. ermanii* Cham., and mount Fujiyama (Japan) - *B. ermanii*. The deciduous subalpine birch forests of the Central Greater Caucasus Mountains in the Kazbegi district of Georgia are represented by a combined species composition where *B. litwinowii* is a dominant treeline species. The main plant species associations in a birch forest habitat are represented by *Betula raddeana* Trautv., *Populus tremula* L., *Salix caprea* L., *S. kazbekensis* A.K.Skvortsov, *Sorbus caucasigena* Kom. ex. Gatsch., *Rhododendron caucasicum* Pall., *Vaccinium myrtillus* L., *Aconitum nasutum* Fisch. ex. Reichenb., *A. orientale* Mill., *Aquilegia caucasica* (Ledeb). Rupr., *Cephalanthera longifolia* (L.) Fritsch, *Cicerbita racemosa* (Willd.) Beauverd, *Dolichorrhiza renifolia* (C.A.Mey.) Galushko, *D. caucasica* (M.Bieb.) Galushko, *Geranium silvaticum* L., *Heracleum roseum* Steven, *Platanthera chlorantha* (Custer) Reichenb., *Swertia iberica* Fisch. & C.A.Mey., etc. (Nakhutsrishvili et al., 2006).

The subalpine birch forest is a very sensitive ecosystem with a key role in the regulation of water resources and the stability of mountain slopes (Kvachakidze, 1979; Sakhokia, 1983; Wielgolaski, 2005; Körner, 2008; Smith et al., 2009). During the last century the birch forest area in the Kazbegi district diminished due to anthropogenic factors such as fires, cutting of trees, and uncontrolled grazing. Forest degradation turned the areas into subalpine secondary meadows used as pastures and hay meadows (Sakhokia, 1983). Historically, birch forests were destroyed and burned by Kazbegi district residents. Fire is the dominant

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disturbance in many forest types, where it profoundly alters the composition and structure of plant communities (Lamont and Wiens, 2003). Forest cutting for firewood is always a problem for the birch and other tree species. Many individuals of *B. litwinowii* were destroyed in the Kazbegi district in this manner. According to the literature, forest habitat degradation is one of the major threats to species diversity of plant and animal populations. It causes lower population viability and genetic variation, which have a serious impact on multiple ecosystem functions (Honnay et al., 2005; St. Clair and Omas, 2011).

Uncontrolled grazing in the Central Great Caucasus Mountain region has been the most important problem for the restoration of degraded birch forests since the 1970s. According to Sakhokia (1983), the birch forest restoration process was inhibited by sheep grazing and recommendations were oriented toward grazing restrictions. Overgrazing by sheep is one of the important reasons for ecosystem degradation (Aradottir and Arnalds, 2001). Grazing affects seeds and their germination process, limiting birch forest species regeneration (Lehtonen and Heikkinen, 1995). Lack of sufficient regeneration of the tree species is a major problem of mountain forests (Krauchi et al., 2000). Although wild herbivores have some impact on the growth and development of forests, the large numbers of domestic sheep and cattle exert a far greater influence on these processes (Suomienen and Olofsson, 2001). Heavy browsing and trampling of young trees can severely suppress their growth and in some cases lead to their death (Kılıç et al., 2003). Control of grazing activities can promote tree regeneration (Honnay et al., 2005), but there are numerous other challenges too, such as seed dispersal, avoidance of predation, and germination of seeds, as well as survival and growth of seedlings (Anschlag et al., 2008; Zolfaghari et al., 2013).

Since the 1990s the sheep population has greatly diminished in the Central Greater Caucasus because of economic problems. The reforestation of birch forests started with changes of species diversity in the habitats of secondary meadows (Akhalkatsi et al., 2006; Hughes et al., 2009). Since this period, huge areas of the northern slopes in the Kazbegi district have been covered by birch seedlings presented by primary successions of the birch forest. Currently, birch trees on the northern slopes reach 4–5 m in height and constitute a logical succession. Some climax successions of subalpine forests, timberline, and tree line remain in this area. This process is known as natural regeneration of birch forests, which is apparently in close relation with the global climate change, but the most important factor is the reduction of uncontrolled sheep grazing in the Kazbegi district (Akhalkatsi et al., 2006; Nakhutsrishvili et al., 2006).

The global climate change limits the number of tree species at high elevations with particular manifestations of low temperatures (Larcher et al., 2010). The problem is determined by critical temperatures for the mean growing season in the climatic tree line (Körner, 2012; Kollas et al., 2014). Climate change is quite intensive in the northern European zones (Gottfried et al., 2012). However, the climate has been more stable in the Central Greater Caucasus in the past century (Gigauri et al., 2013). Therefore, birch forest protection should be dependent on human impact and overgrazing effects (Holtmeier, 2009).

The aim of our study was to determine the variability in plant species composition and diversity during the natural reforestation of the birch forest in the Kazbegi district of the Central Great Caucasus of Georgia. Another interest was the comparison of differences in species composition between primary and degraded subalpine birch forest habitats. Three major constraints must be overcome when determining plant species diversity changes during forest restoration processes: (1) the geographical position and environmental features of different habitat types of the subalpine birch forest; (2) comparison of the species composition, richness, evenness, and Shannon–Wiener diversity index changes during birch forest natural restoration processes; and (3) determination of indicator species in the studied habitat types.

2. Materials and methods

2.1. Study region

Georgia (69,875 km^2) is located in the south Caucasus region (Figure 1). The study region of the Kazbegi district (1081 km^2) is situated to the north of the Main Watershed Range of the Central Greater Caucasus, in the valley of the R. Tergi (42°48′N; 44°39′E) at the border with Russia. This is morphologically the most complex high-mountain region of the Central Greater Caucasus. The ground materials are Jurassic rocks, Palaeozoic and even older granites, young lava, and moraines (Nakhutsrishvili, 2013). The elevation of the region ranges from 1210 m a.s.l. to 5033 m at the highest peak (Mt. Kazbegi). The average elevation is 2850 m a.s.l. About 50 soil types have been described on the territory of Georgia and the following specific soil types are found at subalpine zones: 1) mountain-forest brown skeleton soils of middle and small depth; 2) mountain-forest light brown skeleton soils of middle and small depth; and 3) degraded forest and secondary meadow soils (Neidze, 2003).

The climate of the Kazbegi district is moderately humid with relatively dry, cold winters and long and cool summers. The average annual temperature is 4.9 °C. January is the coldest month with an average temperature of –5.2 °C and the lowest temperature is –30 °C. The maximum average temperature of the warmest months (July and Au-

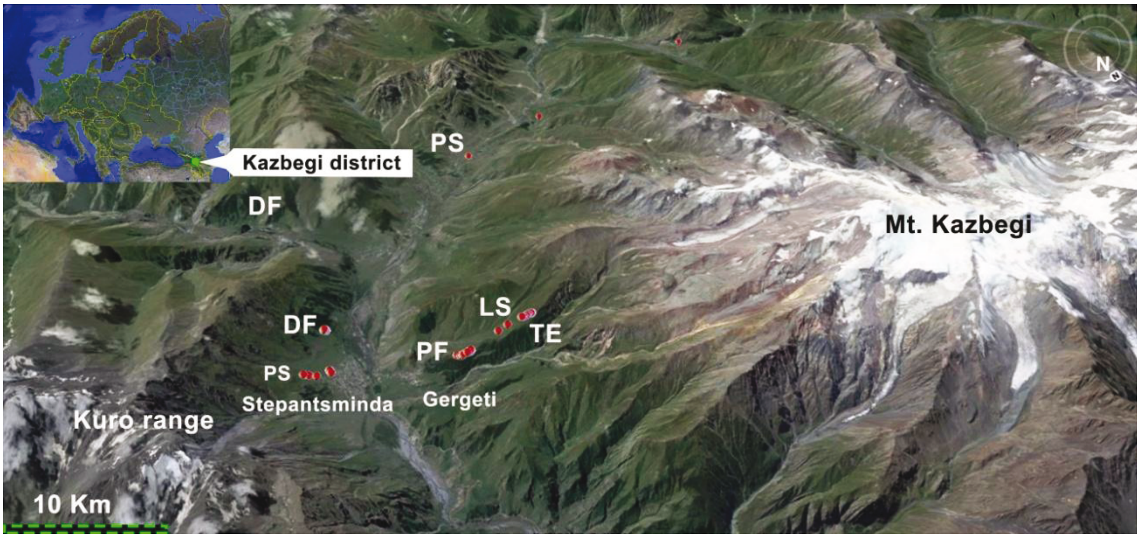

Figure 1. A map of the study site plots in the Kazbegi region with 5 birch forest habitats: PS – Pioneer stage of secondary succession of forest restoration in the surroundings of Stepantsminda and the village of Vardisubani; LS – Logical succession of growing birch forest during natural restoration on the slope of Mt. Kazbegi; PF – primary birch forest "Lifu" near the village of Gergeti and the Sameba Church; DF – degraded forest near Stepantsminda and the village of Sno; TE – Treeline alpine ecosystem on the slope of Mt. Kazbegi.

gust) is about 14.4 °C (the highest temperature is 30 °C). Stable snow cover persists for 5–7 months from November to May and reaches its maximum depth (115–120 cm) in March. The mean air humidity in the summer is 75%. The average annual precipitation is about 1000 mm with peak values in early summer. Fog is frequent in this zone (135 foggy days per year), especially in the summer. Winds of the mountain-gorge type prevail (Nakhutsrishvili, 2013).

The flora of the Kazbegi district contains ca. 1100 species of vascular plants (Sakhokia and Khutsishvili, 1975). The following vegetation zones are represented in the region: middle-mountain (1000–1500 m a.s.l.), upper-mountain (1500–1750 m a.s.l.), subalpine (1750–2500 m a.s.l.), alpine (2500–3000 m a.s.l.), subnival (3000–3600 m a.s.l.), and nival (above 3600 m a.s.l.). The environmental conditions, the morphological and functional types of plants, and the composition and productivity of plant communities in the study region are described by Nakhutsrishvili (2013).

The natural forest habitat type of the Kazbegi district is birch (*Betula litwinowii*) forest. It is located only on the north-facing slopes of east–west ridgelines that extend upward to the high mountain peaks, forms the alpine timberline at higher elevations (2050–2550 m a.s.l.), and reaches its highest tree line limit only when associated with the broadleaf evergreen shrub *Rhododendron caucasicum* (Akhalkatsi et al., 2006). The birch forest is oriented on the north-facing slopes with continuous winter snow cover and is predominantly accompanied by *Rhododendron caucasicum*, *Populus tremula*, *Salix kazbekensis*, *Sorbus caucasigena*, *Vaccinium myrtillus*, *Empetrum caucasicum*, and other species (Nakhutsrishvili et al., 2006). The Kazbegi district is presently sparsely populated and land use change has led to a diminished anthropogenic impact. The primary (not damaged) forest is protected by church territory based on religious traditions not allowing tree cutting and is located near the Sameba monastery, close to the village of Gergeti. There are some degraded forests near other villages, in particular close to the small town of Stepantsminda.

2.2. Study sites

In order to compare species composition and diversity among birch forest types during natural restoration and at degradation levels, five habitat types were selected in the Kazbegi district and human impact effects were evaluated. The degradation steps of these forest types start with disturbances of the primary forest by natural and human factors, leading to degraded forest and nonforest types. Forest restoration started at the secondary subalpine meadows and continued growing at logical succession with 3–5 m trees. Primary forests protected by church traditions and degraded forests near settlements were identified according to a subjective estimate of birch forest restoration and degradation status by evaluating the human impact effects on species composition changes. The preselection was then evaluated during field trips yielding the final set of sample sites (Figure 1). The environmental characteristics such as geographical coordinates, landscape conditions, and above-ground vegetation parameters for each investigated habitat type were collected. The main characteristics of the habitat types are presented in Table 1.

Habitat type 1. A pioneer secondary succession stage (PS) of forest natural restoration with small 1–5-year-old birch seedlings. This habitat type is found on subalpine pasture meadows on the slopes of northern exposure near the town of Stepantsminda, Mt. Ellia of the Kuro range, and near the village of Vardisubani (Figure 1). The vegetation cover is between 70% and 95%. Some shrubs and birch seedlings are growing on dense tussock grass meadows dominated by *Anemone fasciculata*, *Calamagrostis arundinacea*, *Daphne glomerata*, *Dolichorrhiza caucasica*, *Leontodon hispidus*, *Lotus caucasicus*, *Salix kazbekensis*, *S. kuznetzowii*, *Bettonica macrantha*, *Trifolium canescens*, *Vaccinium myrtillus*, *Veratrum lobelianum*, etc.

Habitat type 2. A logical succession of a birch forest with 4–6-m-tall young birch trees (LS), located on the major northern slopes of Mt. Kazbegi (Figure 1). Intensive regeneration of the birch was observed on the slope between the timberline and the ridge. Plant cover index varies between 60% and 90% (Table 1). Other forest species mixed with birch are *Salix kazbekensis*, *S. kuznetzowii*, *Sorbus caucasigena*, *Veratrum lobelianum*, etc.

Habitat type 3. A primary subalpine birch forest (PF) called *"Lifu"*, protected by the Sameba church, situated in the subalpine birch forest zone and composed of 15–20-m-tall trees (Table 1; Figure 1). The plant cover (besides birch) in the understory is about 70%–75% and is represented by the following species: *Aconitum nasutum*, *A. orientale*, *Daphne mezereum*, *Geranium sylvaticum*, *Platanthera chlorantha*, *Polygonatum verticillatum*, *Primula amoena*, *Pyrola media*, *Rubus saxatilis*, *Sorbus caucasigena*, *Swertia iberica*, *Veratrum lobelianum*, etc.

Habitat type 4. A birch forest degraded by anthropogenic impact (DF) called "*Areshistavi*" is situated near the town of Stepantsminda on the Kuro range and in the Sno gorge (Table 1; Figure 1). In this site only dwarf birch trees are found, growing exclusively in the soil depressions. The plane areas are covered by grasses and herbs with plant cover at about 90% and dominated by *Bromopsis variegata*, *Campanula biebersteiniana*, *Carum caucasicum*, *Heracleum roseum*, *Nardus stricta*, *Primula amoena*, *Viola caucasica*, etc. The soil depressions are almost depleted of vegetation.

Habitat type 5. The upper zone of the tree line ecotone (TE), called open alpine tundra and situated above the timberline of a subalpine forest (Table 1; Figure 1). It consists of 2–3-m-tall crook-stemmed birch trees, growing among *Rhododendron caucasicum* shrubs that form a dense cover. Besides these, the vegetation is composed of *Carex tristis*, *Empetrum caucasicum*, *Gentiana pyrenaica*, *Luzula pseudosudetica*, *Poa alpina*, *Salix kazbekensis*, *Sorbus caucasigena*, *Vaccinium myrtillus*, *V. vitis-idaea*, etc.

Twenty plots in each forest habitat type (a total of 100 plots) were analyzed for species composition and diversity. Each plot was square (5 × 5 m). Study sites are located between 1822 and 2660 m a.s.l. (Table 1; Figure 1), with only northern exposure. The description of each plot includes coordinates, altitude, exposure, inclination, cover percentage (vascular plants, stones, lichens, bryophytes, bare ground, and litter), tree height, and vascular plant species cover percentage per plot. Vegetation canopy cover is measured as the percentage of ground cover by a vertical projection of the understory shrubs, herbs, grasses, and other species. Basal cover of trees is determined by measuring their diameter at breast height. We also used the method of fish-eye lenses to evaluate sky exposure

Table 1. Habitat types in the Kazbegi district: location with coordinates, elevation, exposure and slope inclination, bare soil, stone and cryptophytes cover percentage (mean ± SD) (N = 100).

Habitat type	Location	Coordinates	Elevation	Exposition	Inclination°	pH	Bare soil cover %	Stone cover %	Cryptophytes cover %
Pioneer succession (PS)	Stepantsminda Mt. Ellia, v. Vardisubani	N42.578/66 E44.570/66	2030 ± 104.26	N	33.25 ± 6.54	5.6 ± 0.43	6.4 ± 6.47	6.05 ± 6.19	4.83 ± 4.07
Logical succession (LS)	Mt. Kazbegi slope	N42.595 E44.570	2098.2 ± 148.35	N	25 ± 8.4	5.44 ± 0.55	13.15 ± 9.86	4.9 ± 5.12	5.1 ± 2.55
Primary forest (PF)	Lifu forest, v. Gergeti	N42.666 E44.620	2098.35 ± 43.02	N	24.5 ± 7.4	5.47 ± 0.2	17.1 ± 9.81	0.0	9.3 ± 6.83
Degraded forest (DF)	Stepantsminda, Kuro range	N42.642 E44.643/5	1850.75 ± 19.92	N	38 ± 6.36	5.43 ± 0.25	9.65 ± 6.62	0.6 ± 2.26	8 ± 4.79
Tree line alpine zone (TE)	Mt. Kazbegi slope	N42.66 E44.58/60	2536.2 ± 70.43	N	40.5 ± 8.87	4.9 ± 0.37	4.85 ± 5.34	1.475 ± 2.02	4.45 ± 2.52

effects on the vegetation cover of the research plots. Sky exposure was used as a general indicator of illumination influencing the habitat microclimate, which might be affected by climate. Data sampling was performed in July of 2011 and 2013.

2.3. Data analysis

Mean, standard deviation, and minimum and maximum values were calculated for each quantitative data set. One-way ANOVA ($p < 0.05$) was used to test differences in environmental data, species cover, and canopy height of habitat types. Tukey's honestly significant difference test was used to assume equal variances. Pearson's correlation coefficient (r) was calculated by bivariate correlation analyses.

Species richness was determined as the number of vascular plant species per sampling plot used to assess species diversity in the studied habitat types. More aspects of diversity are characterized by evenness, which is emphasized by the Shannon–Wiener index ($H' = -\Sigma P_i \ln P_i$), called α diversity (Tokeshi, 1993), where P_i is the proportion of characters belonging to individuals that species *i* contributes to the total *i* abundance.

Discriminant function analysis (DFA) was used with SPSS 16 to determine the relation among the studied habitat types by species cover percentage per plot, indicating the species composition and richness. Principal components analysis (PCA) was used to determine important characters for the differences in habitat types. Additionally, we performed a detrended correspondence analysis (DCA) using PC-ORD 5.33 software to demonstrate relationships between species distribution and environmental conditions among plots of habitat types. Environmental conditions were passively projected in the ordination. Indicator species analysis (Dufrene and Legendre, 1997) was carried out for all habitat types to describe the value of different species in indicating environmental conditions. Hierarchical cluster analyses were done by Statistica 6.0 software; this method uses an analysis of variance approach to evaluate the distances between clusters. This attempts to minimize the Sum of Squares of any two (hypothetical) clusters that can be formed at each step. The distance measure interval is Euclidean distance, computing distances between objects in a multidimensional space.

3. Results

3.1. Floristic composition

Our results demonstrate that species composition and diversity vary in different habitat types of subalpine birch forests (Supplement, Table S1; on the journal's website). A total of 50 families, 143 genera, and 243 species of vascular plants were found in the 100 study plots of 5 habitat types (Figure 2A). The most dominant families in the total area are Asteraceae (30 species), Fabaceae (25 species), Poaceae (21 species), Caryophyllaceae (15 species), Apiaceae (12 species), and Rosaceae (11 species). The number of species ranges from 15 to 48 per sample plot, and from 75 to 152 per habitat type. The plots within a habitat type vary by some plant species (*Agrostis planifolia*, *Alchemilla rigida*, *Anemone fasciculate*, *Avenella flexuosa*, *Bettonica macrantha*, *Betula litwinowii*, *Calamagrostis arundinacea*, *Campanula collina*, *Festuca ovina*, *Hieracium* × *pannoniciforme*, *Geranium sylvaticum*, *Lapsana grandiflora*, *Ranunculus caucasicus*, *Vicia variabilis*), which are present in all habitat types and most plots (Supplement, Table S1). The number of life forms of vascular plants in the study sites varies among habitat types (Figure 2B). The highest number of species is represented by herbs, especially in open habitats of pioneer succession and in the upper zone of the tree line habitat covered by subalpine shrubbery and crook-stemmed trees. The other life forms from the study sites do not represent all vascular plant species of the habitat types. Only two tree species are dominant in the nondegraded primary forest: *Betula litwinowii* and *Salix caprea*, and the study sites contain these species. In general, the highest number of tree species is observed in this habitat type and it contains two birch species (*Betula litwinowii*, *B. raddeana*), the common aspen (*Populus tremula*) in forest edges, goat willow (*Salix caprea*), and Caucasian rowan (*Sorbus caucasigena*) in higher elevations. *Pinus kochiana* is part of a natural rock pine forest but is planted near a primary birch forest on burned areas and few individuals are germinated within the birch forest. *Quercus iberica* has mainly disappeared as it is being used for firewood. Currently some oak species are restored and protected in the primary forest. The pioneer succession starts with the seedling growth of *Betula litwinowii* and three more trees are added to this area: *Salix caprea*, *S. kazbekensis*, and *S. kuznetzowii*, ranking it as a large area of the logical succession. The upper alpine tree line contains two birch species, all *Salix* spp. and *Sorbus caucasigena*. The shrubs appear in secondary subalpine meadows, starting the forest restoration. Birch seedlings (1–2 years old) are growing in the area with 3–5 year old shrubs: *Daphne glomerata*, *Vaccinium myrtillus*, *Rhododendron caucasicum*, *Rosa* spp., and *Rubus* spp. Generally, these shrubs are not found on typical pasture and hay meadows. Ferns (*Asplenium septentrionale*, *Dryopteris filix-mas*, and *D. oreades*) are present in subalpine birch forest habitats. *Polystichum lonchitis* and *Botrychium lunaria* occur in secondary meadows and alpine tree lines.

3.2. Horizontal and vertical structure of habitats

The total cover of understory vegetation shows similar levels in open and in forest habitats (Table 2) and correlates negatively with bare soil cover data ($r = -0.79$; $P < 0.00001$). Trees canopy cover (subtracted from sky exposure data)

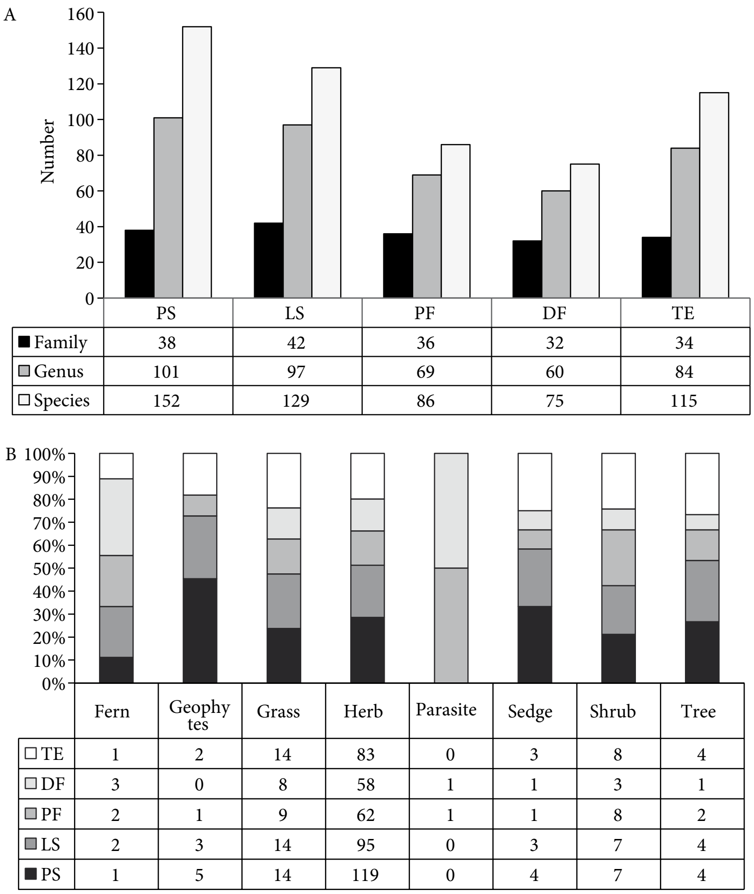

Figure 2. A - Number of families, genera, and species in 5 different habitat types of subalpine birch forest. (See Figure 1 for explanation of the legends); B- Number of species of different growth life forms - tree, shrub, herb, grass, sedge, fern, and parasite in the 5 habitat types (N = 100).

Table 2. Mean ± SD data in parenthesis of soil cover percentage by understory vegetation, tree canopy and basal cover %, shrub, herb, and grass cover %. Tree, shrub, and grass height in centimeters. Sky exposure percentage. Species richness, evenness, Shannon–Wiener and Simpson index. One-way analysis of variance (ANOVA) was conducted for all values. F and significance values are presented (N = 100).

Habitat type / Characters	Pioneer succession (PS)	Logical succession (LS)	Primary forest (PF)	Degraded forest (DF)	Tree line alpine zone (TE)	Df	Mean Square	F	Significance
Understory vegetation cover (%)	82.72 ± 11.31	76.85 ± 8.27	74.73 ± 10.18	81.75 ± 10.79	89.61 ± 7.89	4	670.88	7	0.0001
Tree canopy cover (%)	10.95 ± 4.35	81.84 ± 4.98	83.7 ± 3.04	85.429 ± 4.05	23.2 ± 9.47	4	27007.09	848.8	0.0001
Tree basal cover %	0	28.85 ± 14.17	16.45 ± 7.82	15.8 ± 6.59	8.85 ± 6.40	4	1209.14	16.55	0.0001
Shrub cover (%)	9.27 ± 6.05	11.4 ± 15.1	8.37 ± 4.61	6.9 ± 5.57	51.48 ± 20.03	4	7278.31	50.67	0.0001
Herb cover (%)	46.07 ± 10.02	27.55 ± 12.52	43.96 ± 10.87	48.85 ± 12.4	17.83 ± 10.7	4	3639.8	28.25	0.0001
Grass cover (%)	16.43 ± 7.5	9.05 ± 4.21	8.48 ± 4.65	10.2 ± 5.4	11.45 ± 11.6	4	201.73	3.87	0.006
Tree height (cm)	92.45 ± 34.59	360 ± 80.45	1475 ± 259.3	810 ± 212.5	108.85 ± 45	4	6807178	278.77	0.0001
Shrub height (cm)	19.85 ± 11.95	31.7 ± 13.96	79.75 ± 59.81	55.75 ± 29.16	39.3 ± 5.82	4	10823.32	11.28	0.0001
Grass height (cm)	57.35 ± 15.8	50 ± 17.99	79 ± 9.26	70.65 ± 16.27	51.3 ± 20.29	4	3216.78	12.04	0.0001
Birch trees number per 25 m^2 plot	9.64 ± 8.47	25.55 ± 9.84	6.65 ± 2.6	6.3 ± 2.94	2.6 ± 1.27	4	1607.68	43.3	0.0001
Sky exposition (%)	61.63 ± 6.36	18.16 ± 4.98	16.32 ± 3.01	14.57 ± 4.05	71.06 ± 3.94	4	15250.67	717.54	0.0001
Species richness	36.5 ± 6.24	26 ± 8.5	26.85 ± 5.11	22.1 ± 3.31	28.45 ± 7.67	4	562.91	13.58	0.0001
Evenness	0.87 ± 0.03	0.7 ± 0.14	0.81 ± 0.08	0.84 ± 0.05	0.63 ± 0.12	4	0.21	24.63	0.0001
Shannon–Wiener Index	3.13 ± 0.19	2.29 ± 0.57	2.66 ± 0.28	2.61 ± 0.21	2.12 ± 0.53	4	3.04	19.93	0.0001
Simpson index	0.939 ± 0.01	0.78 ± 0.15	0.89 ± 0.05	0.897 ± 0.03	0.74 ± 0.13	4	0.14	16.91	0.0001

in forest habitats and shrubs, herbs, and grasses projective cover show variability among studied habitats (Table 2; Figure 3A). Tree cover in pioneer succession is projective cover for lower young trees. Tree canopy cover is increased in logical succession with higher trees and sky exposure is covered similarly to subalpine forests (Table 2). The sky exposure correlates negatively with tree canopy cover ($r = -0.96$; $P < 0.00001$). One-way analysis of variance (ANOVA) determined large differences among tree covers in the studied habitats ($F = 848.8$; $P < 0.0001$). Herbs and grasses cover is highest in secondary meadows. However, subalpine forest understory is intensively covered by these life forms (Figure 3A). The shrub cover is extremely high in the alpine tree line habitat (51.48 ± 20.03). These areas are characterized by lower pH (4.9 ± 0.37; Table 1), which is correlated with elevation ($r = -0.61$; $P < 0.00001$).

The tree height in primary forest is much higher, where birch trees reach ca. 20 m in height (Table 2; Figure 3B). The same tree species in a naturally degraded habitat reach ca. 10 m and birch trees in logical succession vary only from 3 to 5 m in height. The secondary meadows are covered by seedlings and young 1–5-year-old trees and have 7 shrubs

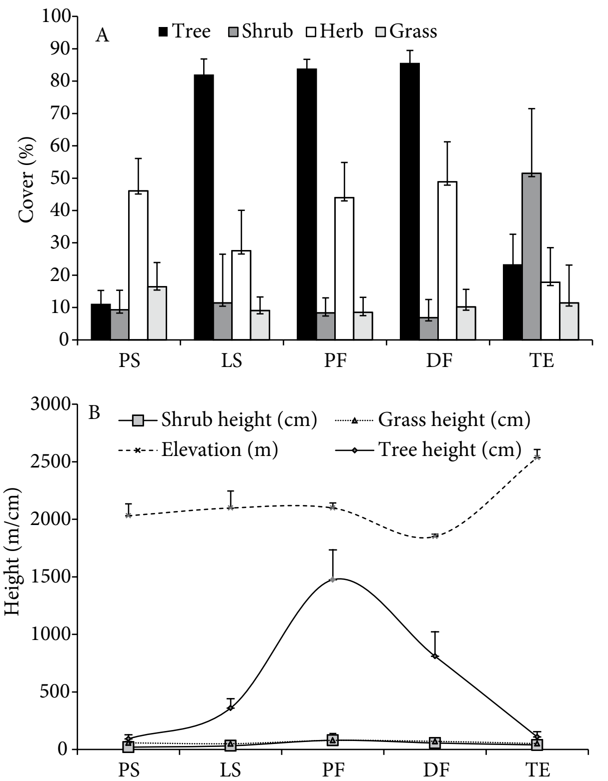

Figure 3. A - Life forms (trees, shrubs, herbs, and grasses) vegetation cover percentage data (mean numbers with SD) in different habitat types of the studied sites. (See Figure 1 for explanation of the legends); B - Trees, shrubs, and grasses height in centimeters of the 5 studied habitat types and elevation of the studied plots in meters (N = 100).

(Figure 2B). Tree height, according to one-way ANOVA, accounts for large differences among the studied habitats ($F = 278.77$; $P < 0.0001$). Tree height positively correlates with tree cover ($r = 0.7$; $P < 0.00001$). Shrub and grass height is taller in the forest understory (Table 2).

3.3. Species diversity

The species richness per plot varies slightly among the studied sites, but differences exist ($F = 13.58$; $P < 0.00001$; Table 2; Figure 4A). The species richness shows higher levels in pioneer succession (36.5 ± 6.24) by meadow and forest species composition. Degraded subalpine birch forests have lower levels of plant species diversity (22.1 ± 3.31; Table 2; Figure 4A). Evenness and Shannon–Wiener index are higher in pioneer succession (Table 2; Figures 4B and 4C) and have a lower rate in logical succession with a large cover of young birch trees, and in the alpine tree line upper zone covered mainly by *Rhododendron* shrubs. Herb cover represented by the highest number of species correlates positively with evenness ($r = 0.81$; $P < 0.00001$) and the Shannon–Wiener index ($r = 0.76$; $P < 0.00001$).

3.4. Comparison of habitat types

We identified 21 environmental, vegetation structure, and species diversity items of data (Tables 1 and 2) as important characters for the differences in habitat types by conducting PCA based on the correlation matrix. Cumulative initial eigenvalues of 5 principal components (PCs) reached 85.01% (42.28%, 20.08%, 10.4%, 7.21%, and 4.99%, respectively). The highest loadings on the 1st PCA axis correspond to characters of the Shannon–Wiener index (0.98), understory vegetation cover (0.97), the Simpson index (0.97), evenness (0.95), shrub cover (0.94), elevation (0.92), grass height (0.92), bare soil cover (0.89), number of birch trees per 25 m^2 (0.88), tree cover (0.88), tree height (0.88), stone cover (0.86), pH value (0.85), sky exposure (0.85), tree basal cover (0.84), herb cover (0.82), species richness (0.76), grass cover (0.76), cryptophytes cover (0.75), shrub height (0.61), and inclination (0.57).

In stepwise DFA, based on the 5 PCs of the study sites resulting from PCA, we obtained a high cumulative percentage of variance that accounted for 98.11% for the first three axes of the canonical DFA (Table 3). Wilk's lambda is very low for the first axis of the analysis (0.01, $P < 0.0001$), but higher for the last axis (0.77, $P < 0.0001$). Classification results show that all 20 studied plots (100%) belong to pioneer succession. The logical succession claims 19 studied plots out of 20 (95%), and the remaining one is associated with pioneer succession (Table 2). Primary forest has a connection with degraded forest at 15% and the opposite is 10% (Table 2). The alpine tree line zone confirms a similarity with pioneer succession with its lower birch trees and shrubs (20%).

The DFA scatter plot shows distribution of the 100 plots of 5 habitat types against the first two canonical

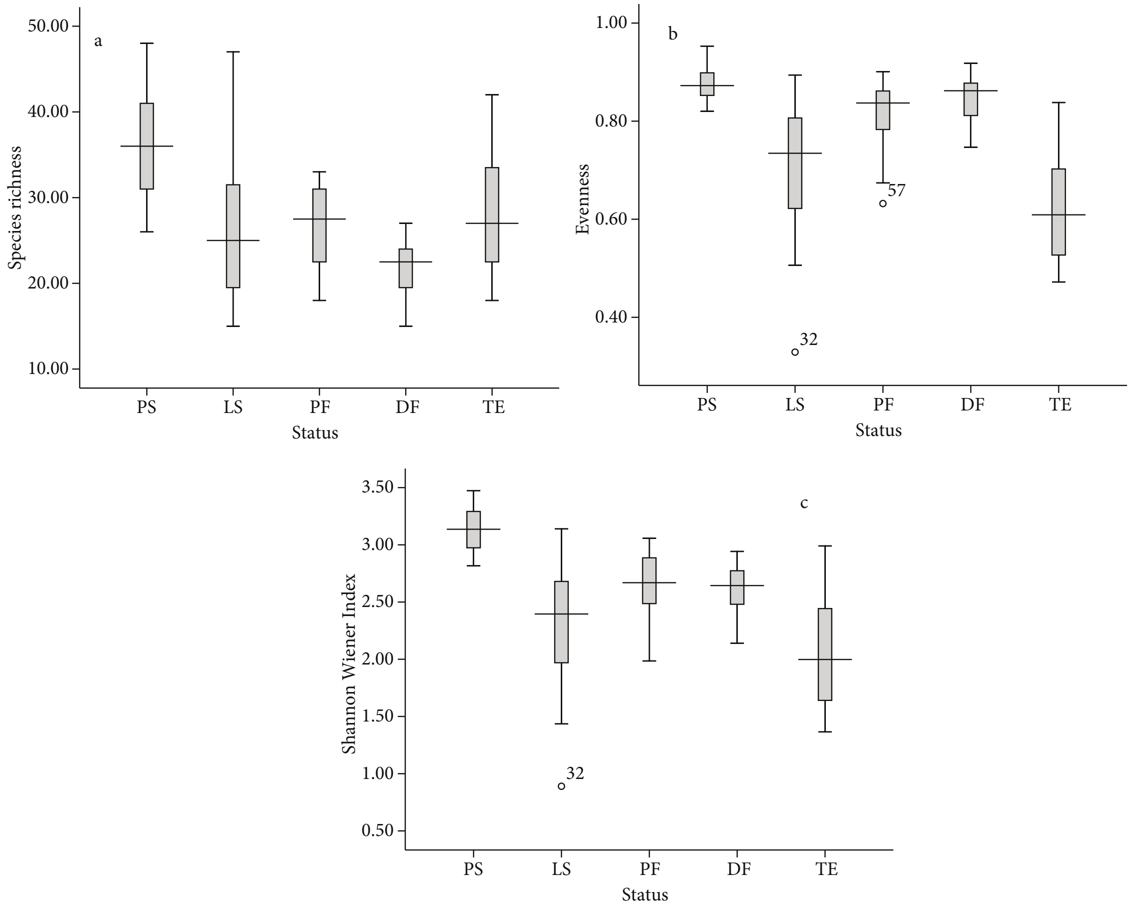

Figure 4. Box plots for species richness (**A**), evenness (**B**), and Shannon–Wiener index (**C**) of different habitat types of the studied sites. (See Figure 1 for explanation of the legends).

discriminant functions axes (Figure 5). The three groups of subalpine birch forest habitats (PF, DF, and LS) are located in the left, lower, and upper part of the plot, respectively. Tree line habitat types (TE) are shown on the right lower part of the plot and pioneer succession of secondary meadows are in the upper part near the tree line habitat. Some plots of logical succession join the pioneer succession on the right part.

DCA ordination revealed correlation between 243 species percentage cover data and all 100 sample plots based on twenty-one characters (Figure 6). The distribution of habitat types along the axes was different and it is similar to the distributions of samples data in the DFA scatter plot (Figure 5). Species covers of PF and DF plots are again located in the left part of the plot. PF is located in the upper part of the first ordination axis and is positively correlated with tree and grass heights and tree canopy cover. Degraded forest is located in the right lower part and is in correlation with herb cover, exposure, evenness, and Simpson index. Logical and primary successions are mixed in the central part of the ordination axes and reach the tree line habitat located on the right. All three habitat types are correlated with elevation, sky exposure, and shrub cover.

The relationships among the 5 habitat types of nondegraded and degraded forests, alpine tree line, and logical and pioneer successions are reflected in the dendrogram of a hierarchical cluster analysis using Euclidean distance (Figure 7). The 5 habitat types in the dendrogram are clustered into three main groups. The first cluster includes pioneer succession (PS) and tree line habitat (TE). Logical succession (LS) is separated from two clusters. The last contains two subalpine forests, however, revealing very long linkage distances.

3.5. Indicator species

Indicator species analysis revealed significant indicator species in the different habitat types of subalpine birch forests (Table 4). On the sites of pioneer succession *Lotus caucasicus* (76.1), *Ranunculus oreophilus* (60.5), *Rhinanthus minor* (54), *Trifolium canescens* (45.3), *Thymus collinus* (43.8), and *Anthoxanthum odoratum* (41.3) have high indicator values.

Table 3. Results of the DFA. Grouping variables of the 5 habitat types of birch subalpine forest areas (See Figure 1 for explanation of the legends) are based on the first 4 axes of the canonical discriminant function analysis with eigenvalues, percentage of variance, cumulative percentage, canonical correlation, probability level and Wilk's lambda. The classification results of the 20 studied plots per each habitat type are distributed as correct data and associated data to other habitat types. The classification percentage data shows percentage of plot numbers as correct data and associated data with other habitat types (N = 100).

Data after grouping variable "beech forest are habitat types"

Functions	Eigenvalue	% of variance	Cumulative %	Canonical correlation	Probability level	Wilk's **Λ**
1	11.67	75.44	75.44	0.96	0.00	0.01
2	2.38	15.37	90.81	0.84	0.00	0.11
3	1.13	7.29	98.11	0.73	0.00	0.36
4	0.29	1.89	100	0.48	0.00	0.77

Classification data after grouping variable "beech forest area habitat types"

Group	PS	LS	PF	DF	TE	Total
PS	19	1	0	0	0	20
LS	1	19	0	0	0	20
PF	0	0	17	3	0	20
DF	0	0	2	18	0	20
TE	4	0	0	0	16	20

Classification percentage data after grouping variable "beech forest area vegetation types"

	PS	LS	PF	DF	TE	Total
PS	95	5	0	0	0	100
LS	5	95	0	0	0	100
PF	0	0	85	15	0	100
DF	0	0	10	90	0	100
TE	20	0	0	0	80	100

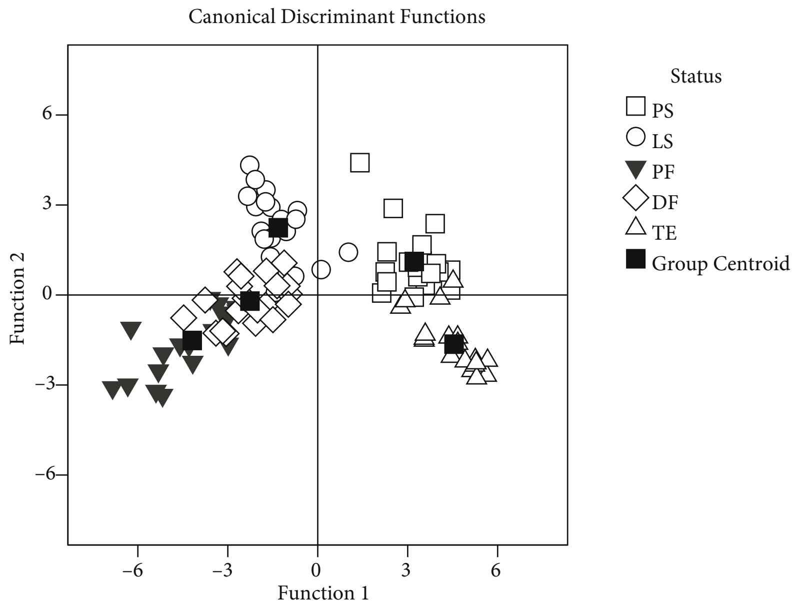

Figure 5. Scatter plot of discriminant function analysis (DFA) of the 100 plots of studied sites based on 5 principal components of 21 characters of species richness and diversity indices, soil and vegetation percentage cover, and canopy vertical structure data resulting from PCA; Scatter plot of the 5 habitat types (See Figure 1 for explanation of the legends) are plotted against two canonical discriminant functions axes (N = 100).

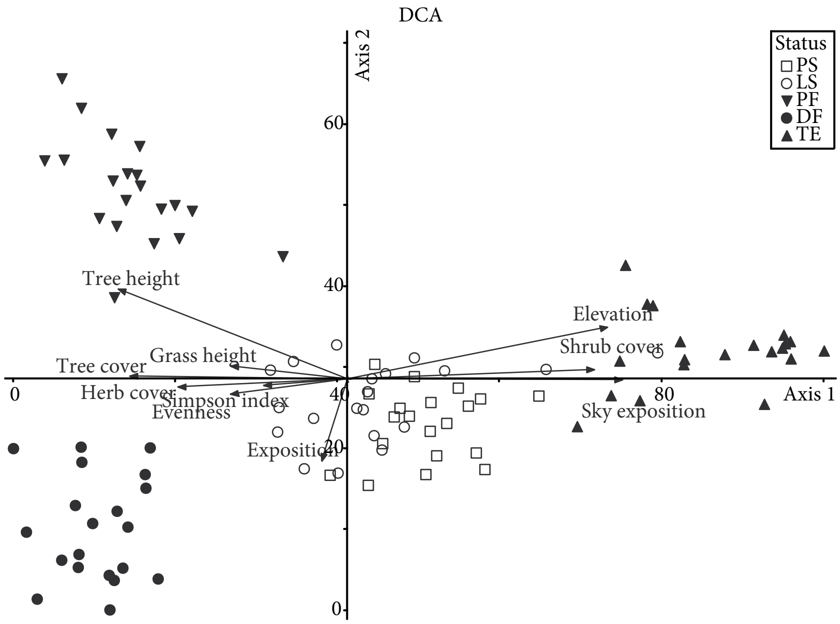

Figure 6. Detrended correspondence analysis (DCA) diagram showing the ordination of 243 species percentage cover data at the 100 studied plots of the 5 habitat types (See Figure 1 for explanation of the legends) in relation with environmental variables of the studied sites (arrows). The first axis is horizontal, the second is vertical. The direction and length of arrows show the degree of correlation between habitat types and environmental variables. E. g. PF is positively correlated with tree and grass height and tree cover; DF with herb cover and evenness; TE and PS with elevation and sky exposure (N = 243; 100).

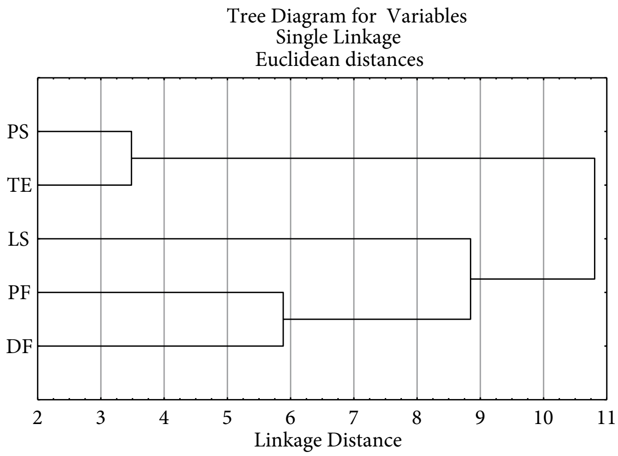

Figure 7. Hierarchical cluster analysis dendrogram of Euclidean similarity distance showing the relationships among the 5 habitat types based on 5 principal components of species richness and diversity indices, soil and vegetation percentage cover, and canopy vertical structure data resulting from PCA (N = 100).

Betula litwinowii (38.4) is the only species with a high indicator value in the logical succession sites. In the climax subalpine birch forest the following indicator species were identified: *Aconitum nasutum* (88.7), *Solidago virgaurea* (81.9), *Geranium sylvaticum* (69.7), *Polygonatum verticillatum* (69.4), *Rubus saxatilis* (60.4), *Lapsana grandiflora* (57.4), *Pyrola media* (53.1), and *Veratrum lobelianum* (50.7). The shrub species *Rubus idaeus* (81.8) has a very high indicator value in the degraded forest habitat, and so does *Rhododendron caucasicum* (90.3) in the tree line plots.

4. Discussion

The results have shown changes in vascular plant species diversity during the natural regeneration of subalpine birch forest from secondary meadows used as pasture in the past. The study sites revealed the highest species richness (36.6 ± 5.9) in pioneer succession because two habitat types of subalpine meadow and birch forest plant species are mixed there. Forest elements, such as tree species seedlings and young trees (*Betula litwinowii*, *Salix caprea*, *S. kazbekensis*, and *S. kuznetzowii*), and different species of shrubs (*Rhododendron caucasicum*, *Daphne glomerata*, *Vaccinium myrtillus*, etc.) are part of this habitat type. Later, these shrubs are absent in closed forest canopy habitats of both subalpine forest and logical succession stages. The shrub cover correlates negatively with sky exposure and open habitats are more covered by subalpine shrub species. According to the literature (Dierschke, 1994; Schmidt et al., 2008), when new species appear in the community, pioneer succession generally changes during the course of 4–5 years. The studied pioneer succession in the Kazbegi district started germination of birch seeds from the soil bank ca. 5 years after this field work in 2011.

Table 4. Indicator value (IV) of indicator species between groups of vegetation types in a birch forest zone. The table shows the indicator values, i.e. the percentage of indication from 0 (no indication) to 100 (perfect indication), and results of the Monte Carlo test of significance (N = 243).

Species	Family	Life form	Observed indicator value (IV)	Mean	SD	Significance
Pioneer succession (PS)						
Lotus caucasicus Kuprian ex Juz.	Fabaceae	Herb	76.1	11.9	3.73	0.0002
Ranunculus oreophilus M.Bieb.	Ranunculaceae	Herb	60.5	11.6	3.66	0.0002
Rhinanthus minor L.	Scrophulariaceae	Herb	54	12	3.66	0.0002
Trifolium canescens Willd.	Fabaceae	Herb	45.3	10.9	3.5	0.0002
Thymus collinus M.Bieb.	Lamiaceae	Herb	43.8	7.8	3.64	0.0002
Anthoxanthum odoratum L.	Poaceae	Grass	41.3	16.3	4.11	0.0004
Helictotrichon adzharicum (Albov) Grossh.	Poaceae	Grass	39.4	8.2	3.73	0.0002
Leontodon hispidus L.	Asteraceae	Herb	37.7	10.4	3.87	0.0002
Trifolium ambiguum M.Bieb.	Fabaceae	Herb	37.7	15.8	3.59	0.0002
Daphne glomerata Lam.	Thymelaeaceae	Shrub	36.8	14.5	3.75	0.0006
Polygonum alpinum All.	Polygonaceae	Herb	36.4	10.3	3.91	0.0002
Logical succession (LS)						
Betula litwinowii Doluch.	Betulaceae	Tree	38.4	24.2	1.97	0.0002
Primary forest (PF)						
Aconitum nasutum Fisch. ex Reichenb.	Ranunculaceae	Herb	88.7	10.7	4.07	0.0002
Solidago virgaurea L.	Asteraceae	Herb	81.9	11.7	4.02	0.0002
Geranium sylvaticum L.	Geraniaceae	Herb	69.7	14.4	3.74	0.0002
Polygonatum verticillatum (L.) All.	Convallariaceae	Geophytes	69.4	11	3.89	0.0002
Rubus saxatilis L.	Rosaceae	Shrub	60.4	12.6	3.64	0.0002
Lapsana grandiflora M.Bieb.	Asteraceae	Herb	57.4	14.1	4	0.0002
Pyrola media Sw.	Pyrolaceae	Herb	53.1	8.4	3.73	0.0002
Veratrum lobelianum Bernh.	Liliaceae	Geophytes	50.7	12.1	3.87	0.0002
Vicia balansae Boiss.	Fabaceae	Herb	49.2	10.8	3.57	0.0002
Rosa mollis Smith	Rosaceae	Shrub	47.8	8.9	3.53	0.0002
Calamagrostis arundinacea (L.) Roth	Poaceae	Grass	47	17.1	3.56	0.0002
Daphne mezereum L.	Thymelaeaceae	Shrub	45	7.9	3.87	0.0002
Anthriscus nemorosa (M.Bieb.) Spreng.	Apiaceae	Herb	40	6.5	3.04	0.0002
Sorbus caucasigena Kom. ex Gatsch.	Rosaceae	Tree	38.7	9.5	3.68	0.0002
Lathyrus pratensis L.	Fabaceae	Herb	38.2	7.5	3.38	0.0002
Degraded forest (DF)						
Rubus idaeus L.	Rosaceae	Shrub	81.8	11.6	3.69	0.0002
Heracleum roseum Steven	Apiaceae	Herb	76.9	11.3	3.83	0.0002
Viola caucasica Kolenati	Violaceae	Herb	74.4	11.8	3.69	0.0002
Polygonum carneum K.Koch	Polygonaceae	Herb	60.8	17.8	3.75	0.0002
Primula amoena M.Bieb.	Primulaceae	Herb	59.6	16.4	3.59	0.0002
Pyrethrum coccineum (Willd.) Worosch.	Asteraceae	Herb	55.8	11.3	3.91	0.0002
Dryopteris oreades Fomin	Dryopteridaceae	Fern	46.3	8.9	3.66	0.0002
Cirsium obvallatum (M.Bieb.) Fisch.	Asteraceae	Herb	43	17.7	3.64	0.0002
Linum hypericifolium Salisb.	Linaceae	Herb	40.1	9.3	3.75	0.0002
Cruciata glabra (L.) Ehrend.	Rubiaceae	Herb	35.4	18.6	2.97	0.0002
Treeline alpine zone (TE)						
Rhododendron caucasicum Pall.	Ericaceae	Shrub	90.3	13.1	3.74	0.0002
Empetrum caucasicum Juz.	Empetraceae	Shrub	64.2	8.8	3.62	0.0002
Arenaria lychnidea M. Bieb.	Caryophyllaceae	Herb	46.7	10.1	3.9	0.0002
Pedicularis wilhelmsiana Fisch. ex M.Bieb.	Scrophulariaceae	Herb	45	6.9	3.17	0.0002
Luzula pseudosudetica (V.Krecz.) V.Krecz.	Juncaceae	Grass	44.7	9.9	4.09	0.0002
Pyrethrum aromaticum Tzvelev	Asteraceae	Herb	42.3	7.6	3.48	0.0002
Poa alpina L.	Poaceae	Grass	42.2	8	3.75	0.0002
Salix kazbekensis A.Skvortsov	Salicaceae	Tree	40.8	12.8	4.16	0.0002
Gentiana pyrenaica L.	Gentianaceae	Herb	40	6.7	3.25	0.0002
Carex tristis M.Bieb.	Cyperaceae	Sedge	37.4	11.1	4.76	0.0002

It is known that the forest regeneration process is determined not only by one tree species, but also by all existing species relationships and functions in the ecosystem (Wang et al., 2014). Our results indicate that when the process of forest regeneration starts on subalpine meadows, the first composition of species is formed by the seedlings of some tree species, dwarf shrubs, and other elements of forest understory that are associated with birch trees. Shrubs and remnant trees facilitate the establishment of woody seedlings (Holl et al., 2000).

The tree line habitat type and the pioneer succession of subalpine meadows revealed close relations in species composition and diversity (Table 2). Multivariate ordination clustered pioneer succession with alpine tree line areas (Figure 7) and the similarity was indicated by dwarf shrubs appearing in the first stages of the natural reforestation process on subalpine meadows. The dwarf shrubs *Daphne glomerata*, *Empetrum caucasicum*, *Rhododendron caucasicum*, and *Vaccinium myrtillus* grow only in open canopy areas and are absent in closed canopy forest habitats of both the subalpine forest and logical succession stages. Tree seedlings and shrubs may help overcome other obstacles to recovery such as ameliorating stressful microclimatic conditions (Vieira et al., 1994; Kremer et al., 2014). In addition, the height of birch trees (about 1–3 m) is similar in tree line and pioneer succession areas.

In our opinion, these similarities show the starting process of forest restoration, which is restricted in the tree line ecotone due to concrete climatic conditions. Seedling growth was slowed by a limited availability of nutrients and microclimatic conditions (Holl et al., 2000). Environmental conditions, including plant–plant interactions, strongly affect tree recruitment; pioneer shrubs facilitate the establishment of woody species and can positively affect reforestation success in many different ecological settings (Gómez-Aparicio et al., 2009). Therefore, we should decide that the starting of forest restoration in secondary meadows depends on the existence of dwarf shrub groups. Analysis of late successional communities showed that several shrub species may act as nurses, effectively facilitating the growth of woody species. This technique could be used to design multispecific reforestation works (Gómez-Aparicio et al., 2009).

Degraded forest showed the lowest species richness (22.7 ± 3.8) because the change in species composition during habitat degradation leads to disappearing of typical forest species (Honnay and Jacquemyn, 2007). Forest degradation caused the decline of species diversity. Research on tropical deforestation describes its negative consequences for biodiversity and ecosystem functioning (Turner, 1996; Laurance et al., 1998). Forest degradation also greatly affects social, cultural, and ecological functions (Sasaki and Putz, 2009).

Thus, the alpine tree line habitat type and the pioneer succession of subalpine meadows revealed close relations in species composition and diversity. In our opinion, these similarities show the starting process of forest restoration, which is restricted in the tree line ecotone due to concrete climatic conditions. The natural regeneration of birch forests is apparently in close relation with the global climate change, but the most important factor in the Kazbegi district is the reduction of uncontrolled sheep grazing. Moreover, the forest restoration process shows quite a few differences in species composition and diversity, and the presence of a particular species depends on the environmental conditions of the habitat types. Forest degradation and clear cutting lead to open habitats and secondary meadows, depending on anthropogenic impacts. High grazing was the main reason in the Kazbegi region for the maintenance of pastures as secondary subalpine meadows. Since the 1990s the number of sheep herds has decreased and grazing has diminished. Forest restoration began during this period and logical succession was reached 10–15 years later. The anthropogenic impact and landscape use should be considered as the main influencing factors on forest restoration by natural reforestation processes.

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Supplementary Materials
Results
Supplement.

Table S1. A species list of the 5 habitat types of the subalpine birch forest restoration process (See Figure 1 for explanation of the legends) with life forms and number of plots in different habitats for plant species. Total plant species number - 243. Number of plots per habitat types - 20. Total number of plots - 100. species list of the 5 habitat types of the subalpine birch forest restoration process (See Figure 1 for explanation of the legends) with life forms and number of plots in different habitats for plant species. Total plant species number - 243. Number of plots per habitat types - 20. Total number of plots - 100.

Family	Species	Life form	PS	LS	PF	DF	TE
Apiaceae	*Anthriscus nemorosa* (M.Bieb.) Spreng.	Herb	0	0	8	0	0
Apiaceae	*Astrantia maxima* Pall.	Herb	0	0	0	3	0
Apiaceae	*Astrantia ossica* Woronow ex Grossh.	Herb	0	0	0	3	0
Apiaceae	*Bupleurum polyphyllum* Ledeb.	Herb	2	5	0	2	0
Apiaceae	*Carum caucasicum* (M.Bieb.) Boiss.	Herb	0	0	0	1	6
Apiaceae	*Chaerophyllum roseum* M.Bieb.	Herb	2	0	0	0	2
Apiaceae	*Heracleum asperum* (Hoffm.) M.Bieb.	Herb	1	0	1	0	0
Apiaceae	*Heracleum roseum* Steven	Herb	0	0	6	18	0
Apiaceae	*Ligusticum alatum* (M.Bieb.) Spreng	Herb	0	0	2	0	0
Apiaceae	*Pastinaca armena* Fisch. & C.A.Mey.	Herb	1	1	0	0	1
Apiaceae	*Pimpinella rhodantha* Boiss.	Herb	9	10	6	1	9
Apiaceae	*Seseli transcaucasicum* (Schischk.) M.Pimen. & Sdobnina	Herb	8	5	3	6	0
Asparagaceae	*Scilla siberica* Haw.	Geophytes	0	1	0	0	0
Aspleniaceae	*Asplenium septentrionale* (L.) Hoffm.	Fern	0	0	0	1	0
Asteraceae	*Antennaria caucasica* Boriss.	Herb	3	1	0	0	8
Asteraceae	*Anthemis sosnovskyana* Fed.	Herb	2	0	0	0	4
Asteraceae	*Aster alpinus* L.	Herb	1	0	0	0	1
Asteraceae	*Centaurea cheiranthifolia* Willd.	Herb	3	1	0	0	0
Asteraceae	*Cephalanthera longifolia* (L.) Fritsch	Herb	3	1	0	0	0
Asteraceae	*Cirsium obvallatum* (M.Bieb.) Fisch.	Herb	16	10	9	17	0
Asteraceae	*Dolichorrhiza caucasica* (M.Bieb.) Galushko	Herb	0	1	9	2	1
Asteraceae	*Dolichorrhiza renifolia* (C.A.Mey.) Galushko	Herb	0	0	2	3	0
Asteraceae	*Doronicum oblongifolium* DC.	Herb	2	0	0	0	1
Asteraceae	*Doronicum orientale* Hoffm.	Herb	0	1	0	0	0
Asteraceae	*Erigeron caucasicus* Steven	Herb	0	0	0	0	1
Asteraceae	*Gnaphalium supinum* L.	Herb	1	0	0	0	0
Asteraceae	*Hieracium* x *pannoniciforme* Litv. & Zahn	Herb	9	12	3	4	12
Asteraceae	*Hieracium prenanthoides* Vill.	Herb	2	0	7	1	0
Asteraceae	*Hieracium umbellatum* L.	Herb	1	0	0	0	0
Asteraceae	*Hieracium vulgatum* Fries	Herb	2	0	0	0	0
Asteraceae	*Inula orientalis* Lam.	Herb	2	1	0	5	0
Asteraceae	*Lapsana grandiflora* M.Bieb.	Herb	4	7	16	2	4
Asteraceae	*Leontodon hispidus* L.	Herb	9	1	0	2	4
Asteraceae	*Podospermum alpigenum* K.Koch	Herb	0	0	0	0	1
Asteraceae	*Pyrethrum aromaticum* Tzvelev	Herb	1	0	0	0	9
Asteraceae	*Pyrethrum coccineum* (Willd.) Worosch.	Herb	2	4	0	16	1

Table S1. (Continued).

Asteraceae	*Scabiosa caucasica* M.Bieb.	Herb	4	0	0	0	6
Asteraceae	*Senecio pseudoorientalis* Schischk.	Herb	0	0	0	6	1
Asteraceae	*Senecio rhombifolius* (Adams) Sch.Bip.	Herb	0	0	2	0	0
Asteraceae	*Solidago virgaurea* L.	Herb	0	0	18	0	5
Asteraceae	*Sonchus oleraceus* L.	Herb	0	0	1	0	0
Asteraceae	*Taraxacum officinale* Wigg.	Herb	8	3	0	0	0
Asteraceae	*Tragopogon filifolius* Rehm. ex Boiss.	Herb	1	0	0	0	4
Asteraceae	*Tragopogon graminifolius* DC.	Herb	0	0	0	0	1
Betulaceae	*Betula litwinowii* Doluch.	Tree	20	20	20	20	19
Boraginaceae	*Aipyanthus pulcher* (Willd. ex Roem. & Schult.) V.Avetissjan	Herb	0	1	0	0	0
Boraginaceae	*Myosotis alpestris* F.W.Schmidt	Herb	0	0	0	0	2
Boraginaceae	*Myosotis arvensis* (L.) Hill	Herb	10	4	0	7	2
Brassicaceae	*Bunias orientalis* L.	Herb	1	0	0	0	0
Campanulaceae	*Asyneuma campanuloides* (M.Bieb. ex Sims) Bornm.	Herb	0	2	6	6	0
Campanulaceae	*Campanula bellidifolia* Adams	Herb	2	5	0	0	1
Campanulaceae	*Campanula biebersteiniana* Schult.	Herb	0	1	0	0	3
Campanulaceae	*Campanula collina* Sims	Herb	14	13	5	13	10
Campanulaceae	*Campanula hohenackeri* Fisch. & C.A.Mey.	Herb	4	0	0	0	0
Campanulaceae	*Campanula sosnowskyi* Charadze	Herb	0	1	0	0	1
Campanulaceae	*Campanula trautvetteri* Grossh. ex Fed.	Herb	1	0	6	1	0
Campanulaceae	*Campanula tridentata* Schreb.	Herb	1	0	0	0	1
Caryophyllaceae	*Arenaria lychnidea* M.Bieb.	Herb	4	2	0	0	11
Caryophyllaceae	*Arenaria serpyllifolia* L.	Herb	0	0	0	0	1
Caryophyllaceae	*Cerastium arvense* L.	Herb	4	2	0	0	0
Caryophyllaceae	*Cerastium multiflorum* C.A.Mey.	Herb	0	0	0	1	6
Caryophyllaceae	*Cerastium purpurascens* Adams	Herb	1	0	0	0	0
Caryophyllaceae	*Dianthus cretaceus* Adams	Herb	1	0	0	0	0
Caryophyllaceae	*Gypsophila elegans* M.Bieb.	Herb	2	0	0	0	0
Caryophyllaceae	*Minuartia circassica* (Albov) Woronow	Herb	2	5	0	0	0
Caryophyllaceae	*Minuartia oreina* (Mattf.) Schischk.	Herb	8	2	0	0	10
Caryophyllaceae	*Silene italica* (L.) Pers.	Herb	1	0	0	0	0
Caryophyllaceae	*Silene linearifolia* Otth	Herb	4	3	0	0	4
Caryophyllaceae	*Silene ruprechtii* Schischk.	Herb	4	4	0	1	0
Caryophyllaceae	*Silene vulgaris* (Moench) Garcke	Herb	0	0	2	0	0
Caryophyllaceae	*Silene wallichiana* Klotzsch	Herb	0	0	0	1	0
Caryophyllaceae	*Stellaria media* (L.) Vill.	Herb	1	2	0	0	1
Cistaceae	*Helianthemum grandiflorum* (Scop.) DC.	Herb	0	3	0	0	0
Clusiaceae	*Hypericum linarioides* Bosse	Herb	0	2	0	0	0
Clusiaceae	*Hypericum perforatum* L.	Herb	4	3	0	0	0
Convallariaceae	*Polygonatum verticillatum* (L.) All.	Herb	0	0	16	4	1
Convolvulaceae	*Cuscuta europaea* L.	Parasite	0	0	0	1	0
Crassulaceae	*Sedum oppositifolium* Sims	Herb	7	6	12	8	0
Crassulaceae	*Sedum stevenianum* Rouy & Camus	Herb	1	0	0	0	0
Crassulaceae	*Sedum stoloniferum* S.G.Gmel.	Herb	0	0	0	0	2

Table S1. (Continued).

Crassulaceae	*Sedum tenellum* M. Bieb.	Herb	2	0	0	0	1
Crassulaceae	*Pseudorosularia sempervivoides* (Fisch. ex M.Bieb.)	Herb	0	0	0	0	1
Cupressaceae	*Juniperus communis* L.	Shrub	5	4	0	0	1
Cyperaceae	*Carex tristis* M.Bieb.	Sedge	4	0	0	1	10
Cyperaceae	*Carex caryophyllea* Latourr.	Sedge	4	2	0	0	0
Cyperaceae	*Carex digitata* L.	Sedge	0	1	0	0	0
Cyperaceae	*Carex meinshauseniana* V.Krecz.	Sedge	10	0	1	0	6
Cyperaceae	*Carex pallescens* L.	Sedge	2	1	0	0	1
Cyperaceae	*Kobresia capiliformis* Ivanova	Herb	0	0	0	0	1
Dipsacaceae	*Cephalaria gigantea* (Ledeb.) Bobr.	Herb	1	0	7	2	0
Dryopteridaceae	*Dryopteris filix-mas* (L.) Schott	Fern	0	0	3	5	0
Dryopteridaceae	*Dryopteris oreades* Fomin	Fern	0	0	4	10	0
Dryopteridaceae	*Polystichum lonchitis* (L.) Roth	Fern	0	1	0	0	0
Empetraceae	*Empetrum caucasicum* Juz.	Shrub	1	0	0	0	13
Ericaceae	*Rhododendron caucasicum* Pall.	Shrub	4	6	1	0	20
Ericaceae	*Vaccinium arctostaphylos* L.	Shrub	0	0	1	0	3
Ericaceae	*Vaccinium myrtillus* L.	Shrub	15	15	5	0	16
Ericaceae	*Vaccinium vitis-idaea* L.	Shrub	11	8	5	0	10
Euphorbiaceae	*Euphorbia macroceras* Fisch. & C.A.Mey.	Herb	1	0	1	0	0
Fabaceae	*Anthyllis caucasica* (Grossh.) Juz.	Herb	0	0	0	0	1
Fabaceae	*Anthyllis lachnophora* Juz.	Herb	1	1	0	0	1
Fabaceae	*Anthyllis variegata* Boiss. ex Grossh.	Herb	4	0	0	0	1
Fabaceae	*Astragalus captiosus* Boriss.	Herb	2	2	0	0	0
Fabaceae	*Cicerbita racemosa* (Willd.) Beauverd	Herb	3	2	8	1	0
Fabaceae	*Galega orientalis* Lam.	Herb	0	0	2	0	0
Fabaceae	*Lathyrus pratensis* L.	Herb	1	1	8	0	0
Fabaceae	*Lotus caucasicus* Kuprian ex Juz.	Herb	18	7	0	0	1
Fabaceae	*Medicago glutinosa* M.Bieb.	Herb	3	3	0	0	0
Fabaceae	*Onobrychis biebersteinii* Sirj.	Herb	0	1	0	0	0
Fabaceae	*Onobrychis petraea* (M.Bieb. ex Willd.) Fisch.	Herb	0	3	0	0	0
Fabaceae	*Orobus cyaneus* Steven	Herb	0	0	0	0	4
Fabaceae	*Trifolium alpestre* L.	Herb	1	1	0	0	2
Fabaceae	*Trifolium ambiguum* M.Bieb.	Herb	15	15	0	1	13
Fabaceae	*Trifolium canescens* Willd.	Herb	14	6	0	0	3
Fabaceae	*Trifolium caucasicum* Tausch	Herb	1	2	0	0	0
Fabaceae	*Trifolium medium* L.	Herb	1	1	0	0	0
Fabaceae	*Trifolium pratense* L.	Herb	3	2	0	0	0
Fabaceae	*Trifolium repens* L.	Herb	9	5	0	0	6
Fabaceae	*Trifolium trichocephalum* M.Bieb.	Herb	2	0	0	0	0
Fabaceae	*Vicia alpestris* Steven	Herb	0	0	2	0	0
Fabaceae	*Vicia balansae* Boiss.	Herb	2	0	13	7	0
Fabaceae	*Vicia grossheimii* Ekvtim.	Herb	0	9	0	0	1
Fabaceae	*Vicia purpurea* Steven	Herb	2	0	0	0	0
Fabaceae	*Vicia variabilis* Freyn & Sint.	Herb	7	1	10	3	1

Table S1. (Continued).

Gentianaceae	*Gentiana angulosa* M.Bieb.	Herb	2	2	0	0	0
Gentianaceae	*Gentiana aquatica* L.	Herb	1	0	0	0	0
Gentianaceae	*Gentiana cruciata* L.	Herb	1	0	0	0	0
Gentianaceae	*Gentiana pyrenaica* L.	Herb	0	0	0	0	8
Gentianaceae	*Gentiana septemfida* Pall.	Herb	1	0	0	0	0
Gentianaceae	*Gentianella caucasea* (Lodd. ex Sims) Holub	Herb	1	0	0	0	0
Gentianaceae	*Swertia iberica* Fisch. & C.A.Mey.	Herb	0	0	3	0	0
Geraniaceae	*Geranium ibericum* Cav.	Herb	0	0	1	0	1
Geraniaceae	*Geranium platypetalum* Fisch. & C.A.Mey.	Herb	1	0	0	0	1
Geraniaceae	*Geranium sylvaticum* L.	Herb	2	9	18	3	3
Juncaceae	*Luzula multiflora* (Ehrh.) Lej.	Grass	10	4	0	2	1
Juncaceae	*Luzula pseudosudetica* (V.Krecz.) V.Krecz.	Grass	1	0	1	1	13
Juncaceae	*Luzula spicata* (L.) DC.	Grass	7	3	0	0	1
Lamiaceae	*Ajuga orientalis* L.	Herb	0	0	0	0	1
Lamiaceae	*Bettonica macrantha* K.Koch	Herb	8	6	15	16	7
Lamiaceae	*Prunella vulgaris* L.	Herb	0	1	0	0	0
Lamiaceae	*Salvia verticillata* L.	Herb	0	2	0	2	0
Lamiaceae	*Thymus collinus* M.Bieb.	Herb	9	1	0	0	0
Lamiaceae	*Thymus nummularius* M.Bieb.	Herb	1	0	0	0	0
Liliaceae	*Fritillaria lutea* M.Bieb.	Herb	7	2	0	1	3
Liliaceae	*Paris quadrifolia* L.	Herb	0	0	1	0	0
Liliaceae	*Veratrum lobelianum* Bernh.	Herb	0	3	18	1	3
Linaceae	*Linum hypericifolium* Salisb.	Herb	0	2	3	10	0
Onagraceae	*Epilobium angustifolium* L.	Herb	2	1	3	0	4
Onagraceae	*Epilobium montanum* L.	Herb	0	0	1	4	0
Ophioglossaceae	*Botrychium lunaria* (L.) Sw.	Fern	6	1	0	0	1
Orchidaceae	*Coeloglossum viride* (L.) C.Hartm.	Geophytes	0	0	0	0	5
Orchidaceae	*Corallorrhiza trifida* Chatel.	Geophytes	0	1	0	0	0
Orchidaceae	*Dactylorhiza euxina* (Nevski) Czer.	Geophytes	1	0	0	0	0
Orchidaceae	*Gymnadenia conopsea* (L.) R.Br.	Geophytes	7	1	0	0	8
Orchidaceae	*Herminium monorchis* (L.) R.Br.	Geophytes	2	0	0	0	0
Orchidaceae	*Platanthera chlorantha* (Custer) Reichenb.	Geophytes	1	0	4	0	0
Oxalidaceae	*Oxalis acetosella* L.	Herb	0	0	7	0	3
Papaveraceae	*Papaver fugax* Poir.	Herb	1	0	0	0	0
Pinaceae	*Pinus kochiana* Klotzsch ex K.Koch	Tree	0	1	0	0	0
Plantaginaceae	*Plantago atrata* Hoppe	Herb	0	1	0	0	5
Plantaginaceae	*Plantago media* L.	Herb	1	0	0	0	0
Poaceae	*Agrostis planifolia* K.Koch	Grass	17	14	2	14	11
Poaceae	*Agrostis tenuis* Sibth.	Grass	0	1	0	0	0
Poaceae	*Anthoxanthum odoratum* L.	Grass	16	10	0	0	17
Poaceae	*Avenella flexuosa* (L.) Parl.	Grass	18	13	8	5	18
Poaceae	*Bromus variegatus* M. Bieb.	Grass	13	7	0	0	6
Poaceae	*Calamagrostis arundinacea* (L.) Roth	Grass	2	9	20	17	2
Poaceae	*Festuca ovina* L.	Grass	3	8	1	4	12

Table S1. (Continued).

Poaceae	*Festuca rubra* L.	Grass	0	1	4	0	0
Poaceae	*Festuca sylvatica* Huds	Grass	0	0	1	0	0
Poaceae	*Festuca valesiaca* Gaudin	Grass	3	0	0	0	0
Poaceae	*Festuca varia* Haenke subsp. *woronowii* (Hack.) Tzvelev	Grass	1	0	0	0	1
Poaceae	*Helictotrichon adzharicum* (Albov) Grossh.	Grass	9	2	0	0	0
Poaceae	*Helictotrichon asiaticum* (Roshev.) Grossh.	Grass	0	0	0	0	1
Poaceae	*Helictotrichon pubescens* (Huds.) Pilg.	Grass	0	0	0	0	2
Poaceae	*Nardus stricta* L.	Grass	0	0	0	0	2
Poaceae	*Phleum phleoides* (L.) Karst.	Grass	3	0	0	1	0
Poaceae	*Poa alpina* L.	Grass	1	0	0	0	9
Poaceae	*Poa iberica* Fisch. & C.A.Mey.	Grass	0	2	2	0	0
Poaceae	*Poa longifolia* Trin.	Grass	0	0	0	0	2
Poaceae	*Poa nemoralis* L.	Grass	0	4	2	6	0
Poaceae	*Trisetum flavescens* (l.) Beauv.	Grass	0	0	1	0	0
Polygalaceae	*Polygala alpicola* Rupr.	Herb	11	4	0	0	3
Polygalaceae	*Oxyria elatior* R.Br. ex Meissn.	Herb	1	0	0	0	0
Polygalaceae	*Polygonum alpinum* All.	Herb	2	3	0	5	2
Polygalaceae	*Polygonum carneum* K.Koch	Herb	9	3	16	20	4
Polygalaceae	*Polygonum viviparum* L.	Herb	12	2	0	1	14
Polygalaceae	*Rumex acetosella* L.	Herb	1	0	1	0	0
Polygalaceae	*Rumex scutatus* L.	Herb	0	2	0	0	0
Polypodiaceae	*Polypodium vulgare* L.	Herb	0	0	2	0	0
Primulaceae	*Primula algida* Adams	Herb	3	2	0	0	1
Primulaceae	*Primula amoena* M.Bieb.	Herb	10	5	7	19	0
Primulaceae	*Primula auriculata* Lam.	Herb	1	0	0	0	0
Primulaceae	*Primula cordifolia* Rupr.	Herb	2	0	1	0	0
Pyrolaceae	*Pyrola media* Sw.	Herb	0	1	11	0	0
Ranunculaceae	*Aconitum nasutum* Fisch. ex Reichenb.	Herb	1	0	18	0	0
Ranunculaceae	*Anemone fasciculata* L.	Herb	4	2	7	3	14
Ranunculaceae	*Aquilegia caucasica* (Ledeb.) Rupr.	Herb	0	0	5	1	0
Ranunculaceae	*Ranunculus caucasicus* M.Bieb.	Herb	3	10	6	11	1
Ranunculaceae	*Ranunculus oreophilus* M.Bieb.	Herb	16	7	3	0	0
Ranunculaceae	*Thalictrum alpinum* L.	Herb	1	3	0	0	0
Ranunculaceae	*Thalictrum foetidum* L.	Herb	1	0	0	1	0
Ranunculaceae	*Trollius ranunculinus* (Smith) Stearn	Herb	0	1	1	8	1
Rosaceae	*Alchemilla laeta* Juz.	Herb	1	1	4	3	0
Rosaceae	*Alchemilla rigida* Bus.	Herb	13	14	13	16	8
Rosaceae	*Alchemilla sericata* Reichenb. ex Bus.	Herb	14	10	0	0	9
Rosaceae	*Dryas caucasica* Juz.	Shrub	5	2	1	0	0
Rosaceae	*Potentilla crantzii* (Crantz) G.Beck ex Fritsch	Herb	5	3	0	0	2
Rosaceae	*Rosa mollis* Smith	Shrub	0	0	12	3	0
Rosaceae	*Rubus idaeus* L.	Shrub	4	1	0	19	1
Rosaceae	*Rubus saxatilis* L.	Shrub	0	2	17	7	4
Rosaceae	*Sibbaldia parviflora* Willd.	Herb	0	1	0	0	2

Table S1. (Continued).

Rosaceae	*Sibbaldia semiglabra* C.A.Mey.	Herb	3	0	0	0	0
Rosaceae	*Sorbus caucasigena* Kom. ex Gatsch.	Tree	1	0	12	0	3
Rubiaceae	*Cruciata glabra* (L.) Ehrend.	Herb	14	12	17	19	0
Rubiaceae	*Cruciata laevipes* Opiz	Herb	1	0	0	0	0
Rubiaceae	*Galium album* Mill.	Herb	1	0	0	0	0
Rubiaceae	*Galium rotundifolium* L.	Herb	0	0	3	0	0
Rubiaceae	*Galium pumilum* Murray	Herb	1	0	0	4	0
Rubiaceae	*Galium verum* L.	Herb	5	7	0	1	0
Salicaceae	*Salix caprea* L.	Tree	6	5	3	0	6
Salicaceae	*Salix kazbekensis* A.Skvorts.	Tree	8	7	0	0	12
Salicaceae	*Salix kuznetzowii* Laksch. ex Goerz	Tree	2	0	0	0	3
Saxifragaceae	*Saxifraga cartilaginea* Willd.	Herb	3	1	0	0	1
Saxifragaceae	*Saxifraga kolenatiana* Regel	Herb	0	0	0	0	1
Scrophulariaceae	*Euphrasia hirtella* Jord. ex Reut.	Herb	4	0	0	0	2
Scrophulariaceae	*Orobanche lutea* L.	Parasite	0	0	1	0	0
Scrophulariaceae	*Pedicularis chroorrhyncha* Vved.	Herb	0	1	3	1	0
Scrophulariaceae	*Pedicularis wilhelmsiana* Fisch. ex M.Bieb.	Herb	0	0	0	0	9
Scrophulariaceae	*Rhinanthus minor* L.	Herb	16	6	0	0	5
Scrophulariaceae	*Scrophularia orientalis* L.	Herb	4	3	0	0	0
Scrophulariaceae	*Veronica gentianoides* Vahl	Herb	6	4	3	0	8
Selaginellaceae	*Selaginella helvetica* (L.) Spring	Herb	1	1	0	0	0
Thymelaeaceae	*Daphne glomerata* Lam.	Shrub	15	8	0	0	14
Thymelaeaceae	*Daphne mezereum* L.	Shrub	0	0	9	0	0
Urticaceae	*Urtica dioica* L.	Herb	0	0	1	5	0
Valerianaceae	*Valeriana alpestris* Steven	Herb	3	2	3	2	6
Valerianaceae	*Valeriana cardamines* M.Bieb.	Herb	0	1	0	0	0
Valerianaceae	*Valeriana tiliifola* Troitzk.	Herb	0	3	0	0	0
Violaceae	*Viola caucasica* Kolenati	Herb	4	3	2	17	0
Violaceae	*Viola rupestris* F.W.Schmidt	Herb	1	1	0	0	0
Violaceae	*Viola somchetica* K.Koch	Herb	5	12	0	1	3
Woodsiaceae	*Woodsia ilvensis* (L.) R.Br.	Fern	0	1	0	0	0