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Biodiversity of under-crown spaces and canopy gaps of forests of the Caucasian Biosphere Reserve (Russia, North-Western Caucasus)

Introduction

The concept of the mosaic-cyclical organisation of forest ecosystems emphasises the importance of the diversity of microsites, in maintaining the biological diversity of flora and fauna (Watt 1947, Oldeman 1983, Whitmore 1990). Currently, the mosaic of microsites is most pronounced in old-growth forests and is associated with the life and death of trees. Well-preserved old-growth forests include the forests of the Caucasian Biosphere Reserve, one of the largest mountain-forest reserves in Europe and the oldest reserves in Russia.

After the falling of old trees and the formation of breakthroughs in the forest canopy (canopy gap), there are cardinal changes in the light and rainfall regimes. Since vegetation is most sensitive to a change in the illumination regime, while both vegetation and soil fauna are more sensitive to a change in the moisture regime, a difference in the floristic and faunistic composition between the under-crown spaces and windows in old-growth forests can be expected.

The aim of this work is to assess the diversity of vegetation and soil macrofauna in two types of microsites of old-growth forests: under-crown spaces and canopy gaps.

Materials and methods

The studies were carried out in the upper reaches of the Belaya River (Russia, Republic of Adygea) on the territory of the Caucasian Biosphere Reserve (Location Guzeripl) (fig. 1).

The Caucasian Reserve was created in 1924 in the south of the Krasnodar Territory. In fact, the time of establishment of the protected status of this territory should actually be attributed to 1886 – the time of the organisation of the Imperial "Kuban Hunt" in the upper reaches of the Belaya and Laba rivers. In 1979, the Caucasian Reserve received the status of a Biosphere Reserve and entered the International Network of Biosphere Reserves. In 1999, the Caucasian Biosphere Reserve was included in the list of UNESCO World Heritage Sites. The modern territory of the reserve is about 300,000 hectares, with more than half of the area being covered by forests (Litvinskaya 2013).

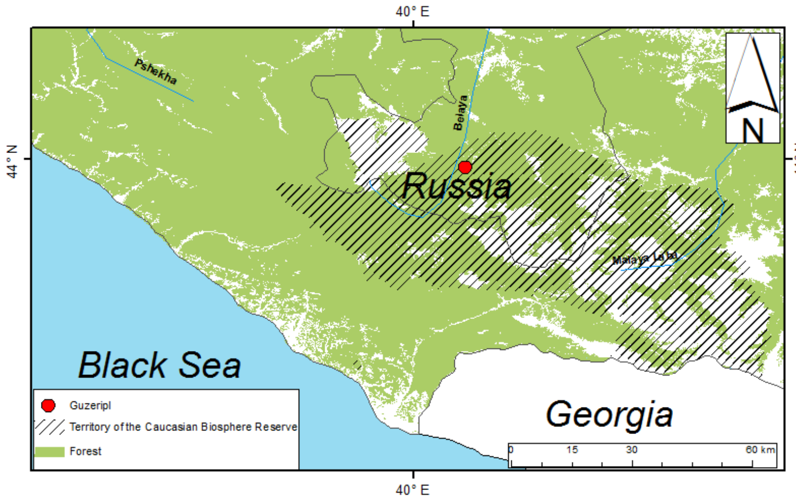

Fig. 1. Map of the Caucasian Biosphere Reserve. Location point Guzeripl – research region

This territory is part of the Western mountain province of the Greater Caucasus (Gvozdetsky 1963, Milkov and Gvozdetsky 1986). The average annual precipitation is 1.200 mm and the average annual temperature is +10.3 °C. Positive air temperatures remain for 292–361 days, and the growth season (T > 10 °C) is 160–234 days (http://meteo.ru). The relief is a complex mountainous terrain. Schist eluvia-based brown soils (Cambisols Dystric, *WRB*… 2015) are common in the soil cover. The thickness of the humus horizon is on average 10–15 cm, the humus content in the upper horizon can reach 10–15% and the pH is acidic or slightly acidic (Shishov et al. 2004). The dominant forest type was chosen as the object of research: this was fir-beech forests, in which under-crown spaces and canopy gaps were examined (fig. 2).

The studies were carried out in the summer seasons of 2016 and 2019. The work included geobotanical, population-ontogenetic and soil-zoological methods.

Geobotanical methods

Square plots of 400 square meters were laid out for plant community description. In each forest type there were 37 geobotanical descriptions in the under-crown area, and 10 descriptions in the canopy gaps. A complete floral list, taking into account the layered structure of vegetation, was made up for each plot. In each layer, the projective cover of species was defined according to the scale of Braun-Blanquet (1964, cited by: Mirkin et al. 1989). The communities' species diversity was evaluated through the indicators of species richness and species saturation (Smirnova et al. 2002).

Fig. 2. Under-crown areas (1–3) and canopy gaps (4–6) of fir-beech forest of the Northwest Caucasus (Caucasian Biosphere Reserve) (photo: N. Shevchenko)

Population-ontogenetic methods

The periodisation of ontogenesis proposed by T.A. Rabotnov (1950) and supplemented by A.A. Uranov (Uranov 1975) and his students (Zaugolnova et al. 1988) is used. The following states are distinguished in the tree ontogenesis: juvenile (j); immature (im); virginal (v); young generative (g1); mature generative (g2); old generative (g3) and senile (s) (Smirnova et. al. 1999, Evstigneev and Korotkov 2016). The composition of tree cenopopulations was determined in under-crown areas and gaps. This type of ontogenetic spectrum was established according to the classification proposed by T.A. Rabotnov (1950), later supplemented and detailed (Uranov and Smirnova 1969, Zaugolnova et al. 1988). The paper is using the classification of the ecological-coenotic groups of vascular plant species developed for European Russia (Smirnova et al. 2002, 2004, 2017).

Soil-zoological methods

Quantitative calculations of soil macrofauna were carried out in gaps and under-crown areas. Records of litter and soil were made by excavation and manual analysis of soil samples (Gilyarov 1975). Invertebrates were fixed in 70–80% ethanol. The size of each separate sample was 25 x 25 cm, with a depth up to 30 cm. 54 soil samples were taken in the under-crown spaces (18 under fir crowns and 18 under beech crowns) and 18 samples in canopy gaps. Invertebrates were fixed in 70% alcohol. Insects, mollusks, crustaceans, and millipedes were identified up to supraspecific taxa (using field guides (Likharev and Rammelmeyer 1952, Lokshina 1969, Mamaev 1972). Earthworm species were identified with field guides (Vsevolodova-Perel 1997).

Results

Under-crown spaces

The stand is only codominated by *Fagus orientalis* Lipsky [nomenclature after *World Flora Online*: A*n Online Flora of All Known Plant*s http://www.worldfloraonline.org] and *Abies nordmanniana* (Steven) Spach, *Acer platanoides* L. and *Carpinus betulus* L. are found as admixtures. The upper sub-layer of the stand is represented exclusively by *F. orientalis*, while the lower sub-layer is represented by *A. nordmanniana* with a small admixture of *F. orientalis*. The projective cover of the stand is 90–95%. The undergrowth layer is dominated by *A. nordmanniana* and *F. orientalis*. *Ribes petraeum* Wulfen, *Ilex colchica* Poljark. and *Rhododendron ponticum* L. are found as singular trees. The projective cover of the layer ranges from 5–20%. The herb-dwarf shrub layer is a dead-soil layer, with a projective cover of 5–7%. Common species are *A. nordmanniana*, *A. platanoides*, and *F. orientalis*. Singular plants of *Cephalanthera rubra* (L.) Rich., *Dryopteris filix-mas* L. Schott, *Fraxinus excelsior* L., *Moehringia trinervia* (L.) Clairv. *Monotropa hypopitys* L., *Neottia nidus-avis* (L.) Rich. and *Tilia bigoniifolia* Steven are found. The species richness of vascular plants is about 15 species. The moss layer is localised on elevations near tree trunks, on tree trunks, in deadwood and in soil. The projective cover is 5–12%. Common species are *Isothecium alopecuroides* (Lam. ex Dubois) Isov., *Neckera complanata* (Hedw.) Huebener, *Eurhynchium angustirete* (Broth.) T.J. Kop., *Hypnum cupressiforme* Hedw., *Leucodon sciuroides* (Hedw.) Schwägr. and *Ulota crispa* (Hedw.) Brid. In total, 17 species of mosses are described in the under-crown space.

Only the cenopopulation of *A. nordmanniana* has the full ontogenetic spectrum in the under-crown area of the fir-beech forest. The cenopopulation of *F. orientalis* has an intermittent spectrum with no virginal individuals. The intermittent spectrum was also observed for the *C. betulus* cenopopulation. Plants of this species with reduced vitality are found very rarely on the area of former gaps. Due to its high growth rate, hornbeam quickly occupies vacant areas. The invasive type is observed in *A. platanoides* and *T. begoniifolia*, while cenopopulations of *F. excelsior*, *Fraxinus pennsylvanica* Marshall, *Prunus avium* (L.) L., and *Populus tremula* L. have the fragmentary type of spectrum. The undergrowth of the above species dies early due to the lack of light. In the under-crown space of fir-beech forests, plants of only two ecological-cenotic groups grow: nemoral and boreal species.

Representatives of 15 families and orders were found in the soil macrofauna in the under-crown spaces. Among the trophic groups, saprophages prevail, the number of which is more than half of the total number and 94% of the total biomass. In the under-crown spaces of fir, the abundance and biomass of invertebrates is significantly higher (46±6 ind./m^2; 6.0±0.3 g/m^2) than under the crowns of beech (30±4 ind./m^2 and 5.0±0.8 g/m^2). In the under-crown spaces of fir in the litter, typical inhabitants are the larvae and adults of click beetles, millipedes, multiped, earwigs (fam. Forficulidae), while in soil, typical inhabitants include predatory millipedes (orders Scolopendrida, Lithobiomorpha, Geophilomorpha) and earthworms (endogeic *Dendrobaena schmidti* and anecic *D. mariupoliensis*). In the under-crown areas of beech, imago of snapping beetles (*Agriotes sputator*) and drupes (Lithobiomorpha) are numerous in litter, while in soil earthworms (*D. schmidti* and *D. mariupoliensis*) were more numerous.

Canopy gaps

Canopy gaps are formed as a result of the natural death of old *F. orientalis* trees in the upper sub-layer (trees 40–60 meters high). 80% of gaps in the fir-beech type of forest were formed as a result of breakage of old beech tree trunks at a height of more than 1 meter, rather than of treefall. During the fall of old trees of the upper sub-layer, *F. orientalis* and *A. nordmanniana* trees of the lower sub-layer are usually the ones that tend to break. The size of gaps in old-aged fir-beech forests ranges from 320 to 380 m^2. Gaps are 10 to 20 years old.

A. nordmanniana and *F. orientalis* codominate along the periphery of gaps in the tree stand. Early-generative *C. betulus* and *F. excelsior* trees are rarely found as an admixture. The projective cover of the layer is 5–15%. The undergrowth is dominated by young *F. orientalis* and *A. nordmanniana*. The admixture contains *C. betulus*, *P. avium*, *Sambucus ebulus* L., *Sambucus nigra* L., *T. begoniifolia*, *F. excelsior* and *Philadelphus coronaries* L. The projective cover of the layer is 30–60%. The herb-dwarf shrub layer is unevenly developed, with the projective cover ranging from 20–100%. *A. nordmanniana*, *A. platanoides*, *Athyrium filix-femina* (L.) Roth, *C. betulus*, *Circaea lutetiana* L., *D. filix-mas*, *F. orientalis*, *Fragaria vesca* L., *F. excelsior*, *Prunus laurocerasus* L., *Rubus caesius* L., *T. begoniifolia*, and *Viola mirabilis* L. are common. *R. caesius* and the undergrowth of *A. nordmanniana*, *A. platanoides*, *C. betulus* and *F. orientalis* often dominate. The species richness of vascular plants is more than 30 species. Moss is developed sporadically on elevations near tree trunks, on deadwood and mounds. The maximum number of moss species was described in the gaps of the fir-beech forest type and was estimated at 33 species. Typical species are *Brachythecium* *rutabulum* (Hedw.) Schimp., *E. angustirete*, *H. cupressiforme*, *I. alopecuroides*, *L. sciuroides*, *N. complanata*, *Pterigynandrum filiforme* Hedw. and *U. crispa*.

Cenopopulations of *A. nordmanniana*, *Acer campester*, *C. betulus*, *F. orientalis, F. excelsior* and *T. begoniifolia* have the full ontogenetic spectrum in the gaps. The invasive type of spectrum was described for *A. pseudoplatanus*, *Quercus hartwissiana* Steven, *P. lauroceracus*, and *Salix caprea*; the intermittent type – for *A. platanoides* and *P. avium* and fragmented for *P. tremula.* Thus, in the gaps, successful forest restoration takes place at the expense of shade-tolerant tree species. 7 ecological-cenotic groups of plants (boreal, meadow-edge, nemoral, nitrophilous, water-marsh, piny and rocky species) are growing in the canopy gaps.

The macrofauna in the gaps of the beech-fir forest includes 14 taxa (orders and families). The total number (40±6 ind./m^2) does not differ significantly from the under-crown areas, but the biomass (25±4 g/m^2) is 2.5 times higher in comparison with the under-crown areas, due to the biomass of soil saprophages (23±3 g/m^2). The density of predators, phytophages and mixophages is low (5–18 ind./m^2). The most common soil predators are drupes (order Lithobiomorpha) – other representatives are low. It is of interest that water-loving invertebrates, not only earthworms, mollusks and larvae of dipterans, but also larvae of caddisflies (order Trichoptera), inhabit this area, which serves as an indicator of high soil moisture in the studied forest gaps.

Discussion

Fir-beech forests of the Caucasian Biosphere Reserve are characterised by the absence of traces of logging or fire (no coal was found in soil) and the tree layer having a complex spatial structure, represented by trees of different ages. This type of forest was described on the territory of the Caucasian Biosphere Reserve, which has preserved well since the end of the 18th century; the remaining local forests are the closest to natural ones. We assume that this type of forest represents the terminal stage of development of coniferous and broad-leaved forests of the Northwest Caucasus. The age of individual fir trees exceeds 450 years; the height of the tree canopy reaches 50±12.1 m. The average stock of stem wood is 1.097±265 m^3/ha, with *F. orientalis* accounting for 66–82% of the total stock of stem wood and *A. nordmanniana* accounting for 16–32% (Lukina et al. 2018).

In the gaps, the species density of vascular plants is more than two times higher than in under-crown communities, which is explained by good illumination and high soil moisture, as the stand does not intercept precipitation. These two factors are usually listed as determinants for a significant increase in the species richness of plants in gaps, in comparison with under-crown areas

(Denslow and Spies 1990). The density of tree undergrowth of different species in the gaps is more than 10 times higher than in under-crown areas. The significant role of gaps in the successful regeneration of tree species was noted in oak-pine forests in the United States (Schumann et al. 2003), beech-dominated forests in Denmark (Ritter et al. 2005), beech forests of Iran (Haghverdi et al. 2012) and in tropical forests of Costa Rica, where experimental felling with the creation of gaps resulted in the successful development of undergrowth, especially that of light-loving species (Dupuy and Chardon 2008).

It is important to note that a group of semi-aquatic plant species is represented only in the gaps. The formation of puddles that that maintain (do not dry out) for a substantial time are often observed in the gaps, and as a result, stagnant moisture is formed. As part of the flora in the windows, the semi-aquatic species *Alisma plantago-aquatica* L., *Juncus effusus* L., *Cardamine tenera* S.G. Gmel. ex C.A. Mey., *Galeopsis tetrahit* L., *Ranunculus repens* L., and even the larvae of caddisflies (order Trichoptera), were found in the soil macrofauna. The composition of the ecological-cenotic groups of plants in the gaps is more then three times higher than in the under-crown spaces, which is associated with the strong shading of the ground cover by the tree canopy and the formation of dead-cover oligodominant forest communities.

In the gaps, in contrast to the floristic diversity, the taxonomic diversity of the macrofauna as a whole, does not differ from the under-crown spaces. At the same time, there are differences in the biomass of functional groups: gaps are important elements of the forest mosaic for the functioning of saprophages, first of all earthworms, which ensure the processing of plant litter. Only the gaps have a high biomass of anecic earthworms – which are important ecosystem engineers, not often found in forest communities, but are instead found in old-growth intact forests (Geraskina 2019). Studies of the effect of tree canopy gaps on the distribution of earthworms in the beech forests of Iran (Kooch and Hosseini 2010, 2014) have shown that the density and biomass of earthworms is lower in gaps than under tree canopies. The authors attribute this fact to the faster drying of the soil in gaps in comparison to a closed canopy space. In our studies, opposite results were obtained. This is most likely due to the fact that in the climatic conditions of Iran, most of the precipitation falls in autumn (Kooch and Haghverdi 2014), while the total amount of precipitation during the year is 1.7 times lower (720 mm annual rainfall) than in the forests of the Caucasian Reserve. In the forests we studied, the maximum precipitation occurs from May to July, during the period of optimum temperature for the activity of soil fauna, while there are no sharp fluctuations into seasons and the total amount of precipitation is at least 1 200 mm annual rainfall. More uniform levels of moisture creates favorable conditions for moisture-loving groups of flora and fauna in the canopy gaps, in comparison with closed under-crown spaces.

Conclusion

This study has demonstrated that in the canopy gaps of fir-beech forests of the forests of the Caucasian Biosphere Reserve, the species saturation of plants is more than two times higher than in the under-crown spaces, due to good illumination and high soil moisture - the forest stand does not intercept atmospheric precipitation. The renewal of tree cenopopulations is much more efficient in gaps in comparison with under-crown spaces. The density of undergrowth of different types of trees in the gaps is more than 10 times higher than in the under-crown spaces. In the gaps, more than three times ecological-cenotic groups of plants were recorded than in the under-crown spaces. In both gaps and under-crown spaces, all the main trophic groups of macrofauna are inhabitant, however their biomass is significantly higher in gaps than in under-crown spaces. Due to the fact that the moisture supply of the soil is also an important factor for the functioning of the macrofauna (especially for the moisture-loving saprophages), in the gaps the biomass of saprophages is on average 2 times higher than in the under-crown spaces. Only the gaps have a high biomass of anecic earthworms, which are very rare in modern forest communities.

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Summary

This research was carried out in the beech-fir forests of the Caucasian Biosphere Reserve, where unique old-growth forests have survived without traces of felling and fires, having been under protection since the end of the 18th century. The aim of this work is to assess the diversity of vegetation and soil macrofauna in two types of microsites of old-growth forests: under-crown spaces and canopy gaps. The research involves geobotanical, population-ontogenetic and soil-zoological methods. It has been well established that in the canopy gaps, due to good illumination and high soil moisture, the species density of plants is more than two times higher than in the under-crown spaces. Also, in comparison with the under-crown spaces, the renewal of tree cenopopulations occurs much more efficiently in the canopy gaps: in the gaps, the density of undergrowth of different types of trees is more than 10 times higher than in the under-crown spaces. In addition, 7 ecological cenotic groups of plants were noted in the canopy gaps, and only 2 groups in the under-crown spaces. With regard to soil macrofauna, the taxonomic and functional diversity of under-crown spaces and gaps is generally comparable, however, the biomass of invertebrates is 2.5 times higher in gaps than in under-crown spaces. In this case, the main contribution to the biomass is made by hygrophilous saprophages, among which earthworms predominate. Only the canopy gaps have a high biomass of anecic earthworms – these are important ecosystem engineers which are rarely found in modern forests.

Key words: Caucasian Biosphere Reserve, Caucasus, species richness, invertebrates, soil fauna, vegetation, forest community

Bioróżnorodność pod koronami drzew i w lukach drzewostanu w lasach Kaukaskiego Rezerwatu Biosfery (Rosja, zachodni Kaukaz)

Streszczenie

Badania przeprowadzono na terenie Kaukaskiego Rezerwatu Biosfery, w unikalnym lesie ze starym drzewostanem bukowo-jodłowym, który, jako obiekt chroniony od końca XVIII wieku, przetrwał do dziś bez wyrębów, wiatrowałów i pożarów. Celem badań była ocena różnorodności gatunkowej roślinności i makrofauny glebowej tego lasu w dwóch typach mikrosiedlisk – pod koronami drzewostanu i w lukach koron drzew. W badaniach stosowano metody z zakresu geobotaniki, zoologii i ekologii populacyjnej. Przeprowadzone analizy wykazały, że w lukach koron drzew, ze względu na dobre warunki świetlne i wysoką wilgotność gleby, liczba gatunków roślin jest ponad dwa razy większa niż pod okapem drzewostanu. Ponadto w lukach, w porównaniu do powierzchni pod koronami, odnowienie cenopopulacji drzew zachodzi bardziej intensywnie. Zagęszczenie podrostu jest tu bowiem ponad 10 razy większe, niż pod koronami drzew. Znaczne różnice zaznaczają się też w liczbie ekologicznych grup gatunków roślin występujących na obu porównywanych siedliskach. Na powierzchniach pod lukami koron wyróżniono 7 grup ekologicznych, podczas gdy pod koronami drzew tylko 2 grupy. W odniesieniu do różnorodności taksonomicznej i funkcjonalnej makrofauny glebowej, mierzonej liczbą gatunków i liczbą ich grup ekologicznych, wyniki badań uzyskanych dla obydwu mikrosiedlisk różnią się nieznacznie. Większe różnice dotyczą jednakże stanów biomasy. Stwierdzono, że biomasa bezkręgowców w lukach jest 2,5 razy większa niż pod koronami drzew. Największy udział w biomasie bezkręgowców glebowych pod okapem drzewostanu mają higrofilne saprofagi, wśród których dominują dżdżownice. Ponadto biomasa bezkręgowców tych mikrosiedlisk charakteryzuje się wysokim udziałem dżdżownic anecicznych – ważnych "inżynierów" ekosystemu, rzadko znajdowanych we współczesnych lasach.

Słowa kluczowe: Kaukaski Rezerwat Biosfery, Kaukaz, gleba, bogactwo gatunkowe, bezkręgowce, fauna glebowa, roślinność, zbiorowisko leśne

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