Ecological Questions 34 (2023) 1: 17–33 http://dx.doi.org/10.12775/EQ.2023.010

Structural and species diversity on North and South slopes in coniferous-deciduous forests of the North-Western Caucasus

Nikolaj Shevchenko, Anna Geraskina*

Center for Forest Ecology and Productivity Russian Academy of Sciences, Moscow, Russian Federation
*corresponding author e-mail: angersgma@gmail.com

Received: 3 January 2022 / Accepted: 23 February 2022

Abstract. The research was conducted in similar soil-orographic conditions of three widespread coniferous-deciduous forest types in the North-Western Caucasus: aspen-hornbeam, beech-fir-hornbeam, and fir-beech. The methods used included geobotanical, population-ontogenetic, and soil-zoological. It was found that the north and south slopes in all the studied forest types, in comparison with the flat areas, are characterised by significantly higher plant species richness. The efficiency of the renewal of arboral cenopopulations was much higher on the slopes, in comparison with the flat areas: the number of tree species (higher by 20–70%); density of tree species (higher by 50–100%); the number of cenopopulations of tree species with a complete ontogenetic spectrum was larger on the slopes, in comparison with the flat areas. A greater number of ecological groups of plants were described on the north and south slopes, in comparison with the flat areas. The proportion of boreal species was higher on the north slopes, in comparison with the south slopes, whereas the majority of meadow-forest edge species were the south slopes. The north and south slopes were characterised by the full functional diversity of soil invertebrates, whereas endemic and sub-endemic macrofauna also preserved. On the north slopes, we revealed a high biomass of large litter and soil saprophages, including species and groups actively participating in transformation of plant litter and soil formation. The south slopes showed high densities of phytophages and predators (among soil macrofauna), which regulate the diversity of other components of forest communities through biotic interactions. All the studied forest types on the north and south slopes exceeded the flat areas in terms of species diversity of plant communities, regeneration of tree species, ecological plant groups, endemic fauna of soil invertebrates, including soil formers. This confirms need to the protection of such territories to preserve and maintain the biological diversity of the coniferous-deciduous forests in the North-Western Caucasus.

Key words: forest community, forest type, undergrowth, undercrown space, species richness, litter, soil invertebrates, trophic groups, earthworms.

1. Introduction

The exposure and steepness of slopes is an important ecological factor in the spatial differentiation of plant complexes and biological diversity of forests. Its role is reduced mainly to the spatial redistribution of the influence intensity of key directly acting environmental factors such as temperature, humidity, and light.

The effects of slope exposure on vegetation and biodiversity have been known for a long time (Braun, 1935; Parma & Jouybari, 2010). Exposure and steepness of slopes affect temperature conditions (Antyufeev, 1978; Kutiel, 1992;

Marcelo & Maxim, 2001), radiation level (Butorina, 1969; Shcherbakov, 1970; Kozhevnikova, 1981), soil moisture content, winter distribution of snow (Richter, 1948; Billings & Bliss, 1959; Galen & Stanton, 1995), wind speed (Isard, 1986; Zhang et al., 2002), and soil fertility (Wang & Cai, 1988). Better warmed south slopes bear more thermophilic and more developed xerophilous vegetation than the north slopes (Butorina, 1969; Shcherbakov, 1970; Kozhevnikova, 1981; Elagin, 1976, 1980; Bennie et al., 2006). At the same time, on the north slopes, the forest belt lies much higher than on the south slopes; soils and air warm up more slowly with a slight moisture evaporation (Odum, 1975; Pikin, 2005).

Soil invertebrates are very sensitive to environmental gradients, depending on the steepness and exposure of slopes. With an increase in aridity and hypothermia, the taxonomic diversity and density of soil fauna decrease (Davis et al., 1998). Nevertheless, with the combined influence of factors, the greatest diversity and density of invertebrates is most often expected on cool and humid slopes (Pryke & Samways, 2010). Therefore, such studies are important to focus on the contrasting north and south slopes.

The diversity of soil fauna is determined by the composition of vegetation, which forms litter of different quality (Sariyildiz, 2008; Sariyildiz & Küçük, 2008; Kuznetsova et al., 2021). Composition of soil invertebrates is also determined by biotic interactions between trophic groups. High taxonomic diversity of soil invertebrates often does not take into account the responses of individual species to a huge number of potential combinations of abiotic and biotic factors. Therefore, combining species into groups, for example, trophic or functional, makes it possible to identify the reactions of a group to changes in environmental conditions on the basis of their common functional traits (Pillar, 1999; Rae et al., 2006).

Comprehensive studies of the species, trophic, ecological, and ontogenetic structure of various forest components are lacking despite the high importance of mountain forests in maintaining biodiversity.

This work aimed to assess the contribution of the north and south slopes to the structural and species diversity of the coniferous-deciduous forests in the North-Western Caucasus.

2. Materials and Methods

The study area (Fig. 1) included mountainous and foothill territories in the south of Krasnodar Territory and in the republics of Adygea and Karachay-Cherkessia, west of Elbrus, between 43.5° and 44.8° N (approximately 120 km long) and between 38.5° and 41.5° E. (approximately 450 km long). According to physical and geographical zoning, these territories belong to the Greater Caucasus, mainly to the Western high-mountain province (Gvozdetsky, 1963), whereas according to botanical-geographical zoning they belong to the Kuban sub-province of the North Caucasian province (Grebenshchikov et al., 1990).

The relief of the North-Western Caucasus is represented by complex mountain structures belonging to the area of alpine faulting and reaching an absolute height of 4,000 m (Dombay-Ulgen mountain) on the eastern border of the study area (Gvozdetsky, 1963). The climate of the study area is moderate and humid: the mean annual temperature is 7.7–11.1°C above zero; the mean January temperature is 4–5°C below zero; the mean temperature in July and August is approximately 15°C above zero; the annual precipitation varies from 500 mm to 3000 mm. With an increase in altitude, the mean annual temperature decreases with a gradient of no more than 0.5°C for every 100 m of absolute height, whereas the annual amount of precipitation increases with a maximum at an altitude of 2,300–2,400 m above sea level (Gavrilov, 1961; Gulisashvili et al., 1975; Makunina, 1986).

The coniferous-deciduous forests of the North-Western Caucasus are dominated by *Fagus orientalis* Lipsky, 1898, *Abies nordmanniana* (Steven) Spach, 1841, and *Carpinus betulus* L., 1753. The study object was aspen-hornbeam, beech-fir-hornbeam, and fir-beech forests. The studied forest types often dominate in the coniferous-deciduous forest belt of the North-Western Caucasus (Orlov, 1951; Grudzinskaya, 1953). According to the ecological-floristic classification, these forests belong to the association *Illici colchicae-Abietetum nordmannianae* Korotkov and Belonovskaja, 1987 of the *Vaccinio-Fagion orientalis* union (Zohary, 1973) Passarge, 1981 (Belonovskaya et al., 1990).

The selected communities were located in similar soil and orographic conditions: height above sea level from 600 m to 700 m, burozems (Cambisols Dystric, according to WRB., 2015) on the eluvium of shales. The thickness of the humus horizon averages 10–15 cm; the humus content in the upper horizon reaches 10–15%; medium reaction is acidic or weakly acidic (Shishov et al., 2004). Each forest type studied was described on three relief elements: flat area (slope steepness did not exceed 50°), north slope (including the north slope itself as well as northeast and northwest slopes with a steepness varying from 15° to 35°), and the south slope (including the south slope itself as well as southeast and southwest slopes with a steepness varying from 15° to 35°). The proportion of west and east slopes is insignificant in the relief of coniferous-deciduous forest belt of the North-Western Caucasus, with the majority of slopes with a steepness varying from 15° to 35° (Gvozdetsky, 1963).

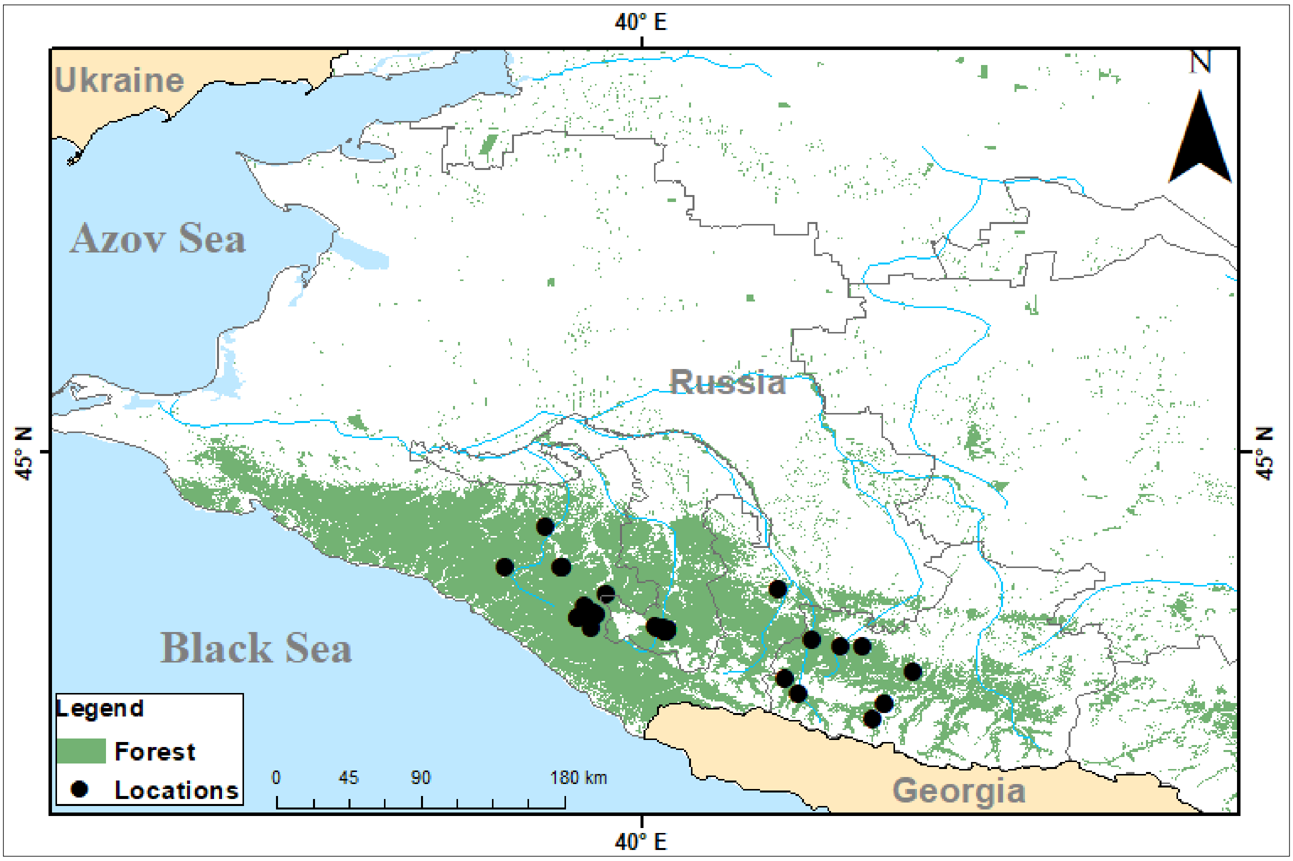

Figure 1. Study area indicating the location of the studied communities

The work used geobotanical, population-ontogenetic, and soil-zoological methods.

Geobotanical methods. To describe the plant communities, we laid 20x20 m square areas. In each type of forest, we made 40 geobotanical descriptions: 20 in the flat areas, 10 on the north slopes, and 10 on the south slopes. Generally of 120 geobotanical descriptions were used. In total the descriptions include 203 species of vascular plants, of which 20 species are found in layer A, 41 species in layer B, and 193 species in layer C (Suppl. Table 1). For all areas we compiled a complete floristic list taking into account the layered structure of vegetation. In each layer, the projective species cover was determined according to the J. Braun-Blanquet cover-abundance scale (Braun-Blanquet, 1964, cited from Mirkin et al., 1989). The names of plant species are given according to worldfloraonline.org. The species diversity of communities was assessed using indicators of species richness and abundance (Smirnova et al., 2002; Metodicheskie..., 2010). Layer A includes young, middle-aged, and old generative trees; to layer B – immature and virginal trees, immature, virginal and generative shrubs; to layer C, grasses, juvenile specimens of trees and shrubs.

Population-ontogenetic methods. We used the periodization of ontogenesis proposed by T.A. Rabotnov (1950) and supplemented by Uranov (1975) and his scholars (Zaugolnova et al., 1988). The ontogeny of trees was divided into the following stages: juvenile (j); immature (im); virginal (v); young generative (g1), mature generative (g2), and old generative (g3) and senile (s) (Smirnova et al., 1999; Evstigneev & Korotkov, 2016). In each type of forest, we determined the composition of arboreal cenopopulations with counting on different-sized areas. Immature, virginal, generative, and senile trees with a height of more than 1.5 m were counted on areas of 0.25 hectares (in 3-fold repetition of all relief elements of each forest type). Immature and virginal trees up to 1.5 m high were counted on areas of 100 m^2 (in 6-fold repetition of all relief elements of each forest type). Juveniles were counted on areas of 1 m^2 (30 times in all relief elements of each forest type). The data obtained were recalculated per hectare. The type of ontogenetic spectrum was established according to the classification proposed by Rabotnov (1950).

In addition to ontogenetic states, the absolute age of trees was determined by counting the number of rings on a core taken at the base of the trunk using an increment borer.

The ecological characteristics of communities (L – light factor, R – pH, F – soil moisture, N – nitrogen content, T – thermal factor, C – continentality, K – Continentality and

H – soil humus richness) were obtained as weighted average points for the corresponding characteristics of species from the ecological E. Landolt's scale (2010). The descriptions were arranged using indirect gradient analysis, or Detrended Correspondence Analysis (DCA), for compliance with the distant trend with determining correlation (r) and significance (p) levels using PC-ORD 5.0, SpeDiv, and Past programs.

The work used the classification of ecological groups of vascular plant species developed for European Russia (Smirnova et al., 2002; Smirnova, 2004). Ecological groups of plants are understood as large groups of ecologically related species, genetically associated with different types of communities. All species were divided into the following ecological groups: Br – boreal species, Md – meadow-forest edge, Nm – nemoral, Nt – nitrophilic, Wt – wetland, Pn – pine, and Other – species of other ecological plant groups.

Soil-zoological methods. In three forest types, soil invertebrates of the macrofauna size group were counted by the method of excavation and manual parsing of soil samples (Gilyarov, 1975). The size of a separate sample was 25x25 cm, the depth up to 30 cm. We took 105 soil samples in the aspen-hornbeam forests (48 in the flat areas, 30 on the north slopes, and 27 samples on the south slopes); 108 soil samples in the beech-fir-hornbeam forests (42 in the flat areas, 39 on the north slopes, and 27 samples on the south slopes); 111 soil samples in the fir-beech forests (48 in the flat areas, 30 on the north slopes, and 33 samples on the south slopes). Earthworms were stored in 95% alcohol; other invertebrates were stored in 70% alcohol. Species membership of insects, molluscs, crustaceans, and millipedes was determined up to supraspecific taxa according to the identification guides (Likharev & Rammelmeyer, 1952; Lokshina, 1969; Mamaev, 1972). Species membership of earthworms was determined according to the identification guide (Vsevolodova-Perel, 1997). The Kruskal-Wallis test was used to identify statistically significant differences in the abundance of macrofauna ($p<0.05$).

3. Results

Forests of aspen-hornbeam type are formed after clear and selective felling; the maximum age of trees is 50–70 years; the height of the tree canopy is 22±3.7 meters; Stem wood stock averages 293±34 m^3/ha with *Carpinus betulus* accounting for approximately 60–75% and *Populus tremula* L., 1753 accounting for approximately 10–20%; the share of other species is less than 5–10%.

Flat areas – the stand is dominated by *Carpinus betulus*; the second largest share belongs to *Populus tremula*. There is a large proportion of *Quercus hartwissiana* Steven, 1857 and a small number of *Betula pubescens* Ehrh., 1789, *Alnus glutinosa* (L.) Gaertn., 1791, *Cerasus avium* (L.) Moench, 1794, and *Fagus orientalis*. Density of the layer is 80–90%. The undergrowth layer is dominated by *Abies nordmanniana*, *Carpinus betulus*, *Corylus avellana* L., 1753, and *Fagus orientalis* with small proportions of *Betula pubescens*, *Crataegus monogyna* Jacq., 1775, *Frangula alnus* Mill., 1768, etc. The share of projective cover of the layer is 10–30%. The herb-dwarf shrub layer is dominated by *Lonicera caprifolium* L., 1753 and *Polygonatum glaberrimum* K.Koch, 1849 with large proportions of *Abies nordmanniana*, *Carex sylvatica* Huds., 1762, *Carpinus betulus*, *Cerasus avium*, *Fraxinus excelsior* L., 1753, *Hedera helix* L., 1753, *Vincetoxicum scandens* Sommier & Levier, 1892, etc. The projective cover of the layer varies from 30% to 70%.

The forest community (Fig. 2) contains mainly photophilous tree species, whereas shade-tolerant species are represented only by undergrowth. The demographic spectrum of the species cenopopulation is represented by all ontogenetic groups. A complete ontogenetic spectrum is noted only for the cenopopulation of *Carpinus betulus*. The spectrum of the invasive type is represented only by juvenile and immature plants. This type is characteristic of the cenopopulations of *Acer campestre* L., 1753, *Acer platanoides* L., 1753, *Fagus orientalis*, *Fraxinus excelsior*, and *Tilia begoniifolia* Steven, 1856. *Populus tremula* and *Quercus hartwissiana* are included in a discontinuous spectrum (the spectrum lacks one or more ontogenetic groups).

The total number of soil macrofauna is 100±12 ind./m^2, while the density of invertebrates in the mineral horizons is more than two times higher than in the litter horizon (Fig. 3). Trophic groups are predominated by saprophages, the number of which is 4–8 times higher than that of predators, phytophages, and mixophages (Fig. 4). In terms of biomass, the saprophagous group is predominated by earthworms and molluscs; proportions of millipedes and woodlice in biomass are significantly smaller (Fig. 5). Among saprophages, the litter is dominated by earthworms (14±5 ind./m^2) and forest cockroaches (12±3 ind./m^2), soil is dominated by earthworms (46±6 ind./m^2) and larvae of Diptera (12±4 ind./m^2). Among saprophages, a large proportion in the total abundance belongs to Ectobiidae and Diptera, although their proportion in the total biomass is less than 0.5±0.05 g/m^2. The litter is inhabited by predators such as spiders and rove beetles, rarely ground beetles and pseudoscorpions. The soil contains numerous predatory millipedes: Lithobiomorpha (8±3 ind./m^2) and Geophilomorpha (6±3 ind./m^2). Among phytophages that are few in number, click beetle larvae (Elateridae family) are the most numerous, whereas Mixophages, including Cucujoidea and Forficulidae, are rare.

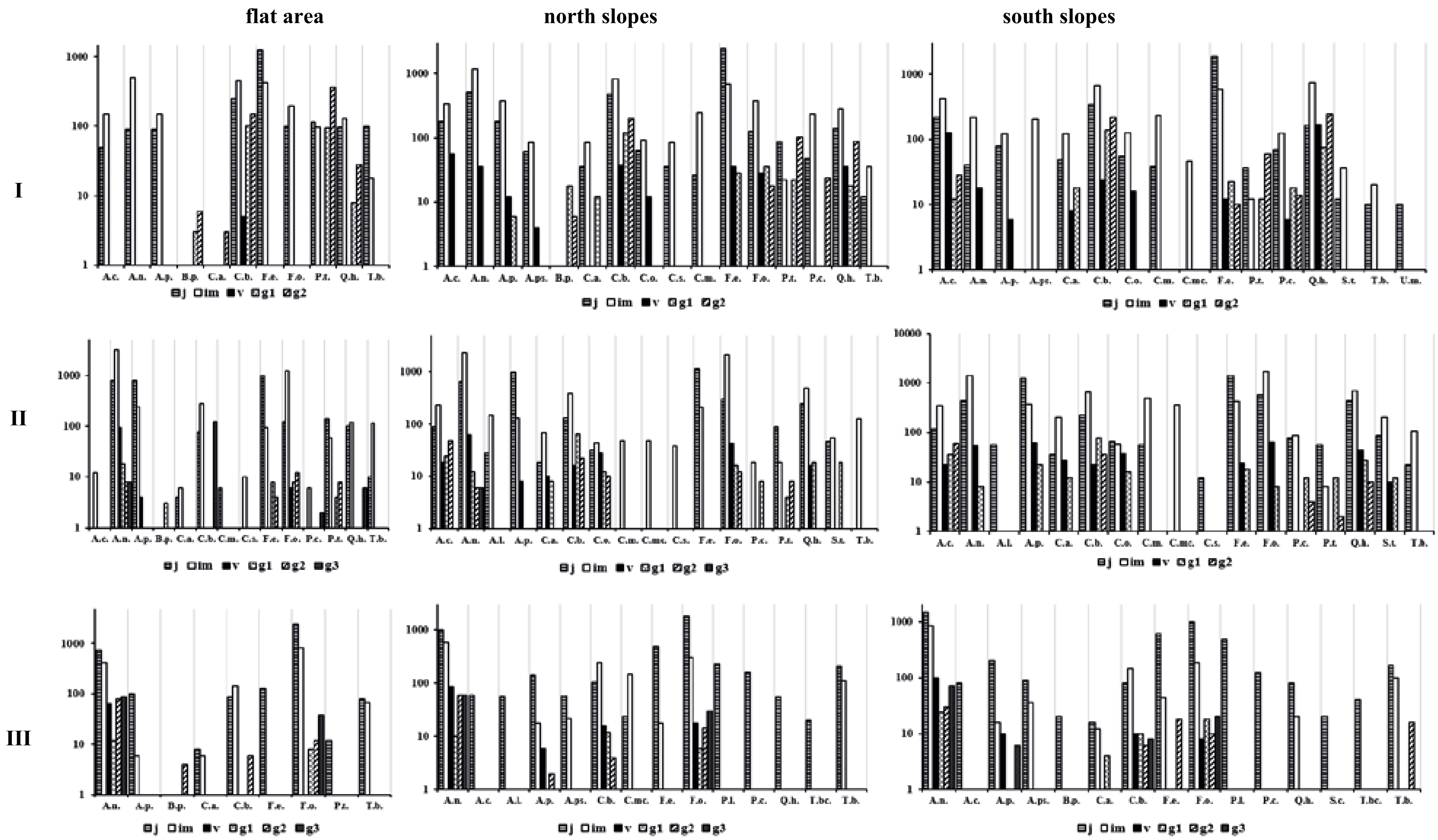

Figure 2. Population-demographic structure of trees in different relief elements of dominant forest types. Note: I – aspen-hornbeam forests; II – beech-fir-hornbeam forests; III – fir-beech forests Abscissa axis – ontogenetic states of tree species: j – juvenile; im – immature; v – virginal; g1 – young generative; g2 – mature generative; g3 – old generative.

Ordinate axis – number of individuals per hectare. Species of trees: A.n. – *Abies nordmanniana*, A.p. – *Acer platanoides*, A.c. – *Acer campestris*, A.l. – *Acer laetum*, A.ps. – *Acer pseudoplatanus*, B.p. – *Betula pubescens*, C.a. – *Cerasus avium*, C.b. – *Carpinus betulus*, C.m. – *Crataegus monogyna*, C.o. – *Carpinus orientalis*, C.s. – *Castanea sativa*, C.ms. – *Crataegus microphylla*, F.e. – *Fraxinus excelsior*, F.o. – *Fagus orientalis*, P.c. – *Pyrus caucasica*, P.l. – *Padus laurocerasus*, P.t. – *Populus tremula*, Q.h. – *Quercus hartwissiana*, S.c. – *Salix caprea*, S.t. – *Sorbus torminalis*, T.b. – *Tilia begoniifolia*, T.bc. – *Taxus baccata*, U.m. – *Ulmus minor.*

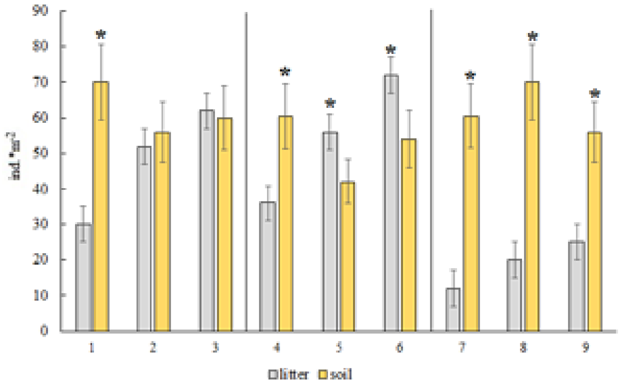

Figure 3. Average number of macrofauna in litter and mineral soil horizons of flat areas (1, 4, 7), north slopes (2, 5, 8), and south slopes (3, 6, 9) of three forests types: aspen-hornbeam forests (1, 2, 3), beech-fir-hornbeam forests (4, 5, 6), fir-beech forests (7, 8, 9)

Note: * – statistically significant differences in numbers of macrofauna between litter and soil horizons within one forest community of one relief element, Kruskal-Wallis test ($p<0.05$).

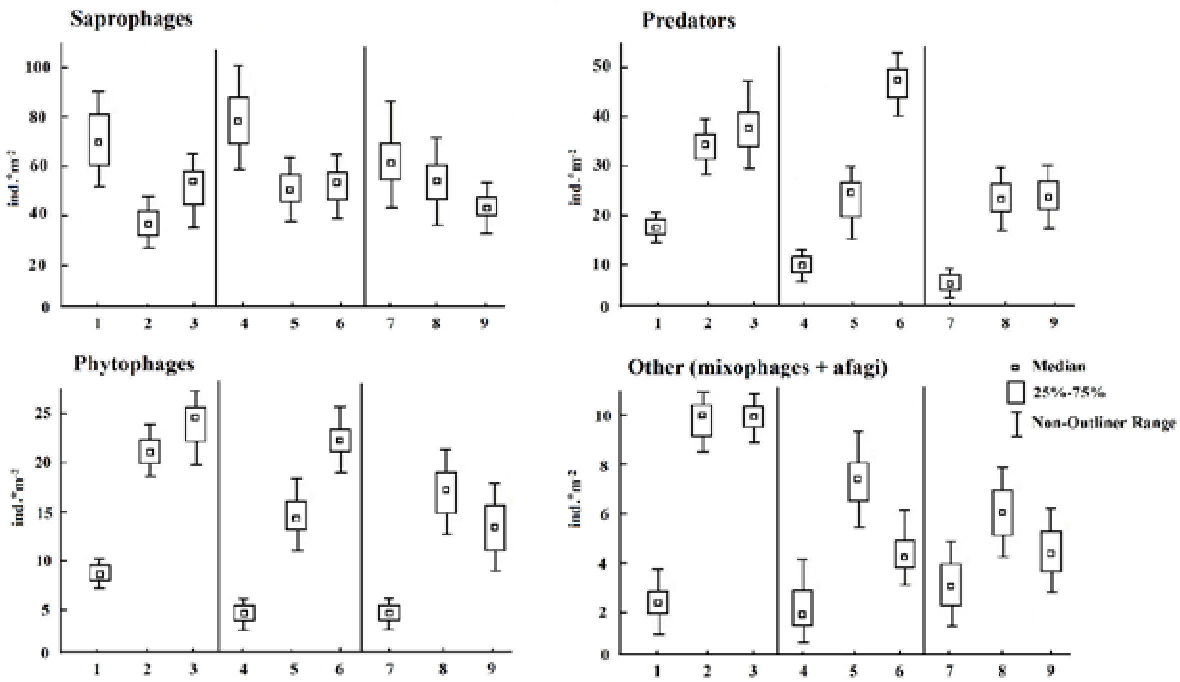

Figure 4. Average biomass of trophic macrofauna groups (1–9 plant community numbers as in Figure 3)

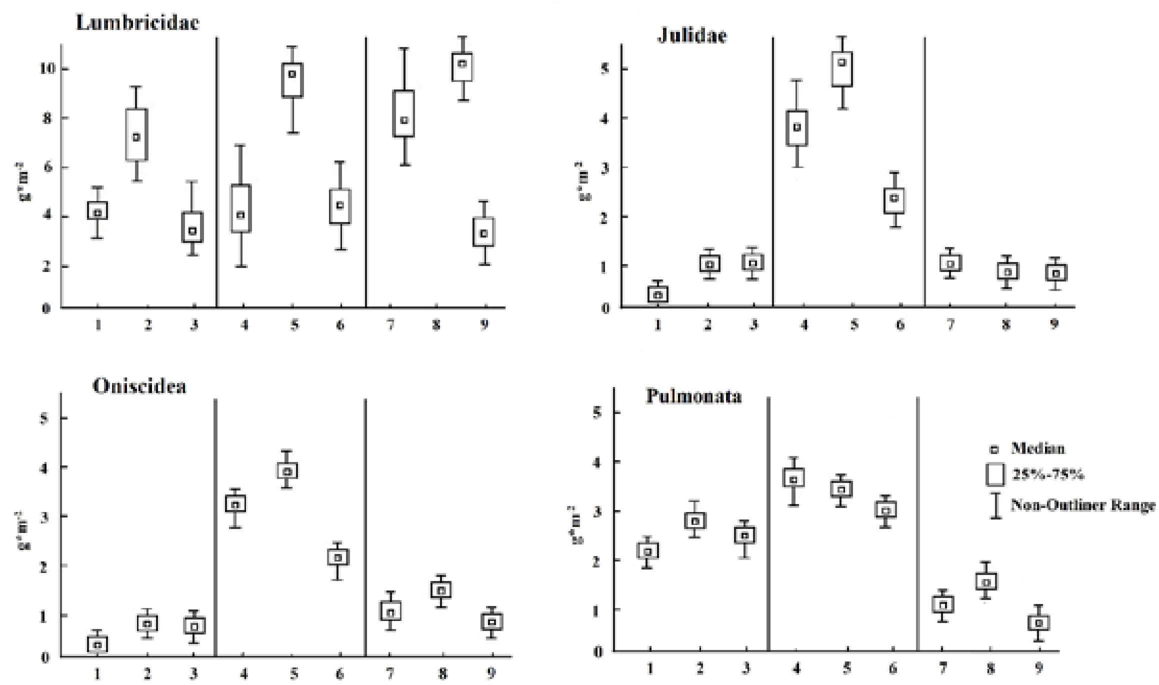

Figure 5. Average biomass of dominant taxa of macrophages (1–9 plant community numbers as in Figure 3)

Earthworms account for a large proportion in the abundance and biomass of invertebrates. The litter horizon is inhabited by four species of epigeic earthworms: *Dendrobaena octaedra* (Savigny, 1826), *Dendrodrilus rubidus tenuis* (Eisen, 1874), *Eiseniella tetraedra* (Savigny, 1826), and the litter form of the polymorphic species *Dendrobaena schmidti* Michaelsen, 1907. The mineral horizons are inhabited by a large number of endogeic species: *Aporrectodea jassyensis* (Michaelsen, 1891), *Dendrobaena tellermanica* Perel, 1966, and endogeic form *Dendrobaena schmidti*. It is these species that account for a large proportion in the total abundance of the macrofauna in the mineral horizons. The epi-endogeic *Lumbricus rubellus* Hoffmeister, 1843 is rare, as is the epi-endogeic form *Dendrobaena schmidti. Dendrobaena mariupolienis* Wyssotzky, 1893 anecic species are found singularly.

North slopes – the stand is dominated by *Carpinus betulus* with large proportions of *Fagus orientalis* and *Betula pubescens*. *Cerasus avium*, *Fraxinus excelsior*, *Populus tremula*, and *Quercus hartwissiana* are presented in small numbers. The share of projective cover of the layer is 80–90%. The undergrowth layer is dominated by *Abies nordmanniana*, *Carpinus betulus*, and *Fagus orientalis*. *Corylus avellana*, *Quercus hartwissiana*, *Pyrus caucasica* Fed., 1952, and *Ligustrum vulgare* L., 1753 are common. The share of projective cover of the layer is 20–40%. The herb-shrub layer is dominated by *Lonicera caprifolium*, *Rubus caesius* L., 1753, *Athyrium filix-femina* (L.) Roth, 1799, *Carex remota* L., 1753, *Fragaria vesca* L., 1753, *Galeobdolon luteum* Huds., 1778, *Polygonatum glaberrimum*, *Quercus hartwissiana*, *Tamus communis* L., 1753, and *Viola odorata* L., 1753. The projective cover of the layer varies from 50% to 90%.

On the north slopes, the cenopopulations of *Carpinus betulus*, *Fagus orientalis*, and *Quercus hartwissiana* are represented by a complete ontogenetic spectrum (Fig. 2). The complete spectrum of *Fagus orientalis* is explained by the omission of mature beech trees on the slopes during clear felling for seeding and soil anchorage. A discontinuous spectrum was noted for the cenopopulations of *Cerasus avium*, *Populus tremula*, and *Pyrus caucasica*; invasive type was noted for *Acer campestre*, *Abies nordmanniana*, *Acer platanoides*, *Acer pseudoplatanus* L., 1753, *Carpinus orientalis*, *Castanea sativa* Mill., 1768, *Crataegus monogyna*, *Fraxinus excelsior*, and *Tilia begoniifolia*; regressive type was noted only for *Betula pubescens*.

The abundance of macrofauna on the north slopes is 106±13 ind./m^2. On the north slopes and in the flat areas, the density of macrofauna in the litter and mineral soil horizons is the same (Fig. 3). Among trophic groups, the number of predators and saprophages is approximately the same, while density of saprophages is two times lower than in the flat areas; the density of phytophages and predators is, on the contrary, more than two times higher, and the total density of groups of myxophages and aphages is five times higher (Fig. 4). Despite the lower total number of saprophages the biomass of earthworms and millipedes was significantly higher on the north slopes in comparison with the flat areas (Fig. 5). The decrease in the total number of saprophages is associated with the low numbers of dipteran and wood cockroach larvae on the north slopes (no more than 6 ind. m^2). The increase in the biomass of earthworms is associated with the predominance of larger endogeic species and a low proportion of small epigeic species, which were found to be few in number on the north slopes. Millipedes on the north slopes include a large representative of the family Julidae *Pachyiulus krivolutskyi* Golovatch, 1977, which is endemic to the forests of the Western Caucasus. Predators are represented by numerous rove beetles (11±3 ind./m^2), spiders (9±4 ind./m^2), labiopods (8±2 ind./m^2), and ground beetles (6±4 ind./m^2); mixophages are represented by Cucujoidea (5±3 ind./m^2), Forficulidae (5±4 ind./m^2), and Lepidoptera cocoons (aphages).

South slopes – the stand is dominated by *Carpinus betulus*. The second largest share often belongs to *Populus tremula*. *Fagus orientalis*, *Cerasus avium*, *Quercus hartwissiana*, and *Acer laetum* C.A.Mey., 1831 are presented in small numbers. The share of projective cover of the layer is 70–80%. The undergrowth layer is dominated by *Abies nordmanniana*, *Acer campestre*, *Fagus orientalis*, and shrubs *Corylus avellana* and *Staphylea colchica* Steven, 1848. The share of projective cover of the layer is 30–50%. The herb and shrub layer is dominated by *Athyrium filix-femina*, *Carex sylvatica*, *Carpinus betulus*, *Circaea lutetiana* L., 1753, *Dryopteris filix-mas* (L.) Schott, 1834, *Fraxinus excelsior*, *Hedera helix*, *Polygonatum glaberrimum*, *Rubus caesius*, *Tamus communis*, and *Viola odorata*.

On the south slopes, *Acer campestre*, *Carpinus betulus*, *Fraxinus excelsior*, *Pyrus caucasica*, and *Quercus hartwissiana* are represented by a complete ontogenetic spectrum; discontinuous spectrum is noted only for *Populus tremula*; invasive type is noted for *Abies nordmanniana*, *Acer platanoides*, *Acer pseudoplatanus*, *Cerasus avium*, *Carpinus orientalis*, *Crataegus microphylla* K.Koch, 1853, *Crataegus monogyna*, *Sorbus torminalis* Garsault, 1764, *Tilia begoniifolia*, and *Ulmus glabra* Mill., 1768 (Fig. 2).

The abundance of macrofauna on the south slopes is slightly higher than on the north slopes and flat areas and amounts to approximately 130±15 ind./m^2. The density of macrofauna in litter and mineral horizons is the same (Fig. 3). The abundance of macrofauna is higher due to the groups of predators and phytophages (Fig. 4). The south slopes are registered higher densities of predators such as Araneidae (12±4 ind./m^2), Staphylinidae (13±2 ind./m^2), and Hemiptera (10±3 ind./m^2); phytophages such as Chrysomelidae (14±4 ind./m^2) and Scarabaeidae (10±2 ind./m^2). The south slopes are inhabited by a relatively large number (10±4 ind./m^2) of adults of firefly beetles of the Lampyridae (aphages) family. The biomass of earthworms on the south slopes is significantly lower than on the north slopes (Fig. 5). Among the Lumbricidae dominate endogeic species *Aporrectodea jassyensis* and endogeic form of *Dendrobaena schmidti*.

Forests of beech-fir-hornbeam type are formed in the places of old clear and selective felling, the maximum age of trees of the first post-felling generation is 80–110 years, the height of the stand is 32±5.7 meters. Stem wood stock averages 319±87 m^3/ha with *Carpinus betulus* accounting for 40–50%, *Abies nordmanniana* accounting for 20–30%, and *Fagus orientalis* accounting for 20–25%. Forests of this type gradually lose photophilous tree species that formed the first post-felling generation. Young shade-tolerant species *Abies nordmanniana* and *Fagus orientalis* enter the upper tree layer.

Flat areas – the forest stand is dominated by *Abies nordmanniana*, *Carpinus betulus*, and *Fagus orientalis*; *Fraxinus excelsior*, *Pyrus caucasica*, and *Quercus hartwissiana* are presented in large numbers. The share of projective cover of the layer is 80–90%. The undergrowth layer is dominated by *Abies nordmanniana*, *Fagus orientalis*, *Acer platanoides* and shrubs of *Corylus avellana* and *Ilex colchica* Pojark., 1947. The share of projective cover of the layer is 40–50%. The herb-shrub layer is dominated by *Athyrium filix-femina*, *Carex sylvatica*, *Fagus orientalis*, *Fraxinus excelsior*, *Hedera helix*, *Lonicera caprifolium*, *Pachyphragma macrophyllum* (Hoffm.) N.Busch, 1908, *Polygonatum orientale* Desf., 1807, *Rubus caesius*, and *Viola odorata*. The share of projective cover of the layer is 20–40%.

In the flat areas (Fig. 2), only the cenopopulations of *Abies nordmanniana*, *Fagus orientalis*, and *Fraxinus excelsior* are represented by a complete ontogenetic spectrum. The discontinuous type is represented by *Carpinus betulus*, *Pyrus caucasica*, *Populus tremula*, and *Quercus hartwissiana*; invasive type is represented by *Acer platanoides*, *Cerasus avium*, and *Tilia begoniifolia*; fragmented type is represented by *Acer campestre*, *Betula pubescens*, and *Castanea sativa*.

In the vertical structure of soil macrofauna distribution, the density of the inhabitants in the mineral horizons is significantly higher than that of the inhabitants of the litter (Fig. 3). In comparison with the aspen-hornbeam type of forest, their total number is slightly lower and amounts to approximately 90±11 ind./m^2. At the same time, saprophages account for the largest share (Fig. 4). They include earthworms, millipedes, woodlice, and molluscs, which account for a large proportion of the biomass (Fig. 5). The litter horizon is inhabited by four species of epigeic earthworms: *Dendrobaena octaedra*, *Dendrobaena attemsi* Michaelsen, 1902, *Dendrodrilus rubidus tenuis*, and the litter form *Dendrobaena schmidti*. Endogeic species, such as *Aporrectodea jassyensis* and endogeic form of *Dendrobaena schmidti*, are numerous in the mineral horizons. Epi-endogeic *Eisenia fetida* (Savigny, 1896), epi-endogeic form of *Dendrobaena schmidti*, and anecic species *Dendrobaena mariupolienis* are found singularly. Predator species include staphyllinids (5±3 ind./m^2) and carnivorous millipedes Lithobiomorpha and Geophilomorpha (5±2 ind./m^2). Phytophages are few in number; the larvae of click beetles (Elateridae) and lamellar beetles (Scarabaeidae) are the most common. Representatives of mixophages, i.e. Cucujoidea and Forficulidae, are rare.

North slopes – the forest stand is dominated by *Abies nordmanniana*, *Carpinus betulus* and *Fagus orientalis* with a large proportion of *Quercus hartwissiana*. The share of projective cover of the layer is 70–80%. The undergrowth layer is dominated by *Abies nordmanniana*, *Fagus orientalis*, *Acer laetum*, *Carpinus orientalis*, and *Crataegus microphylla* trees. The share of projective cover of the layer is 30–70%. The herb-shrub layer is dominated by *Lonicera caprifolium*, *Fragaria vesca*, *Fraxinus excelsior*, *Abies nordmanniana*, *Polygonatum glaberrimum*, *Rubus caesius*, *Tamus communis*, and *Viola odorata*. The share of projective cover of the layer is 20–70%.

On the north slopes (Fig. 2), the cenopopulations of *Acer campestre*, *Abies nordmanniana*, *Carpinus betulus*, *Carpinus orientalis*, *Fagus orientalis*, *Cerasus avium*, and *Quercus hartwissiana* are represented by a complete ontogenetic spectrum; intermittent type is represented by *Populus tremula* and *Populus tremula*; invasive type is represented by *Acer laetum*, *Acer platanoides*, and *Fraxinus excelsior*; intermittent type is represented by *Populus tremula* and *Sorbus torminalis*; fragmented type is represented by *Crataegus microphylla*, *Crataegus monogyna*, *Castanea sativa*, *Pyrus caucasica*, and *Tilia begoniifolia*.

On the north slopes, the abundance of macrofauna in the litter horizon is significantly higher than in the mineral horizons (Fig. 3) and totals 98±9 ind./m^2. The number of saprophages on the north slopes is 1.5 times lower than in the flat areas of this forest type; the number of predators and phytophages, on the contrary, is 2–3 times higher (Fig. 4). Despite the decrease in the number of saprophages, on the north slopes the biomass of some groups is higher than in the flat areas – the number of earthworms is two times higher; the number of millipedes and woodlice is 1.5 times higher (Fig. 5). Among earthworms, a large proportion of the biomass belongs to endogeic species and forms, such as *Aporrectodea jassyensis* and *Dendrobaena schmidti,* and anecic species *Dendrobaena mariupolienis.* Among millipedes, high abundance is registered for *Cylinroiulus caeruleocinctus* (Wood, 1864) (12±4 ind./m^2), whereas other saprophages, such as Diptera larvae and Ectobiidae adults, are rare.

Among the predators, the most numerous are spiders (10±2 ind./m^2), rove beetles (8±2 ind./m^2), and predatory millipedes – Lithobiomorpha and Geophilomorpha (8±3 ind./m^2); among phytophages, the largest shares belong to larvae of Elateridae (8±4 ind./m^2) and Scarabaeidae (6±3 ind./m^2) families. Representatives of mixophages, i.e. Cucujoidea and Forficulidae, were found more often than in the flat areas.

South slopes – the stand is dominated by *Carpinus betulus*, the second largest share belongs to *Abies nordmanniana* and *Fagus orientalis* with large proportions of *Carpinus orientalis* and *Acer campestre*. The share of projective cover of the layer is 70–80%. The undergrowth layer is dominated by *Abies nordmanniana*, *Acer campestre*, *Carpinus orientalis* Mill., 1768, *Fagus orientalis* and shrubs *Cornus mas* L., 1753 and *Corylus avellana*. The share of projective cover of the layer is 40–50%. The herb-shrub layer is dominated by *Festuca drymeja* Mert. & W.D.J.Koch, 1823; *Abies nordmanniana*, *Acer campestre*, *Acer laetum*, *Cornus mas*, *Fragaria vesca*, *Lonicera caprifolium*, *Polygonatum glaberrimum*, *Rubus caesius*, *Tamus communis*, and *Viola odorata* are common. The share of projective cover of the layer is 40–80%.

On the south slopes, the cenopopulations of *Abies nordmanniana*, *Acer campestre*, *Acer platanoides*, *Carpinus betulus*, *Carpinus orientalis*, *Cerasus avium*, *Fagus orientalis*, *Fraxinus excelsior*, *Quercus hartwissiana*, and *Sorbus torminalis* are represented by a complete ontogenetic spectrum; intermittent type is represented by *Pyrus caucasica* and *Populus tremula*; invasive type is represented by *Acer laetum*, *Castanea sativa*, *Crataegus monogyna*, and *Tilia begoniifolia*; fragmentary type is represented by only *Crataegus microphylla* (Fig. 2).

The abundance of macrofauna on the south slopes is 126±13 ind./m^2, while the abundance of invertebrates in the litter is significantly higher than in the mineral horizons (Fig. 3). The total number of saprophages on the south slopes is comparable to the north slopes (no differences were found), while the number of predators and phytophages on the south slopes is 2 times higher than on the north slopes (Fig. 4). On the south slopes, the biomass of earthworms is more than two times lower than on the north slopes (Fig. 5), which is associated with the rare occurrence of large anecic earthworms, which make a greater contribution to the biomass on the north slopes. Also, the biomass of millipedes, woodlice, and molluscs is also significantly lower on the south slopes than on the north slopes, which is due to their low density on the latters (no more than 10±4 ind./m^2). Among the predators, spiders (16±4 ind./m^2) and rove beetles (14±4 ind./m^2) as well as the pubescent centipedes, Lithobiomorpha and Geophilomorpha (18±2 ind./m2), which live mainly in the soil, make up the majority of litter fauna in these forests. Phytophages are represented mainly by larvae of Scarabaeidae (12±4 ind./m^2) and Elateridae (10±3 ind./m^2) families. Among mixophages, the litter was inhabited by representatives of the family Forficulidae (4±4 ind./m^2).

Fir-beech forest type – these forests lack traces of fellings and fires (coal was not found in the soil); the tree layer has a complex spatial structure, represented by trees of different ages. This type of forest was described in the Caucasian Biosphere Reserve, which has been well protected since the late 18th century; therefore, the forests preserved here are the best preserved natural forests. We assume that this type is the final stage in the development of the coniferous-deciduous forests in the North-Western Caucasus (Carbon accumulation ..., 2019). The age of some fir trees exceeds 450 years; the height of the tree canopy reaches 50±12.1 meters. Stem wood stock averages 1097±265 m^3/ha, with *Fagus orientalis* accounting for 66–82% of the total stock and *Abies nordmanniana* accounting for 16–32%.

Flat areas – the stand is dominated by *Fagus orientalis* and *Abies nordmanniana* with small proportions of *Acer laetum* and *Carpinus betulus*. The share of projective cover of the layer is 90–95%. The undergrowth layer is dominated by *Abies nordmanniana* and *Fagus orientalis* with large proportions of *Daphne caucasica* Pall., 1784, *Ilex colchica*, and *Taxus baccata* Thunb., 1784. The share of projective cover of the layer is 5–10%. The herb-dwarf shrub layer is dead-cover layer; the share of projective cover of the layer is 5–7%; the common species are *Abies nordmanniana*, *Acer platanoides*, *Fagus orientalis*, *Cephalanthera rubra* (L.) Rich., 1817, *Dryopteris filix-mas*, *Fraxinus excelsior*, *Moehringia trinervia* (L.) Clairv., 1811, *Monotropa hypopitys* L., 1753, *Neottia nidus-avis* (L.) Rich., 1817, and *Tilia begoniifolia* are found singularly.

In the flat areas, only the *Abies nordmanniana* cenopopulation is represented by complete ontogenetic spectrum; discontinuous spectrum was represented by *Fagus orientalis* and *Carpinus betulus*; invasive type was represented by *Acer platanoides*, *Cerasus avium*, *Fraxinus excelsior*, and *Populus tremula*; fragmentary type was represented only by *Betula pubescens* (Fig. 2).

The abundance of macrofauna in flat areas of fir-beech forests is 73±12 ind./m^2. The abundance of litter macrofauna is 5 times lower than that of soil macrofauna (Fig. 3). The number of saprophages is comparable to the flat areas of other forest types and amounts to 85% of the total number of the entire macrofauna. The densities of predators, phytophages, mixophages, and aphages are very low (Fig. 4). Among saprophages dominate earthworms (48±8 ind./m^2), which make up a large proportion of the biomass (Fig. 5). In the flat areas, four ecological groups of earthworms are well represented: epigeic *Dendrobaena octaedra*, *Dendrodrilus rubidus tenuis*, and the epigeic form of *Dendrobaena schmidti*;

epi-endogeic *Lumbricus rubellus* and *Eisenia fetida*; endogeic *Aporrectodea jassyensis* and endogeic form *Dendrobaena schmidti*; and anecic *Dendrobaena mariupolienis*, which are found in beech-fir forests much more often than in other types of forests. The biomass of woodlice, molluscs, and millipedes is very low (Fig. 5), as is their abundance (in total, for three groups, no more than 12±4 ind./m^2).

North slopes – the stand is dominated by *Fagus orientalis* and *Abies nordmanniana* with a large proportion of *Carpinus betulus* and a small proportion of *Quercus hartwissiana*. The share of projective cover of the layer is 90%. The undergrowth layer is expressed better than in the flat areas; the share of projective cover of the layer is 15–20%, the layer is dominated by the undergrowth of *Fagus orientalis* and *Abies nordmanniana* with large proportions of the undergrowth of *Acer platanoides*, *Crataegus microphylla*, *Rhododendron luteum* Sweet, 1830, and *Tilia begoniifolia*. The herb-dwarf shrub layer is dead-cover layer; the share of projective cover of the layer is 5–10%. The species common for the layer are *Abies nordmanniana*, *Acer platanoides*, *Athyrium filix-femina*, *Carpinus betulus*, *Cephalanthera rubra*, *Fagus orientalis*, *Fraxinus excelsior*, *Rubus caucasicus* Focke,1874, *Tilia begoniifolia*, and *Viola odorata*.

On the north slopes, a complete ontogenetic spectrum is represented by cenopopulations *Abies nordmanniana* and *Fagus orientalis*; intermittent type is represented by *Acer platanoides*; invasive type is represented by *Acer campestre*, *Acer laetum*, *Acer pseudoplatanus*, *Carpinus betulus*, *Crataegus microphylla*, *Fraxinus excelsior*, *Padus laurocerasus* (L.) Mill., 1768, *Pyrus caucasica*, *Quercus hartwissiana*, *Taxus baccata*, and *Tilia begoniifolia* (Fig. 2).

The abundance of macrofauna on the north slopes of fir-beech forests is 90±13 ind./m^2; the number of inhabitants of the litter in the flat areas is several times lower than that of the soil (Fig. 3). The number of saprophages is almost equal to that in the flat areas; the number of predators, phytophages, and mixophages is significantly higher on the north slopes than in the flat areas (Fig. 4). The biomass of three groups of saprophages, i.e. molluscs, woodlice, and millipedes, is low; the biomass of earthworms is high and comparable to that in the flat areas (Fig. 5). The north slopes are also inhabited by different groups of earthworms with the largest proportion of endogeic species, among which the most numerous is Crimean-Caucasian endemic *Dendrobaena schmidti* (30±6 ind./m^2). Millipedes include an endemic Caucasian species *Pachyiulus krivolutskyi* (8±2 ind./m^2). The predators include numerous labipod millipedes, i.e. Lithobiomorpha and Geophilomorpha (14±4 ind./m^2); spiders (6±3 ind./m^2) and rove beetles (5±3 ind./m^2) are less common. Phytophages are mainly represented by Elateridae family (16±4 ind./m^2); mixophages are represented by adults of Forficulidae family (6±3 ind./m^2).

South slopes – the stand is dominated by *Fagus orientalis* and *Abies nordmanniana* with a small proportion of *Carpinus betulus*. The share of projective cover of the layer is 85–90%. The undergrowth layer is dominated by *Abies nordmanniana*, *Fagus orientalis*, and *Ilex colchica*; *Cornus mas*, *Corylus avellana*, *Frangula alnus*, *Rhododendron luteum*, and *Sambucus nigra* L., 1753 are common. The share of projective cover of the layer is 20–30%. The herb-shrub layer is poorly developed; the share of projective cover of the layer is 5–10%; common species are *Abies nordmanniana*, *Acer platanoides*, *Carpinus betulus*, *Cephalanthera rubra*, *Circaea lutetiana* L., 1753, *Fagus orientalis*, *Fraxinus excelsior*, *Paris incomplete* M.Bieb., 1808, *Ribes biebersteinii* Berland. ex DC., 1826, *Tilia begoniifolia*, and *Viola odorata*.

On the south slopes, the cenopopulations of *Abies nordmanniana*, *Fagus orientalis*, and *Carpinus betulus* are represented by a complete ontogenetic spectrum; discontinuous type is represented by *Carpinus betulus*, *Cerasus avium,* and *Fraxinus excelsior*; invasive type is represented by *Acer campestre*, *Acer pseudoplatanoides*, *Betula pubescens*, *Padus laurocerasus*, *Pyrus caucasica*, *Quercus hartwissiana*, *Sorbus torminalis*, and *Taxus baccata* (Fig. 2).

The abundance of macrofauna on the south slopes is 81±9 ind./m^2, as in other landscape elements of this forest type; the number of litter fauna is several times lower than the number of soil fauna (Fig. 3). The number of saprophages, phytophages, and mixophages is approximately the same as on the north slopes; the number of predators on the south slopes is slightly higher than on the north slopes (Fig. 4). The biomass of earthworms on the south slopes is two times lower than on the north slopes; the biomass of woodlice and molluscs is 1.5 times lower; the biomass of bipeds is the same as on the north slopes (Fig. 5). Among earthworms prevail endogeic species, i.e. *Dendrobaena schmidti* (16±2 ind./m^2) and *Aporrectodea jassyensis* (8±4 ind./m^2). Representatives of other groups are rare. Large proportions of the millipedes include *Pachyiulus krivolutskyi* (8±4 ind./m^2) and *Cylinroiulus caeruleocinctus* (6±3 ind./m^2). Among the predators, the largest proportion belongs to labiopods, i.e. Lithobiomorpha and Geophilomorpha orders (16±3 ind./m^2), while spiders, rove beetles, ground beetles are less common. Phytophages are represented mainly by Elateridae larvae; mixophages are represented by adult Forficulidae.

4. Discussion

Thus, in all the studied coniferous-broad-leaved forests on the north and south slopes of the North-Western Caucasus, compared with the flat areas, arboral cenopopulations (Fig. 2) are renewed much better. Aspen-hornbeam forests in the flat areas were noted the renewal of 11 tree species; on the north and south slopes 16 species were renewed. In the flat areas, only one cenopopulation of trees (*Carpinus betulus*) was represented by a complete ontogenetic spectrum with a stable turnover of generations; for the north slopes, this indicator was equal to five; for the south slopes, this indicator was equal to six. The beech-fir-hornbeam type of forest in the flat areas was noted the renewal of 14 species, of which only cenopopulations of *Abies nordmannina* and *Fagus orientalis* have a stable generation turnover; the north and south slopes were noted the renewal of 17 species each. Of these, on the north slopes, cenopopulations of seven tree species are represented by a complete ontogenetic spectrum; for the south slopes this indicator is equal to 10. Old-growth fir-beech forests in the flat areas were noted the renewal of nine tree species; for the north slopes, this indicator was equal to 14; for the south slopes, this indicator was equal to 15 species, of which only one species was represented by a complete ontogenetic spectrum in the flat areas; for the north and south slopes, this indicator was equal to three tree species. A more successful renewal of arboral cenopopulations on slopes compared with flat areas is explained, in our opinion, by better illumination of the ground cover on the slopes due to lateral illumination and a pronounced mosaic of the stand and ground cover.

As can be seen from the graph (Fig. 6), the highest species richness (the number of plant species per 400 m^2) in all the studied coniferous-deciduous forests in the North-Western Caucasus was noted on the north and south slopes; the lowest richness was noted for the flat areas. At the same time, the indicators of species richness on the south and north slopes of the same forest type do not differ. The high species richness on the slopes compared to the flat areas in all the studied forest types can also be explained by better illumination on the slopes. Species richness largely depends on the forest types. The highest level is noted for beech-fir-hornbeam forests; the lowest level is noted for old-growth fir-hornbeam forests; the species richness in the aspen-hornbeam type of forest is medium. Beech-fir-hornbeam forests are noted the tree canopy decay – the trees of the first generation that appeared at the felling site gradually die off forming numerous gaps in the tree canopy and adding lighting to the ground cover and, as a result, facilitating the introduction of photophilous flora. Old-growth fir-beech forests lack ground cover due to strong shading. This adds illumination to the ground cover and, as a result, facilitates the introduction of photophilous flora. Old-growth fir-beech forests lack the ground cover due to strong shading.

The diagram (Fig. 7) shows vectors of environmental factors, the length and direction of which reflect the

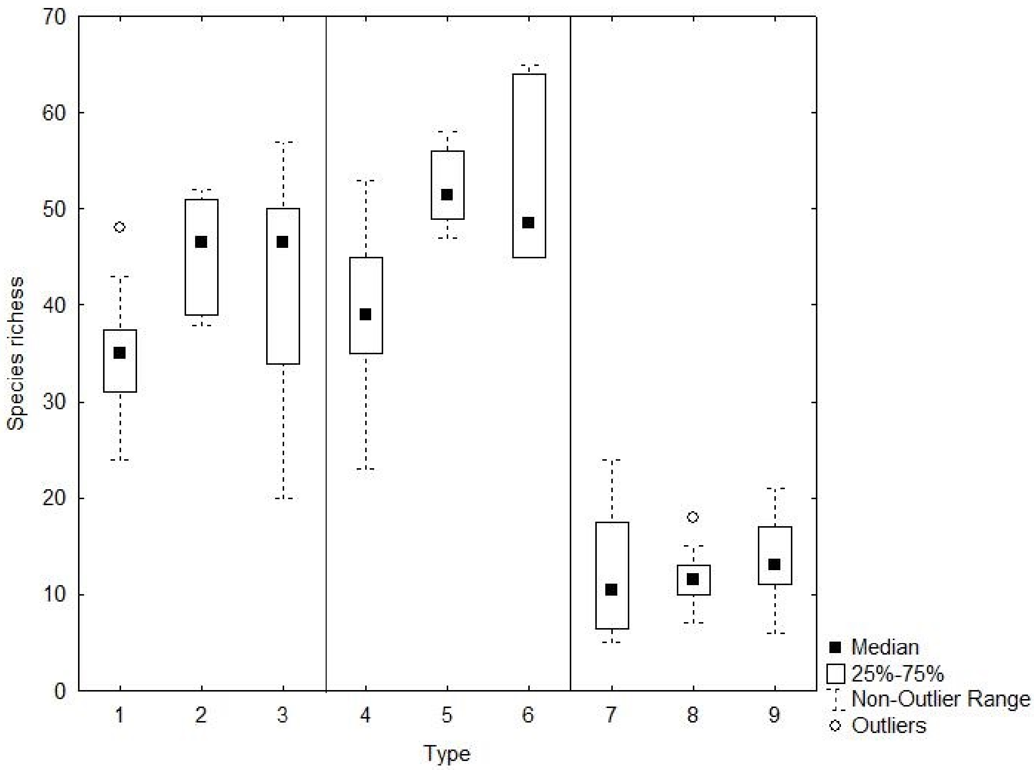

Figure 6. Species richness in the dominant coniferous-deciduous forest types in different relief elements (1–9 plant community numbers as in Figure 3)

correlation of these factors with the axes not being regression lines in the strict sense. The highest correlation with the first axis of DCA ($p<0.005$) is registered for light factor ($r=-0.96$), continentality ($r=-0.94$), soil alkalinity/acidity ($r=-0.78$), heat supply ($r=-0.77$), soil moisture ($r=0.74$) and soil humus ($r=0.71$) content without any significant strong correlation with the second axis. The third axis is correlated only with an indicator of soil nitrogen content ($r=-0.45$).

Multivariate analysis of the geobotanical communities' descriptions for the studied forest types was conducted according to the ecological scale of E. Landolt (Landolt, 1977) (Fig. 7). The results clearly showed that the descriptions for the flat areas of all three studied forest types have the greatest similarity. North and south slopes in old-growth fir-beech forests hardly differ from flat areas in terms of geobotanical descriptions and the ratio of ecological plant groups. This is due to the high canopy density and level of the tree layer (more than 50 meters); even the slopes lack ground cover. In old-growth fir-beech forests, the proportion of hygrophilous, shade-tolerant, and cold-resistant plant species growing on

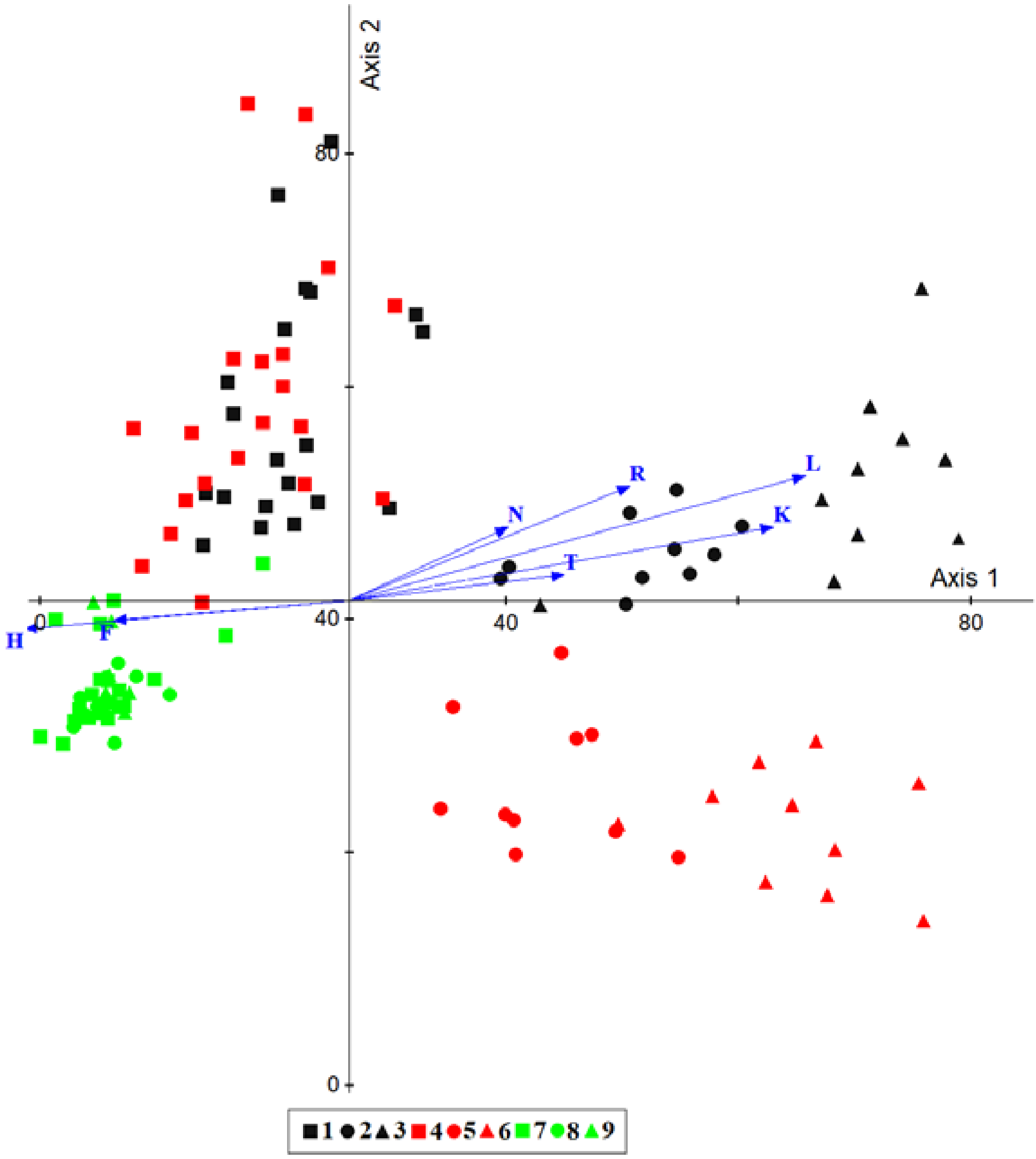

Figure 7. Apposition of the geobotanical descriptions of the studied communities in the first two axes of the DCA and the vectors of ecological factors (E. Landolt's ecological scale; 1–9 plant community numbers as in Figure 3)

Note: L – light factor; R – pH; F – soil moisture; N – nitrogen content; T – thermal factor; C – continentality; H – soil humus richness; K – Continentality.

well moisturized weakly acidic soil is higher than in aspen-hornbeam and beech-fir-hornbeam forests. North and south slopes of the aspen-hornbeam and beech-fir-hornbeam forests also have significant similarities and differ from the flat areas in terms of communities. On the north and south slopes of aspen-hornbeam and beech-fir-hornbeam forests, the proportion of photophilous, thermophilic, nitrophilic plant species growing on neutral soils is higher than in the flat areas. Thus, the multivariate analysis of geobotanical descriptions confirmed that on the north and south slopes, as compared to the flat areas, the illumination of the ground cover is better, since the proportion of photophilous plant species is much higher. In the ecological structure of slopes and flat areas (Fig. 8) of all the studied coniferous-deciduous forests in the North-Western Caucasus, the main core of the flora is composed of nemoral species (from 45% to 78% of all species); the second largest share belongs to boreal species (from 3% to 7%). On the slopes, in comparison with the flat areas, the proportion of meadow (from 3% to 5%) and nitrophilic (from 3% to 5%) species is higher. On the north slopes, in comparison with the south slopes, the proportion of boreal species is higher (from 5% to 7%); on the south slopes, the proportion of meadow-forest edge species is higher (from 4% to 7%). Only on the north slopes of all the studied forest types were found moisture-loving and near-water species such as *Agrostis gigantean* Roth, 1788, *Equisetum ramosissimum* Desf., 1799, *Galium uliginosum* Pall. ex M. Bieb., 1808, *Petasites hybridus* (L.) G.Gaertn., B.Mey. & Scherb., 1801, *Juncus effuses* L., 1753, *Cardamine tenera* S. Gmelin ex C. Meyer, 1831, *Ranunculus repens* L., 1753, etc., whereas pine forest species, such as *Dracocephalum ruyschiana* L., 1753, *Festuca ovina* L., 1753, *Hylotelephium maximum* (L.) Holub, 1979, *Pinus sylvestris* L., 1753, *Vaccinium vitis-idaea* L., 1753, etc., were found only on the south slopes. The presence of hygrophilous plant species on the north slopes and their absence on the south slopes and in the flat areas confirms the stronger humidification of the slopes due to low evapotranspiration. At the same time, the presence ecological groups of pine species on the south slopes in all the studied forest types is explained by dryness.

North and south slopes of all the studied forest types (Fig. 8) differ from the flat areas in terms of the number of ecological plant groups – we described four groups for flat areas of aspen-hornbeam and beech-fir-hornbeam forests and six for the north and south slopes each; for fir-beech forests we described only two groups for flat areas and four for each slope. Thus, on the north and south slopes, compared to flat areas of all the studied forest types, the number of ecological plant groups is higher due to the greater variability of ecological conditions.

The composition and structure of soil macrofauna, on the one hand, depends on the forest type, on the other hand,

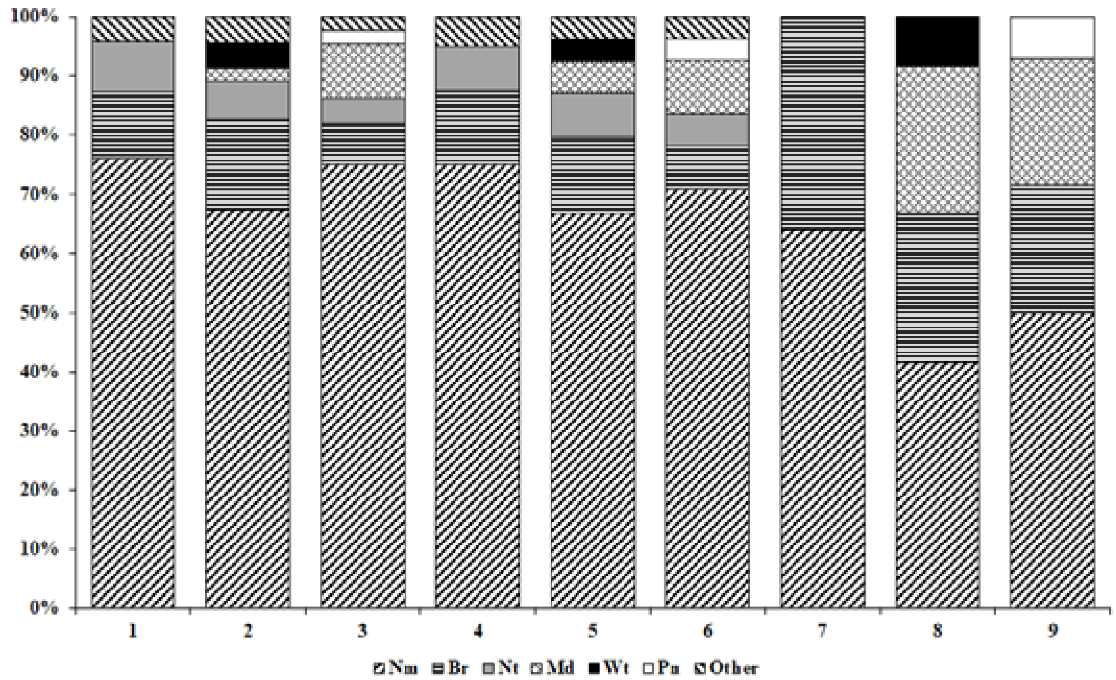

Figure 8. The ratio of ecological plant groups in communities of different forest types on the slopes and in the flat areas (1–9 plant community numbers as in Figure 3)

Note: Nm – nemoral; Br – boreal; Nt – nitrophilous; Md – meadow-forest edge; Wt – water-marsh; Pn – pine; Other – species of other ecological plant groups.

on the position of plant communities in the relief elements. The influence of forest type on the composition of soil macrofauna is largely realized through the quality of litter and the influence of environmental factors that also determine the composition of plant communities (Fig. 4). As in the case of geobotanical descriptions of plant communities, the most similar characteristics of the soil macrofauna population, i.e. total abundance, biomass of trophic groups, distribution of invertebrates over horizons (litter, soil), were obtained: 1. for flat areas of aspen-hornbeam and beech-fir-hornbeam forests 2. for north and south slopes of the aspen-hornbeam and beech-fir-hornbeam forests, and 3. for all communities of the fir-beech forests, regardless of the relief elements. Such connections with plant communities are determined by a similar effect of environmental factors on vegetation and soil fauna. The factors the most significant for soil animals are: humus (H) and soil moisture (F) contents, acidity/alkalinity (R), soil nitrogen content (N) and, for some species, heat supply (T). The combined influence of the properties of plant litter and abiotic factors determines the population of soil macrofauna (Fig. 4). It is known that the most favorable environment for the soil fauna, especially for the group of macrosaprophages, is mixed litter, i.e. the litter containing both rapidly and slowly decomposing fractions (Sariyildiz et al., 2008; Sariyildiz & Küçük, 2008; Kuznetsova et al., 2021). The plants producing slowly decomposing litter are characterized by a high content of secondary metabolites and a low content of nutrients. They facilitate the formation of a thick forest litter, since such litter is slowly processed by the soil biota. These plants include genera *Abies*, *Picea*, *Populus*, *Fagus*, *Quercus*, and boreal shrubs. The plants that produce high quality litter with a high content of nutrients and a low content of secondary metabolites, on the contrary, contribute to decomposition of plant residues by soil saprophages (Prescott et al., 2000; Huang et al., 2020). Such litter is formed by *Acer*, *Fraxinus*, *Tilia*, *Carpinus*, *Betula*, and nitrophilic herbs. The highest density and biomass of macrophages were found in beech-fir-hornbeam forests, in which a mixed litter is formed. This litter serves as a habitat and a trophic resource primarily for bipeds, woodlice, molluscs, and earthworms (Fig. 5). In aspen-hornbeam forests, litter is also formed from different fractions close to mixed forests in terms of properties. This contributes to the maintenance of the diversity and density of soil macrophages, which partly explains the similarity of these two forest types in the way they are inhabited by earthworms. In dead-cover fir-beech forests, despite the well-developed thick litter (Kuznetsova et al., 2021), the composition of litter fauna is poorer and less abundant than in other forest types, which is due to the almost complete absence of rapidly decomposing litter components. This determines the general characteristics of macrofauna composition in this forest type, regardless of the position in the relief. However, the high humus and soil moisture contents in these forests provide a high biomass of macrosaprophages (endogeic and anecic earthworms) in deeper soil horizons. At the same time, it can be assumed that the indicators of soil humus content and worm biomass are interdependent. Estimation of the biomass of macrosaprophage group is more important in mountain soils than on a plain, since this group is better at soil formation in extreme conditions (Pryke & Samways, 2010).

Populations of the soil macrofauna on the north and south slopes differ in all forest types. Colder and wetter north slopes are characterised by the maximum biomass of large litter and soil saprophages: earthworms, molluscs, and millipedes dominated by endemic and subendemic species of the North-Western Caucasus. Warmer and less humid south slopes are characterised by the highest densities of phytophages and predators, which are less dependent on the moisture and trophic properties of the substrate than the densities of large saprophages. At the same time, lower densities and biomass of saprophages on the south slopes are associated, on the one hand, with less favorable abiotic factors (temperature and humidity), on the other hand, with a higher density of predators that regulate through biotic interactions the composition of macrophages as well. The latters can act as the victims of the firsts. However, some studies show that such regularities are not always realized in one size group of soil fauna, because carnivorous species of soil macrofauna also feed on representatives of the mesofauna, the composition of which can also vary greatly in different communities (Rae et al., 2006).

5. Conclusion

It was found that in all the studied forest types, north and south slopes, in comparison with the flat areas, are characterized by significantly higher plant species richness. On slopes, in comparison with flat areas, the efficiency of renewal of arboral cenopopulations is higher: there is a greater number of tree species (by 20–70%); their density is higher (by 50–100%); the number of cenopopulations of tree species with a complete ontogenetic spectrum is larger. The number of ecological plant groups described for the north and south slopes is greater than for the flat areas. The proportion of boreal species is higher on the north slopes than on the south slopes, whereas the south slopes are characterised by a larger proportion of meadow-forest edge species.

The north and south slopes ensure the maintenance of the functional diversity of soil invertebrates, as well as the preservation of endemic fauna. The north slopes were revealed a high biomass of large epigeic and soil saprophages represented by species and groups playing an especially significant role in the transformation of plant litter and in soil formation. These species include millipedes and earthworms. The south slopes show high densities of phytophages and predators, which regulate the diversity of other components of forest communities through biotic interactions.

North and south slopes in all the studied forest types, in comparison with the flat areas, were characterised by higher species diversity of plant communities, more effective regeneration of arboral species, more diverse ecological plant groups, and wider range of endemic soil invertebrates, including soil formers. This confirms the need to protect these territories to preserve and maintain biological diversity of coniferous-deciduous forests in the North-Western Caucasus.

Acknowledgment

The work was carried out as part of an additional agreement to the state task of the CEPF RAS (registration number 123030300031-6) in accordance with the Decree of the Government of the Russian Federation dated September 2, 2022 No. 25–15 p for the implementation of the most important innovative project of national importance aimed at creation of a unified national monitoring system for climatically active substances.

References

Antyufeev V.V., 1978, Dinamika produktivnosti lugovo--stepnyh soobshchestv krymskoj yajly v svyazi s izmenchivost'yu solnechnoj radiacii [Productivity dynamics of meadow-steppe communities of the Crimean yayla in connection with the variability of solar radiation], [in:] Regularities in the development of the organic world. Nauka i tekhnika, Minsk, 5 pp.

Belonovskaya E.A., Grebenshchikov O.S., Davydova M.V., 1990, Biota ekosistem Bolshogo Kavkaza [Biota of ecosystems of the Greater Caucasus]. Nauka, Moscow, 221 pp.

Bennie J., Hill M., Baxter R. & Huntley B., 2006, Influence of slope and aspect on long-term vegetation change in British chalk grasslands. Journal of Ecology 94(2): 355–368.

Billings W.D. & Bliss L.C., 1959, An alpine snowbank environment and its effects on vegetation, plant development, and productivity. Ecology 40(3): 388–397.

Braun E.L., 1935, The vegetation of Pine Mountain, Kentucky: an analysis of the influence of soils and slope exposure as determined by geological structure. American Midland Naturalist 16(4): 517–565.

Butorina T.N., 1969, Tipy lesa Vostochnogo Sayana [Forest types of the Eastern Sayan], [in:] Proceedings of the fifth scientific conference at Tomsk University. TGU, Tomsk, 234 pp.

Davis A.J., Lawton J.H., Shorrocks B. & Jenkinson L.S., 1998, Individualistic species responses invalidate simple physiological models of community dynamics under global environmental change. Journal of Animal Ecology 67(4): 600–612.

Elagin I.N., 1976, Sezonnoe razvitie sosnovyh lesov [Seasonal development of pine forests]. Nauka, Novosibirsk, 230 pp.

Elagin I.N., 1980, Fenologiya lesov Krasnoyarskoj lesostepi [Phenology of Krasnoyarsk forest-steppe forests], [in:] Dynamics of forest biogeocenoses in Siberia. Nauka, Novosibirsk, 174 pp.

Evstigneev O.I. & Korotkov V.N., 2016, Pine Forest Succession on Sandy Ridges within Outwash Plain (Sandur) in Nerussa-Desna Polesie. Russian Journal of Ecosystem Ecology 1(3): 1–18.

Galen C. & Stanton M.L., 1995, Responses of snowbed plant species to changes in growing-season length. Ecology 75(5): 1546–1557.

Gavrilov V.P., 1961, Agroklimaticheskij spravochnik po Krasnodarskomu krayu [Agroclimatic guide to the Krasnodar Territory]. Knizhnoe izdatelstvo, Krasnodar, 466 pp.

Gilyarov M.S., 1975, Metody pochvenno-zoologicheskih issledovanij [Methods of soil and zoological research]. Nauka, Moscow, 304 pp.

Grebenshchikov O.S., Shanina A.A. & Belonovskaya E.A., 1990, Lesa krajnej zapadnoj chasti Bolshogo Kavkaza [Forests in the extreme western part of the Greater Caucasus], [in:] Biota of ecosystems of the Greater Caucasus, p. 63–84. Nauka, Moscow.

Grudzinskaya I.A, 1953, Shirokolistvennye lesa predgorij Severo-Zapadnogo Kavkaza [Broad-leaved forests in the foothills of the North-Western Caucasus], [in:] Broad-leaved forests in the North-Western Caucasus, p. 5–186. Izdatelstvo Akademii Nauk SSSR, Moscow,

Gulisashvili V.Z., Makhatadze L.B. & Prilipko L.I., 1975, Rastitelnost Kavkaza [Vegetation of the Caucasus]. Nauka, Moscow, 234 pp.

Gvozdetsky O.N., 1963, Kavkaz. Ocherki prirody [Caucasus. Essay on nature]. Geografgiz, Moscow, 264 pp.

Huang W., Gonzalez G. & Zou X., 2020, Earthworm abundance and functional group diversity regulate plant litter decay and soil organic carbon level: A global meta-analysis. Applied Soil Ecology 150: 1–15.

Isard S.A., 1986, Factor influencing soil moisture and plant community distribution on Niwot Ridge, Front Range, Colorado, USA. Arctic and Alpine Research 18: 83–96.

Kozhevnikova L.I., 1981, K fenologii stepnyh sklonov [Phenology of steppe slopes], [in:] Scientific notes of the Voronezh branch of the All-Union Botanical Society, p. 49–53. Publishing house of the Academy of Sciences of the USSR, Moscow.

Kutiel P., 1992, Slope aspect effect on soil and vegetation in the Mediterranean ecosystem. Israel Journal of Botany 41(4–6): 243–250.

Kuznetsova A.I., Geraskina A.P., Lukina N.V., Smirnov V.E., Tikhonova E.V., Shevchenko N.E., Gornov A.V., Ruchinskaya E.V. & Tebenkova D.N., 2021, Linking vegetation, soil carbon stocks, and earthworms in upland coniferous – broadleaf forests. Forests 12(9): Article 1179.

Landolt E., 1977, Ökologische Zeigerwerte zur Schweizer Flora [Ecological pointer values for Swiss flora]. Vol. 64. Veroff. Geobot. Inst. ETH, Zurich, 208 pp.

Landolt E., Bäumler B., Ehrhardt A., Hegg O., Klötzli F., Lämmler W., ... & Wohlgemuth T., 2010, Flora indicativa – Ökologische Zeigerwerte und biologische Kennzeichen zur Flora der Schweiz und der Alpen [Flora indicativa – ecological indicator values and biological characteristics for the flora of Switzerland and the Alps]. 2nd Edition. Bern, Haupt, 384 pp.

Likharev I.M. & Rammelmeyer E.U., 1952, Nazemnye molljuski fauny SSSR [Ground mollusks of the fauna of the USSR]. AS USSR, Moscow-Leningrad, 511 pp.

Lokshina I.E., 1969, Opredelitel dvuparnonogih mnogonozhek (Diplopoda) ravninnoj chasti Evropejskoj territorij SSSR [Key two-legged millipedes (Diplopoda) of the flat part of the European territory of the USSR]. Nauka, Moscow, 78 pp.

Makunina A.A., 1986, Fizicheskaya geografiya gornyh regionov SSSR [Physical geography of mountain regions of the USSR]. Izdatel'stvo MGU, Moscow, 166 pp.

Mamaev B.M., 1972, Opredelitel nasekomyh po lichinkam: posobie dlja uchitelej [Identifier of insects on larvae: a manual for teachers]. Prosveshhenie, Moscow, 400 pp.

Marcelo S. & Maxim S., 2001, Influence of slope aspect on Mediterranean woody formation: Comparison of semiarid and an arid site in Israel. Ecology Research 16: 335–345.

Metodicheskie podhody k ekologicheskoj ocenke lesnogo pokrova v bassejne maloj reki, 2010, [Methodological approaches to ecological assessment of forest cover in the small river basin] L.B. Zaugolnova & T.Yu. Braslavskaya (eds.), KMK, Moscow, 383 pp.

Mirkin B.M., Rosenberg G.S., & Naumova L.G., 1989, Slovar ponjatij i terminov sovremennoj fitocenologii [Dictionary of concepts and terms of modern phytocenology]. Nauka, Moscow, 223 pp.

Odum Yu., 1975, Osnovy ekologii [Fundamentals of Ecology]. Mir, Moscow, 738 pp.

Orlov A.Ya., 1951, Temnohvojnye lesa Severnogo Kavkaza [Dark coniferous forests of the North Caucasus]. Izdatelstvo Akademii Nauk USSR, Moscow, 256 pp.

Parma R. & Jouybari S.S., 2010, Impact of physiographic and human factors on crown cover and diversity of woody species in the Zagros forests (Case study: Ghalajeh forests, Kermanshah province). Iranian journal of Forest and Poplar Research 18(4): 539–555.

Pikin S.F., 2005, Gravitacionno-kineticheskaya model relefa [Gravitational-kinetic relief model]. SGU, Stavropol, 2005, 380 pp.

Pillar V.D.P., 1999, On the identification of optimal plant functional types. Journal of Vegetation Science 10(5): 631–640.

Prescott C.E., Zabek L.M., Staley C.L., & Kabzems R., 2000. Decomposition of broadleaf and needle litter in forests of British Columbia: influences of litter type, forest type, and litter mixtures. Canadian Journal of Forest Research 30: 1742–1750.

Pryke J.S. & Samways M.J., 2010, Significant variables for the conservation of mountain invertebrates. Journal of insect conservation 14 (3): 247–256.

Rabotnov T.A., 1950, Zhiznennyj cikl mnogoletnih travjanistyh rastenij v lugovyh cenozah [The life cycle of perennial herbaceous plants in meadow cenoses]. Trudy Botanicheskogo instituta AN SSSR. Series 3. Geobotany 6: 7–204.

Rae D.A., Armbruster W.S., Edwards M.E. & Svengård-Barre M., 2006, Influence of microclimate and species interactions on the composition of plant and invertebrate communities in alpine northern Norway. Acta Oecologica 29(3): 266–282.

Richter G.D., 1948, Rol snezhnogo pokrova v fizikogeograficheskom processe [The role of snow cover in the physical and geographical process]. Izdatelstvo Akademii Nauk USSR, Moscow, 245 pp.

Sariyildiz T. & Küçük M., 2008, Litter mass loss rates in deciduous and coniferous trees in Artvin, northeast Turkey: Relationships with litter quality, microclimate, and soil characteristics. Turkish Journal of Agriculture and Forestry 32(6): 547–559.

Sariyildiz T., 2008, Effects of tree canopy on litter decomposition rates of *Abies nordmanniana*, *Picea orientalis* and *Pinus sylvestris*. Scandinavian journal of forest research 23(4): 330–338.

Shcherbakov Yu.A., 1970, Iz opyta izucheniya roli ekspozicii v landshaftovedenii [Experience of studying the role of exposure in landscape science], [in:] Influence of exposure on landscapes. Izdatelstvo Akademii Nauk USSR, Moscow, 399 pp.

Shishov L.L., Tonkonogov V.D., Lebedev A.I. & Gerasimova M.I., 2004, Klassifikacija i diagnostika pochv Rossii

[Classification and diagnostics of Russian soils]. Ojkumena, Smolensk, 342 pp.

Smirnova O.V., 2004, Prirodnaja organizacija biogeocenoticheskogo pokrova lesnogo pojasa Vostochnoj Evropy [The natural organization of the biogeocenotic cover of the forest belt of Eastern Europe], [in:] O.V. Smirnova (ed.), Eastern European forests: history in the Holocene and modernity. Book 1, p. 16–50. Nauka, Moscow.

Smirnova O.V., Chistyakova A.A., Zaugolnova L.B., Evstigneev O.I., Popadiouk R.V. & Romanovsky A.M., 1999, Ontogeny of a tree. Botanical Journal 84(12): 8–20.

Smirnova O.V., Zaugolgova L.B., Khanina L.G., Bobrovsky M.V. & Toropova N.A., 2002, Populjacionnye i fitocenoticheskie metody analiza bioraznoobrazija rastitelnogo pokrova [Population and phytocenotic methods for the analysis of biodiversity of the plant cover], [in:] Conservation and restoration of biodiversity, p. 145–194. Izdatelstvo Nauchno-obrazovatelnogo Centra, Moscow.

Uranov A.A., 1975, Vozrastnoj spektr fitocenopopuljacij kak funkcija vremeni i jenergii volnovyh processov [Age spectrum of phytocenopopulations as a function of time and energy wave processes]. Biological Sciences 2: 7–34.

Vsevolodova-Perel T.S., 1997, Dozhdevye chervi fauny Rossii: kadastr i opredelitel [Earthworms of the fauna of Russia: Cadastre and determinant]. Nauka, Moscow, 101 pp.

Wang Y.F. & Cai Y.C., 1988, Studies on genesis, types and characteristics of the soils of the Xilin River basin. IMGERS, Research on Grassland Ecosystem 3: 23–83.

WRB, World reference base for soil resources, 2015, International soil classification system for naming soils and creating legends for soil maps. World Soil Resources Reports No. 106. FAO, Rome, 192 pp.

Zaugolnova L.B., Zhukova L.A., Komarov A.S. & Smirnova O.V., 1988, Cenopopuljacii rastenij (ocherki po populjacionnoj biologii) [Coenopopulations of plants (essays on population biology)]. Nauka, Moscow, 236 pp.

Zhang Y.Z., Zheng D. & Yang Q.Y., 2002, Physical geography in Tibet. Science press, Beijing, 178 pp.

World Flora Online, 2012, online version at http://www.worldfloraonline.org/ [Accessed: 14.06.2022)].