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Ecological Gradients (West-East) and Vegetation of the Central Great Caucasus

Abstract

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The Great Caucasus is well known for its impressive plant cover. Uneven topography, rich geology, pronounced climatic gradients, and position between Asia, Europe, and the Mediterranean have contributed to biological diversity of this biodiversity hotspot. The mountain chain covers a pronounced west to east climatic gradient with its western part being more humid and eastern more continental. The paper shows how vegetation follows the climatic gradient and how local orographic environment allows meso-/xerophillous plant communities break in places the general west to east humid to continental pattern through regions located along the gradient. Special emphasis is made on 'small refugia' of mesophillous Tertiary relict flora still preserved in some gorges of the eastern Great Caucasus.

Key words: The Great Caucasus, Ecological gradient, Alpine vegetation, Plant diversity.

Introduction

The Great Caucasus is stretched from the Taman peninsula in the north-west to the Apsheron peninsula in the south-east along a distance of about 1500 km. To the north the Main Watershed range of the Great Caucasus is paralleled by a side range, in the central part of which the highest peaks of the Great Caucasus (> 5000 m a.s.l.) are located. Two other relatively low latitudinal ranges run (rocky and pasture ranges) to the north of the side range (Maruashvili 1971).

The Great Caucasus is well known for its impressive plant cover. Uneven topography, rich geology, pronounced climatic gradients, and position between Asia, Europe, and the Mediterranean have contributed to biological diversity of this biodiversity hotspot. The Great Caucasus has all elevational vegetation zones from semi-deserts of the Caspian depression (28 m a. s. l.) to the nival zone of the ice-capped Mt. Elbrus (5642 m a.s.l.) (Zazanashvili & al. 2000; Nakhutsrishvili 2013; Nakhutsrishvili & Abdaladze 2017a).

The Great Caucasus at the eastern edge of Europe and the Alps in central Europe share young geological age, west-east orientation, belong to the Eurasian mountain chain formed as a result of southern continents moving northwards. In view of 1000 m elevation minimum, the Great Caucasus runs from 41º15' N to 43º 45'N (central part at 43ºN) and the Alps from 44º 10' N to 47º 40' N (central part at 46º 30' N); both chains belong in the temperate zone (Körner & Paulsen 2017).

The Great Caucasus covers a pronounced west to east climatic gradient (Fig. 1). The highlands of the western Caucasus are humid (up to 2200 mm annual precipitation) dominated by mesophilic taxa, while those of the eastern Caucasus are more continental, with dry summers and an increasing ratio of xerophylic taxa (< 800 mm annual precipitation). Half of the annual amount of precipitation falls on the cold season, therefore on large areas of mountains snow and glaciers persist. The annual temperature range is narrow. One of the features of the Caucasus high mountains, which distinguishes this mountain system from other mountains of Europe are sharp climatic and thus, vegetation changes over relatively small distances. For instance, a south-north transect along the "Georgian Military Road" starts on lowland with semi-desert vegetation substituted by steppe, open arid woodland, mesophilous beech forest including the beech forest types with Colchic elements, then high mountain meadows, chiono- and kryophilous herbaceous and relict scrub communities even in snowbeds, and near-glacier micro-habitats. Within this transect mountains create in places shelters with continental oroxerophilous vegetation islands.

Interior valleys are protected from both cold and humid air mass penetration from the north, which supports many relict xerophilous species of past xerothermic periods (Kharadze 1948).

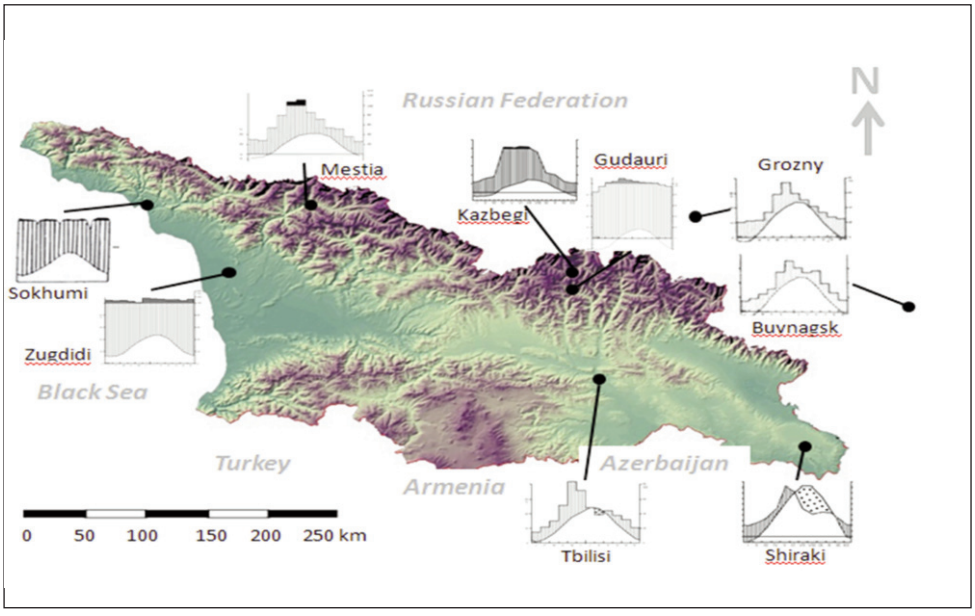

Fig. 1. Climatic diagrams of various parts of the Great Caucasus.

The comparative analysis of the vegetation of two different macro-regions of the Great Caucasus, in particular, the western part of the Central Caucasus–Svaneti and Racha-Lechkhumi, and the Eastern part of the Central Caucasus-Kazbegi, indicates a clear difference between both regions. The major western landmark of the considered area is Mt. Ushba (4710 m) in Svaneti region, and major eastern landmark is Mt. Kazbegi (5047 m) in Kazbegi region. In the following we first provide a general floristic overview, followed by a description of individual vegetation units.

Apkhazeti belongs in the botanical-geographic province of Colchis, past climate of which never bore features of continentality. In the warmest portion of the Pliocene humid subtropical climate dominated the coastal areas, which supported evergreen forest vegetation. At the end of the Tertiary many thermophillous evergreen plants went extinct. The local climate acquired characteristics of the present-day Mediterranean climate. At the same time glaciation of the Quaternary was not characterized by extremely low temperatures, while in places, in conditions of high precipitation montane glaciation was rather strong. Owing to narrow amplitude of climatic changes Colchis kept the features referring to the Tertiary (Shatilova & al. 2011), which made Colchis an important refugium of the Tertiary flora (Kolakovsky 1961). Presence of well-formed terraces is noteworthy. Limestone rocky areas with peculiar flora (Fig. 2a) formed on foothills. Alluvial valleys are in places covered by wetlands (Maruashvili 1971). Vegetation of the Western Great Caucasus (South macro-slope of Apkhazeti) has the following vertical zonation scheme: at 0–20 m coastal rocky area vegetation is present (*Pinus brutia* subsp. *pithyusa, Cistus tauricus, Arbutus andrachne, Alnus barbata, Dioscorea caucasica* (Fig. 2c), *Matteuccia struthiopteris* (Fig. 2d)); at elevations of 20-1400 m natural vegetation is represented by the Colchic forest (*Carpinus caucasica* (= *C. betulus*), *Castanea sativa*, *Fagus orientalis*) with lianas and evergreen understory (*Buxus colchica* (Fig. 2b), *Ilex colchica, Hedera colchica, Ruscus hypophyllum, Rhododendron ponticum*, etc.); at 1400-2000 m coniferous forest is present (*Pinus sylvestris* subsp. *hamata, Abies nordmanniana* (Fig. 3a)*, Picea orientalis*) along with deciduous forest (*Fagus orientalis*) with evergreen shrub understory; at 2000-2300 m the montane forest is substituted by subalpine crooked stem forest (*Betula litwinowii, Acer trautvetteri, Fagus orientalis, Quercus macranthera*) ("Krummholz"), tall herbaceous vegetation (*Heracleum ponticum, H. mantegazzianum, Angelica silvestris*), scrub (*Rhododendron caucasicum, Corylus colchica*); at 2300-2800 m alpine meadows dominate (*Carex pontica, Geranium gymnocaulon, G. platypetalum, Brachypodium rupestre*) (Kolakovsky 1985; Dolukhanov 2010; Nakhutsrishvili & Abdaladze 2017a, b; Nakhutsrishvili & Batsatsashvili 2017).

In Svaneti pronounced glacial landscapes and high peaks (4000-5200 m) are (Maruashvili 1971). The vegetation is remarkably diverse and dominated by meso- and hygrophilous types; high ration of meso- and hygrophilous species (*Geranium gymnocaulon* (Fig. 3b)*, G. platypetalum, Ranunculus lojkae*) is even observed in relict (interglacial) oro-xerophillous formations (*Festucetum variae, Kobresietum macrolepis*). Svaneti is a region with the most mesophillous plant species on the Great Caucasus.

This phenomenon is best represented by presence of relict meso- and hygrophilous vegetation of the Tertuary – the tall herbaceous vegetation ("megaphorbia"), which does not have analogues in other high-mountainous regions, including the Alps. Megaphorbia is composed of gigantic (2-3.5 m tall) herbs: *Heracleum mantegazzianum, Inula magnifica,*

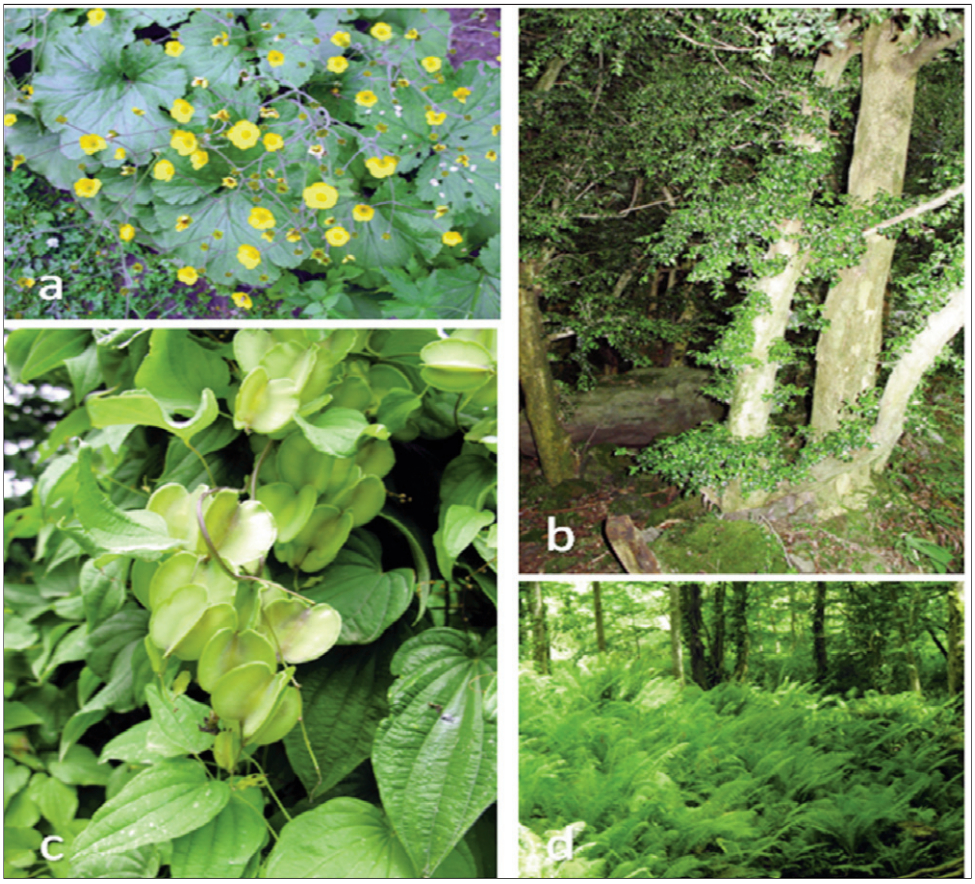

Fig. 2. a) *Woronowia speciosa*; b) *Buxus colchica*; c) *Dioscorea caucasica*; d) *Matteuccia struthiopteris*.

Senecio rhombifolius, etc. (Gagnidze 1974). Vegetation of the Central Great Caucasus (south macro-slope in Svaneti region) has the following vertical zonation scheme: at 0 to 500 m the Black Sea coastal and Colchic lowland vegetation is present; at 500–1900 m there is a zone of mixed, dark coniferous (*Abies nordmanniana, Picea orientalis*) and deciduous (*Fagus orientalis*) forests with evergreen understory (*Ilex colchica, Hedera colchica, Ruscus hypophyllum, Rhododendron ponticum*, etc.); *Quercus iberica* and *Pinus sylvestris* subsp. *hamata* forests occur on dry south-facing slopes; at 1900–2500 m sub-alpine crooked stem forest (*Fagus orientalis, Acer trautvetteri, Sorbus caucasigena = S. aucuparia*) grows along with tall herbaceous vegetation, grass-forb meadows, *Rhododendron caucasicum* scrub (Fig. 3c); at 2500–2750 m landscape is dominated by low alpine meadows with *Geranium gymnocaulon*, as well as "alpine carpets", special attention might be paid to meadows with rare *Pulsatila aurea* (Fig. 3d); at 2750-3200 m upper alpine meadows (dense tussock communities) mainly dominated by *Festuca varia* subsp. *woronowii* make up the major vegetation type present; at 3200-4000 m subnival and

nival patchy vegetation on screes and rocks as well as cryptogams thrive (Kharadze 1944; Dolukhanov & al. 1946; Nakhutsrishvili 2013; Nakhutsrishvili & Abdaladze 2017a, b; Nakhutsrishvili & Batsatsashvili 2017).

The stony and gravel-covered northern macro-slope, particularly, around Mt. Elbrus is covered by communities of *Kobresia macrolepis, K. schoenoides* as well as those of *Dryas caucasica*, a dwarf semi-shrub with bryophytes, lichens and participation of *Salix kazbekensis, Vaccinium vitis-idaea*. On watersheds with plain tops, in the upper alpine zone patchy communities of *Kobrezia humilis, Carex oreophila, Eritrichium caucasicum, Polygonum viviparum* with bryophytes and lichens are found on skeleton substrates, which frozes deeply in winter. According to I. Tumajanov (1980), these communities are phygnomically and ecologically close to alpine tundra. High mountains of the Central Great Caucasus prevent humid air penetration into this area; high peaks with permanent snow cover strengthen the continentality of the local climate, which causes xerophytization in all the vertical zones. The zonation scheme for the Central Great Caucasus (north macro-slope in Baksan valley-Mt. Elbrus area) looks as follows: at 450-700 m steppe and semidesert (*Salvia canescens, Berberis vulgaris*) is present; at 700-1200 m forest-steppe and steppe (*Carpinus orientalis, C. caucasica*) dominate the landscape; at 1200-2200 m pine (*Pinus sylvestris* subsp. *hamata*) and birch (*Betula litwinowii*) forests grow; in places *Juniperus* spp. and *Berberis* communities as well as secondary steppes occur; at 2200-2600 m still steppe fragments are present with subalpine meadows, subalpine crooked stem birch and pine forests, evergreen prostrate shrub *Rhododendron* communities; at 2600-3400 m alpine meadows, "alpine carpets", scree and rock vegetation dominate; at 3400-4000 m only subnival and nival vegetation patches on screes and rocks and cryptogams find relevant ambience for growth (Onipchenko 2004; Nakhutsrishvili 2013; Nakhutsrishvili & Abdaladze 2017a, b; Nakhutsrishvili & Batsatsashvili 2017).

Vegetation profile of the southern macro-slope of the central Great Caucasus (Mtskheta-Cross Pass region) is distinguished by great diversity of types. The lower section has semiarid climate, whereas the middle section has moderately humid climate, which supports mesophillous broad-leaved forest. Spruce (*Picea orientalis*) forest remnants are also present of the left bank of the river Aragvi, and yew (*Taxus baccata*) is found in some narrow ravines. At 1500 m a.s.l. the motorway serpentine ascends to the Cross pass on the Main Watershed Range (on its southern macro-slope). Although south-facing, the slope is much more humid than the opposite side of the range. Vegetation of the Central Great Caucasus (south macro-slope in Mtskheta-Cross Pass region) has the following vertical zonation scheme: at 400-600 m semidesert (*Artemisia lerchiana, Salsola ericoides, Gamanthus pilosus*), steppe (*Stipa stenophylla*), open woodland remnants (*Pistacia atlantica, Juniperus* spp., *Pyrus* spp.), spiny scrub or shibliak-type vegetation (*Paliurus spina-christi, Rhamnus pallasii, Spiraea hypericifolia*) are present; on areas from 600-800 m foothill deciduous forest (*Quercus iberica, Carpinus orientalis, C. caucasica*) grows; at 800-1000 m middle montane forest (*Quercus iberica, Q. pedunculiflora, Ulmus foliacea, Carpinus caucasica*), beech forest with evergreen understory (*Laurocerasus officinalis, Ilex colchica, Hedera pastuchovii*), degraded riparian forest (*Populus nigra, Salix australis*) along riv. Aragvi are present; at 1000-1600 m upper montane deciduous forest (*Fagus orientalis, Carpinus caucasica, Quercus iberica*), beech forest in places mixed with *Picea orientalis* (this is the eastern border of spruce distribution in the Greater

Caucasus), remnants of deciduous forest (*Q. iberica, Fraxinus excelsior, Pyrus caucasica, Populus tremula, Corylus avellana*) at the upper layer of this zone, *Rhododendron luteum* scrub grow; at 1600-1900 m remnants of subalpine forest (*Acer trautvetteri, Betula litwinowii, Sorbus caucasigena = S. aucuparia*, *Populus tremula*) and subalpine tall herbaceous vegetation (*Gadellia lactiflora, Senecio othonnae*) are found; at 1900-2500 m the land is covered by subalpine meadows dominated by: *Nardus stricta, Cynosurus cristatus, Deschampsia caespitosa, Trifolium trichocephalum, Geranium ibericum, Betonica macrantha* (Fig. 3e); snowbed vegetation occurs in moist areas (*Galanthus platyphyllus, Fritillaria latifolia, Dactylorhiza* spp.); rock vegetation (*Campanula hypopolia*) is present; at 2500–3000 m landscapes dominate by alpine meadows with species of *Alchemilla, Sibbaldia parviflora, Kobresia macrolepis, Poa longifolia*; on south-facing slopes we found communities of *Festuca varia* subsp. *woronowii* (Fig. 3e), and on north-facing slopes those of *Rhododendron caucasicum*; along streams: *Primula auriculata, Caltha polypetala*, species of *Batrachium* are usual; "alpine carpets" are also an important component of the landscape; above 3000 m subnival vegetation patches on screes and rocks as well as cryptogams thrive (Sakhokia & Khutsishvili 1975; Nakhutsrishvili 2013; Nakhutsrishvili & Abdaladze 2017a, b; Nakhutsrishvili & Batsatsashvili 2017).

The Central Great Caucasus (north macroslope, Cross Pass-Kazbegi-Chmi) has the following vertical zonation scheme: at 4000 to 3700 m nival vegetation on screes and rocks is present with individual plants of *Cerastium kasbek* and *Alopecurus laguroides* as well as cryptogams; at 3700-3000 m subnival vegetation patches occur on screes and rocks (*Tripleurospermum subnivale, Anthemis iberica, Delphinium caucasicum, Saxifraga exarata* subsp. *moschata, S. sibirica, S. flagellaris, Draba supranivalis, Cerastium kasbek, Alopecurus glacialis, A. laguroides, Nepeta supina, Pseudovesicaria digitata*); at 3000-2750 m landscape is made up of upper alpine meadows (*Carex tristis, Festuca varia* subsp. *woronowii, Nardus stricta*), "alpine carpets" (*Campanula biebersteiniana, Carum caucasicum, Veronica gentianoides, Sibbaldia semiglabra, Poa alpina, Festuca supina, Pedicularis crassirostris, Taraxacum stevenii, T. porphyranthum, Gnaphalium supinum, Alchemilla sericea, A. chlorosericea, Chamaesciadium acaule*); at 2750-2500 m – lower alpine meadows (*Nardus stricta, Carex tristis, Kobresia* spp. and on south-facing slopes *Festuca varia* subsp. *woronowii*), *Rhododendron caucasicum* scrub on north-facing slopes, prostrate elfin scrub dominated by *Dryas caucasica*; at 2500-1900 m subalpine meadows (*Hordeum violaceum, Bromopsis variegata, Agrostis planifolia, Deschampsia caespitosa*) dominate, subalpine park-like forest (*Betula litwinowii, B. raddeana, Populus tremula, Sorbus caucasigena = S. aucuparia, Salix caprea, S. kazbekensis*), crooked-stem birch timberline and prostrate evergreen scrub (*Rhododendron caucasicum, Vaccinium vitis-idaea, Daphne glomerata, Linnaea borealis*) are present on north-facing slopes, rock pine forest (*Pinus sylvestris* subsp. *hamata* (Fig. 4a)*, Berberis vulgaris, Rosa didoensis*), xerophytic scrub (*Juniperus communis, Spiraea hypericifolia*); remains of tall herbaceous vegetation (*Lilium monadelphum* subsp. *georgicum* (Fig. 4b), *Heracleum asperum, H. leskovii, H. sosnowskyi* (Fig. 4d), *Senecio rhombifolius,*) also grow in this zone, on south-facing slopes tragacanth steppe (*Astragalus denudatus* (Fig. 4c)*, A. captiosus, A. kazbekii*) occurs, rock and scree vegetation (*Saxifraga juniperifolia, Draba bryoides, Onosma caucasica*) is also present; at 1900-

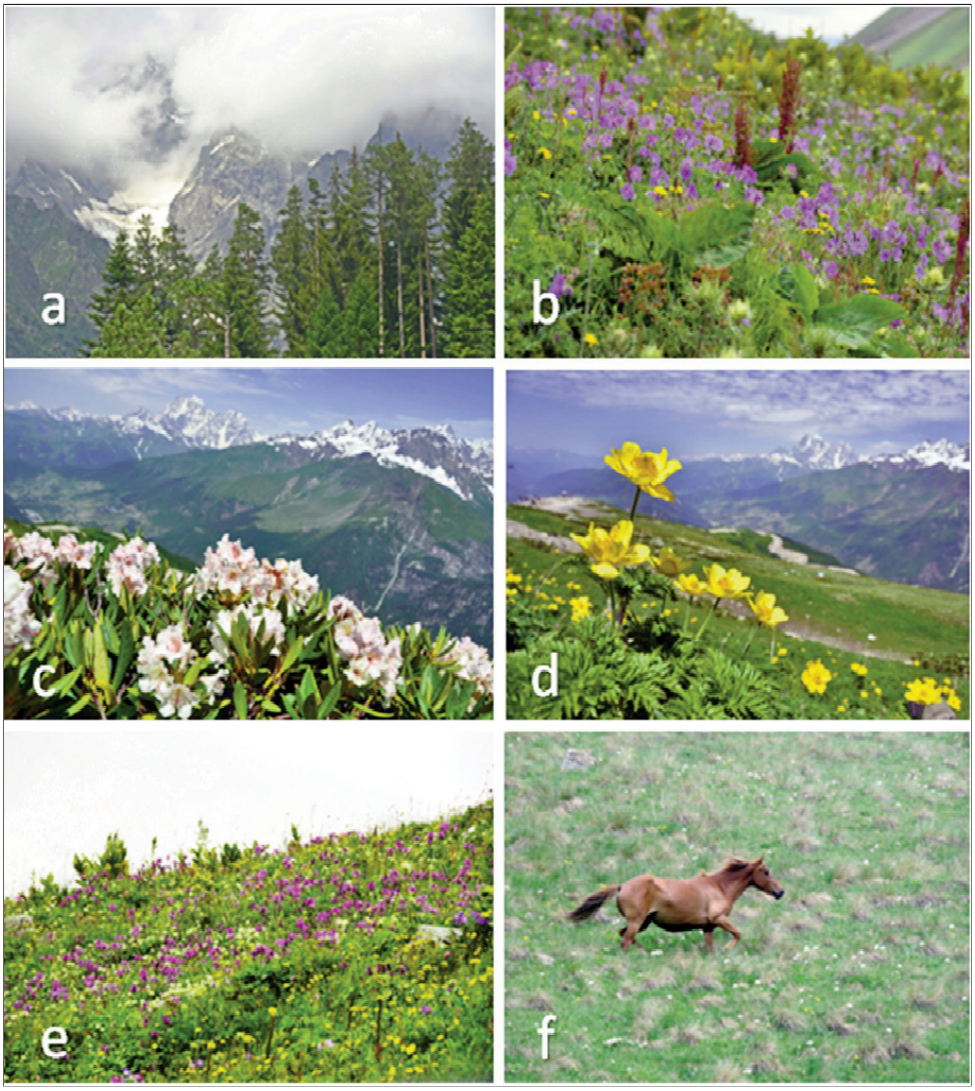

Fig. 3: a) *Abies nordmanniana*; b) Subalpine meadow dominated by *Geranium gymnocaulon*; c) *Rhododendron caucasicum*; d) *Pulsatilla aurea*; e) Subalpine meadow dominated by *Betonica macrantha*; f) Subalpine meadow dominated by *Festuca varia* subsp. *woronowii.*

1500 m rock herbaceous vegetation (*Campanula darialica, C. ossetica*), rock pine forest (*Pinus sylvestris* subsp. *hamata*), xerophytic scrub (*Juniperus communis, Spiraea hypericifolia*) occur; at 1500-800 m tragacanth steppe (*Astragalus denudatus*), steppe and secondary meadows are usual; below 800 m landscapes are constituted by semidesert (*Artemisia lerchiana, A. sosnowskyi*) and steppe (*Stipa stenophylla*) (Sakhokia & Khutsishvili 1975; Nakhutsrishvili & al. 2004, 2005, 2006; Nakhutsrishvili 2013;

Tepnadze & al. 2014; Nakhutsrishvili & Abdaladze 2017a, b; Nakhutsrishvili & Batsatsashvili 2017).

In subnival and nival zones the numbers of sensitive species and communities are especially high; among them snow-bed and near-glacier communities are noteworthy (Nakhutsrishvili & Gamtsemlidze 1984; Abdaladze & al. 2015).

Along with human impact (Nakhutsrishvili & al. 2009), on-going global climate change is the major potential threat to the vegetation diversity of the region (Erschbamer & al. 2010; Gigauri & al. 2013). The Cross-pass-Chmi section is exhibit clear contrasts in its vegetation structure.

Interglacial oroxerophyte communities are found here along with typical subalpine-alpine meso- and hygromesophillous meadows; however, the dominant landscape types are still more xeromorphic (mostly made up of grass species).

In Kazbegi-Chmi section there are narrow ravines, where precipitation does not condense and as a result the ravines are particularly dry supporting only xerophillous and very peculiar flora (Ivanishvili 1973).

We mentioned above that the aridity gradient runs in the north-weest to south-east direction along the Great Caucasus and shows maximim aridity in Dagestan. A. Dolukhanov (1966) recognizes two sub-provincesin the Dagestan province: foothill Dagestan and limestone middle montane Dagestan. In the former montane xerophyte and montane dry steppe communities are joined with sections hemixerophillous forests and its shrub understory remnants.

In the latter montane dry steppe, montane xerophytes, phrygana-like vegetation, hemixerophillous forests, mewdow transformed steppe and, as small islands, pine and birch forest make up the landscapes.

It is noteworthy that on the xerophytic (in certain places ultra-xerophytic) background of Dagestan, on the Side range, much taller than the main Watershed Range, crook-stem birch forest with *Rhododendron caucasicum* and floristically pauperized tall herbaceous vegetation occurs. At the highest elevations shallow snow cover and low temperatures makes the evergreen shrub aquire prostrate growth habit (the shoots grow up to 15-20 cm).

The Eastern Great Caucasus (north macroslope, Dagestan-Chechenya-Ingushetya) has the following vegetation zonation pattern: below 400 m wormwood and grass steppe on foothills, in places with saline halophytic communities and hemixerophytic shrubwoods (shibliak-like vegetation) as well as oak open woodlands; at 400-600 m oak and oak-hornbeam forests on foothills; at 600-1000 m hornbeam-beech forests, in middle-mountain zone mountain xerophytic communities and shibliak-like vegetation (*Paliurus, Spiraea, Crataegus, Rosa*, etc.), in places on north-facing slopes pine forests (*Pinus sylvestris*); at 1000-1900 m secondary and steppe meadows on foothills, mountain xerophytic communities and steppe meadows on south-facing slopes, pine-birch forests and secondary meadows on north-facing slopes in middle-mountain zone; at 1900-2500 m forest vegetation and steppe meadows and forest with subalpine meadows at the upper part, rock and scree vegetation; at 2500-3000 m subalpine and alpine meadows with *Rhododendron* and *Vaccinium* scrub on north-facing slopes (in the western part), meadows (in the more dry eastern part); above 3000 m subnival vegeta-

tion patches on screes and rocks, and cryptogams (Murtazaliev 2009; Nakhutsrishvili & Abdaladze 2017a, 2017b; Nakhutsrishvili & Batsatsashvili 2017).

Even in the most arid sections along the aridity gradient of the Great Caucasus humid ravines are found with well preserved "small refugia" of the Tertiary Gavashelishvili & Tharkhnishvili 2016). One of such small refugia is a small humid ravine with typical plants of Colchis (such as *Vaccinium arctostaphylos, Rhododendron luteum, Ilex colchica, Laurocrasus officinalis, Daphne pontica*) the Batsara Protected Area (the eastern Great Caucasus) surrounded by xerophillous vegetation.

Lagodekhi region is also rich in humid nano-refugia. Below the southern macroslope of the Major watershed range of the Great Caucasus river Alazani valley is located; its width is 30-35 km.

In this part of the Great Caucasus mountains are relatively lower (3000-3500 m a.s.l.). Precipitation remarkably increases close to mountains, which is well reflected by vegetation cover: only 20-25 km apart from the mountains forest vegetation is composed of hemi-xerophillous forest types (*Carpinus orientalis, Quercus iberica = Q. petrea*), steppe and semi-desert, while near the range typical mesophillous forests (with *Quercus pedunculiflora, Populus hybrida, Ulmus foliacea, Acer velutinum*) although rather pauperized occur. Within the Lagodekhi Protected Areas primeval and old-growth mesophillous montane broad-leaved forests are spread.

In some ravines of the Lagodekhi Protected Area the following species are found: *Pterocarya fraxinifolia, Acer velutinum, Taxus baccata*. Of other relicts *Gymnospermium smirnovii* (Fig. 4d)*, Vaccinium arctostaphylos, Staphylea pinnata* are worth mentioning.

Vegetation of the eastern Great Caucasus (South macroslope, Lagodekhi National Park area) has the following pattern: at 200–500 m Alazani floodplain forest and lowland forests (*Alnus barbata, Quercus pedunculiflora, Ulmus foliacea, Acer velutinum, Pterocarya fraxinifolia*, with lianas such as *Smilax excelsa, Clematis vitalba, Hedera helix, H. pastuchowii, Vitis sylvestris*); at 500–1000 m deciduous forests (*Quercus iberica, Carpinus caucasica, Fagus orientalis, Acer laetum, Castanea sativa, Staphylea pinnata*); at 1000–1800 m deciduous forests (*Fagus orientalis, Tilia begoniifolia*); at 1800–2500 m subalpine open woodlands and crooked stem forest near the upper limit (*Betula litwinowii, Acer trautvetteri,* on south-facing slopes *Quercus macranthera*), subalpine tall herbaceous vegetation (*Heracleum sosnowskyi, Telekia speciosa, Gadellia lactiflora*), and meadows; at 2500–3050 m alpine meadows; "Alpine carpets", rock and scree vegetation; above 3050 m subnival vegetation patches on screes and rocks and cryptogams (Nakhutsrishvili & Abdaladze 2017a, b; Nakhutsrishvili & Batsatsashvili 2017).

Conclusions

In the Great Caucasus a high number of vegetation has been revealed. This is due to a great diversity of ecological conditions along the climatic gradient across the Great Caucasus range. All differences in plant communities are caused not only by altitudinal variabilities but location on opposite sides of the Great Caucasus, and therefore, on differ-

Fig. 4. a) *Pinus sylvestris* subsp. *hamata* and rock pine forest; b) *Lilium monadelphum* subsp. *georgicum;* c) *Astragalus denudatus* (thorny tragacanth steppe); d) *Heracleum sosnowskyi* and tall herbaceous vegetation; e) *Gymnospermium smirnovii*.

ent macro expositions. Humid climate of the Black Sea also has an influence: on the West Caucasus prevails mesophilous vegetation compared to the East Caucasus; And vegetation zones are slightly offset upwards.

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