RESEARCH PAPER

PATTERNS OF THE RED-LISTED EPIPHYTIC SPECIES DISTRIBUTION IN CONIFEROUS-DECIDUOUS FORESTS OF THE MOSCOW REGION

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Received: May 27th, 2022 / Accepted: February 15th, 2023 / Published: March 31st, 2023
https://DOI-10.24057/2071-9388-2022-101

ABSTRACT. Epiphytes model the diversity of forest communities and indicate the integrity of natural ecosystems or the threat to their existence. The high sensitivity of epiphytic species to the environmental quality makes them good indicators in anthropogenic landscapes. The study deals with the distribution patterns of rare indicator epiphytic species at the border of their range in the broad-leaved–coniferous forest zone, in the central part of the East European Plain within the Moscow region. The distribution and abundance of eight lichen species *Anaptychia ciliaris, Bryoria fuscescens, B. implexa, Usnea dasopoga, U. glabrescens, U. hirta, U. subfloridana* and the epiphytic moss *Neckera pennata* were studied. The main environmental factors at the regional level were climate variables based on the Worldclim database, water indices based on Sentinel-2 multispectral remote sensing data, and the anthropogenic impact factor in terms of the Nighttime lights of the earth's surface based on the Suomi NPP satellite system. It was revealed that the vast majority of records were in the western and northern sectors of the region, i.e. in the broad-leaved–coniferous forest zone, while the vast majority of 0-records were in the southern and eastern sectors, in the area of broad-leaved and pine forests and extensive reclaimed wetlands. The association with different types of communities and biotopes, as well as tree species, was assessed at the ecosystem level, using field data. It has been established that the distribution of the studied species is governed by natural-geographic features of the territory. The principal limiting factors are air pollution, ecological restrictions (high humidity requirement of sites), cutting of mature forests and formation of local anthropogenic infrastructure. In perspective the study of ecology and living conditions of the studied rare species will help determine the optimal conditions contributing to biodiversity conservation in forests near large metropolitan areas and optimization of habitat diversity.

KEYWORDS: the red-listed epiphytic, forests, bioindicators, climate, anthropogenic impact, community ecology, biotope, urbanized landscapes, Moscow region

CITATION: Chernenkova T. V., Belyaeva N. G., Suslova E. G., Aristarkhova E. A., Kotlov I. P. (2023). Patterns of the red-listed epiphytic species distribution in coniferous-deciduous forests of the Moscow Region. Geography, Environment, Sustainability, 1(16), 119-131
https://DOI-10.24057/2071-9388-2022-101

ACKNOWLEDGEMENTS: The authors would like to thank the non-commercial Verkhovye Conservation Fund (www.verhovye.ru) for organizing field surveys and providing materials; and T.Yu.Tolpysheva, E.E. Muchnik, and I.N. Urbanavichene for identifying species of epiphytic lichens.

Conflict of interests: The authors reported no potential conflict of interest.

INTRODUCTION

The long-term transformation of forest cover is accompanied by a wide range of disturbances at the ecosystem and species levels of organization. Biodiversity change occurs mainly due to the reduction in the area and quality of sites, forest silviculture, decreasing number of native species, and introduction of alien species (Maron and Marler 2008; Aerts and Honnay 2011; Jönsson et al. 2011; Vilà et al. 2011; Lanta et al. 2013; "The Problem of Biodiversity Loss | Saving Earth | Encyclopedia Britannica," n.d.; "Threats to Biodiversity | GEOG 30N: Environment and Society in a Changing World," n.d.). The absence or declining numbers of rare organisms in suitable biotopes is a first sign of disturbance of native ecosystems (Barkman 1969; Case 1980; Folkeson and Andersson-Bringmark 1988; Hauck et al. 2013; Blackburn et al. 2019) indicating a certain threat to the integrity and the very existence of natural ecosystems (Hanski and Ovaskainen 2000).

For the forest community as a whole, the presence of epiphytic lichen and moss cover is very important, providing and maintaining biodiversity and «fullness» of the ecosystem. First of all, they indicate satisfactory air quality; then, their presence indicates the complexity and diversity of forest communities; and finally, such epiphytes fulfill certain ecosystem functions (Pettersson et al. 1995; Antoine 2004; Gunnarsson et al. 2004; Glime 2007).

Traditionally, many species of epiphytic mosses and lichens are considered as objects of indication and monitoring of air quality (Barkman 1969; LeBlanc et al. 1974; Scott and Hutchinson 1990; Byazrov 1994; Chernenkova 2002). More than half a century ago, it was noted that along with the higher pollution levels, the factor of drying, or aridization, could also increase the death of lichens and mosses in a large city (LeBlanc and Sloover 1970). The fact is that lichens and bryophytes are unable to regulate their water status by themselves with the help of a specialized system, available in vascular plants. Instead, they respond directly to environmental conditions, saturating their thalli or tissues with water when it is available, losing it also very quickly, and withstanding desiccation during dry periods. It is this flexibility to adapt to rapid environmental changes that makes such organisms well suited to epiphytic lifestyles (Kranner et al. 2008; Ellis et al. 2015). However, under high temperature and low air humidity, most lichen species seize their physiological activity. This happens at 20% or less saturation of the lichen thallus with moisture (Hawksworth and Rose 1970). Mosses are even worse adapted to droughts than lichens. The study of a wider range of distribution features of cryptogamic organisms makes it possible to assess the level of air pollution, as well as to identify the limiting ecological-coenotic conditions of the habitat, including the ecological state of forests, or inadequate forest management (Johansson and Gustafsson 2001; Boudreault et al. 2008).

Particular environmental features manifest themselves at different hierarchical levels, with dissimilar influence of physiographic (upper level) and biotopic (lower level) factors (Ellis and Coppins 2009; Ellis et al. 2015). For example, the most species of epiphytic lichens and bryophytes are recorded in the northern Holarctic and just sporadically to the south, along the large swamps on the Russian Plain, thereby indicating their obvious relationship with climatic parameters (Ignatov 1993; Shafigullina 2012). There is some evidence that a number of epiphytic lichens tend to open habitats (Halonen and Puolasmaa 1995; Suslova et al. 2017). At the same time, *Bryoria nadvornikiana* grows more slowly in the forests of Quebec under habitat openness of more than 40%, and for *Evernia mesomorpha* it happens under more than 70% openness (Boudreault et al. 2013). Studies of broad-leaved forests in the northwestern part of Germany found that the number of epiphytic lichens has significantly decreased over 100–150 years due to smaller numbers of over-mature and decay trees, lesser soil moisture, as well as deposition of sulfur and nitrogen compounds from the atmosphere (Hauck et al. 2013). The fact that some lichens give preference to certain tree species is also widely reported in the literature (Wirth 1995; Golubkova 1996a 1996b; Tolpysheva and Suslova 2019). Moreover, some species of epiphytes are thought to depend on microbiological habitats that are uniquely associated with the properties of the bark of old trees in late successional forests (Ellis 2012; Ellis et al. 2015; Notov and Zhukova 2015; Llewellyn et al. 2020). *Bryoria capillaris* in the UK (Rose 1976) and *B. nadvornikiana* in Sweden (Karström 1992) are thought to be indicators of mature indigenous forests. The presence of the rare lichens definitely proves the maturity of the stands and favorable environmental conditions for their growth.

An inventory of rare epiphytic cryptogamic organisms makes it possible to find out that the distribution of these organisms is closely associated with the remaining undisturbed forests, including those within the protected areas. This is particularly important for the natural environment of the Moscow region, in terms of the preservation of species and coenotic diversity of forest cover. The Red Data Book of the Moscow Region (2018) (*Red Data Book of the Moscow Region 2018*) includes 25 moss species and 40 rare lichen species out of 334 and 355 species, respectively, which were recorded in the region during the period of its study since the early 19th century. However, just few of them are characteristic of the least disturbed mature coniferous stands of the zonal type, as well as swamps and the margins of wetlands and peatlands. A number of studies deal with the distribution of certain species of epiphytic lichens and mosses in the Moscow region (Suslova et al. 2017; Tolpysheva et al. 2017; Tolpysheva and Suslova 2019); however, their ecological conditions have not been identified in full, and the patterns and factors of their distribution are not statistically confirmed.

The purpose of the study was to establish patterns of distribution of the red-listed epiphytic species on the southern border of the coniferous-deciduous forest zone in the East European Plain as in the case of the Moscow region. The following tasks were completed: 1) collection of data on the distribution and abundance of rare epiphytic forest species; 2) study of the influence of the principal environmental factors (climatic, coenotic, biotopic), explaining the variability in the distribution of species at different spatial levels; 3) assessment of the contribution of anthropogenic factor to the distribution patterns of the studied rare species; 4) identification of the preferability of the studied species in the indication of suitable habitats within an anthropogenic landscape.

MATERIALS AND METHODS

Study area

The Moscow region is a territory in the central part of the East European Plain with an area of 4.58 million hectares (Fig. 1). After the expansion of administrative boundaries in 2012, Moscow has moved from 11th to 6th place in the ranking of the world's largest cities in terms of the area, and the pressure on the region has increased significantly because of the transport infrastructure and construction. The diversity of forest cover in the study area has been formed over the past 100–150 years mainly through spontaneous natural succession within former arable lands or forest cuttings, as well as a result of pine and spruce planting. Silviculture has partially changed the ecological and coenotic features of zonal coniferous and broad-leaved-coniferous communities and the boundaries of their range.

The main part of the Moscow region is located within the zone of coniferous-deciduous forests; a border with the zone of deciduous forests goes through the south of the region (Petrov 1968; Kurnaev 1973). Despite the relatively high forest cover percentage (above 50%), the present-day forest cover is very mosaic and includes a large area of secondary forests with small-leaved species; most of the latter arose from forest plantations (Chernenkova et al. 2019). However, broad-leaved–coniferous, nemoral spruce, subnemoral and boreal forests, as well as broad-leaved forests close to natural zonal ones, have been preserved on the territory due to the protection status of forests. Spruce *(Picea abies)*, pine (*Pinus sylvestris*), birch (*Betula* spp.), aspen (*Populus tremula*), oak (*Quercus robur*), and linden (*Tilia cordata*) are the principal tree species in the forests near Moscow.

According to the schematic map of climatic provinces and regions of Europe, the Moscow region is classified as a temperate continental region (Rivas-Martínez et al. 2004). The mean annual air temperature is 2.7°-3.8° C, the annual precipitation is 479–644 mm. The relief of the territory is in general gently hilly, the heights vary slightly from 90 to 320 m a.s.l., on average 174 m a.s.l., the mean slope is 2.06° (0 to 30.9°). Variations of the main climatic characteristics within the physiographic provinces (PgP) of the Moscow region: 1 – Verkhnevolzhskaya, 2 – Moskovskaya, 3 – Smolenskaya, 4 – Moskvoretsko-Okskaya, 5 – Mescherskaya, 6 – Zaokskaya and 7 – Srednerusskaya (Annenskaya et al. 1997), are shown in Fig. 2. In general, the temperature and precipitation gradient is sub-latitudinal.

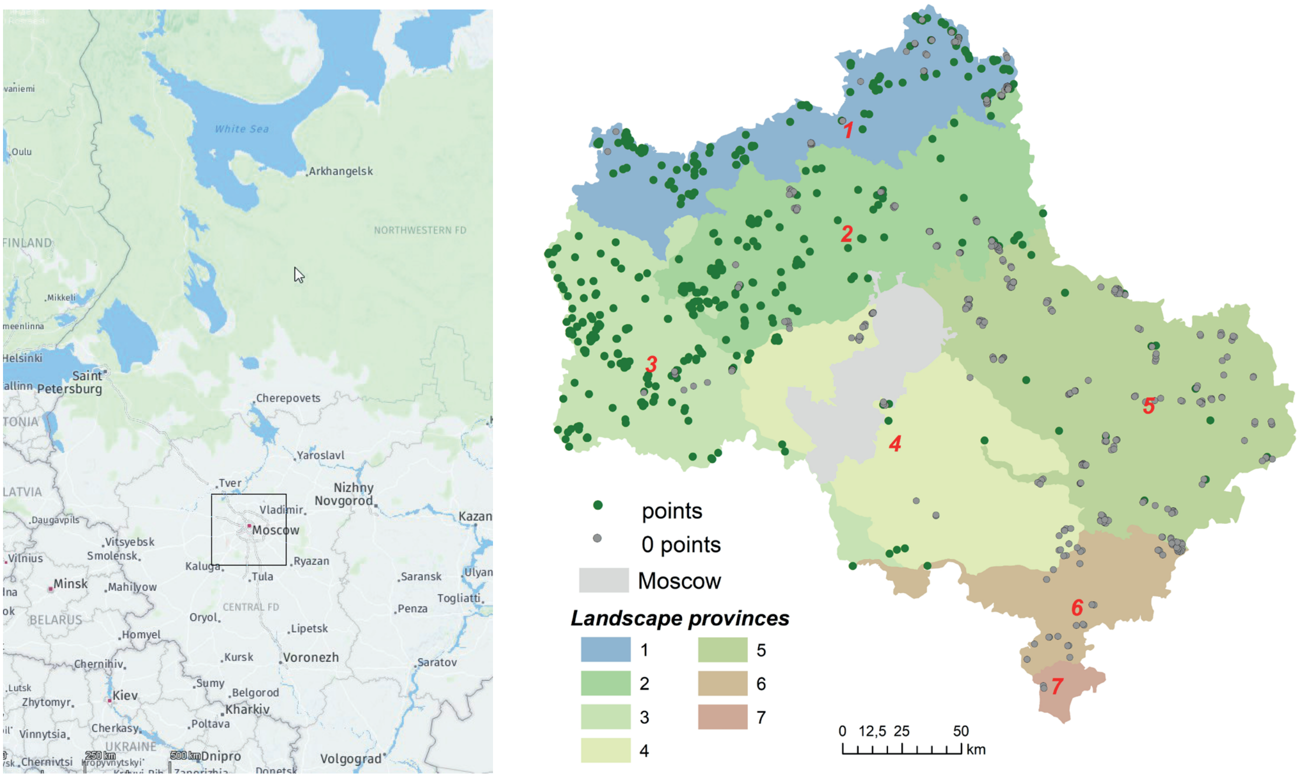

Fig. 1. Location of observation points within the physiographic provinces (PgPs) of the studied territory. 1 – Verkhnevolzhskaya, 2 – Moskovskaya, 3 – Smolenskaya, 4 – Moskvoretsko-Okskaya, 5 – Mescherskaya, 6 – Zaokskaya and 7 – Srednerusskaya (Annenskaya et al. 1997).

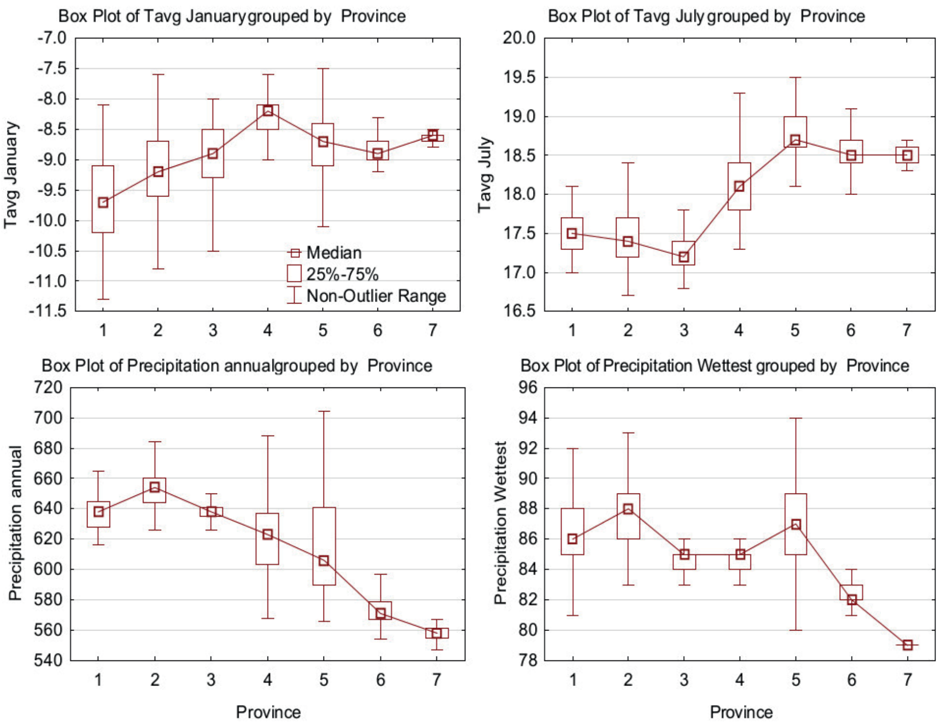

Fig. 2. Climatic characteristics of the Moscow region – the mean temperature of the coldest month ($T_{avg\ jan}$) (A) and the mean temperature of the warmest month ($T_{avg\ july}$) (B), annual precipitation (C) and precipitation of the warmest month (D)

Sampling methods

The following red-listed epiphytic lichen species: *Anaptychia ciliaris, Bryoria fuscescens, B. implexa, Usnea dasopoga, U. glabrescens, U. hirta, U. subfloridana*, as well as the epiphytic moss *Neckera pennata* were used as indicators of the state of forests. All these species are listed in the Red Data Book of the Moscow Region (2018) (*Red Data Book of the Moscow Region 2018*) (Figure 3). Compared to the rest of the red-listed epiphytic species, these species are noted not singly, which gave us reason to use them in statistical analysis in accordance with the objectives of the study.

The territory under study, including more than 150 Nature Protection Area (NPA), among them several newly organized ones, was surveyed by the route method. Surveys and sampling were carried out on the trunks and branches of trees at a height of 0-2 m from the ground. The territory of the city of Moscow was excluded from the survey.

When studied rare species were recorded, they were assessed in terms of the following characteristics: type of plant community, type of biotope, tree species, nature of anthropogenic disturbance, location within a SPNA. A scale for the abundance of particular species within the area of 1 km^2 was developed based on the expert assessment: 0 – the absence of species (378 sites in all), 1 – rarely and sporadically, 2 – occasionally in groups, 3 – very often and abundantly.

The total number of records of the above-mentioned eight species was 875, of which epiphytic lichens were found in 730 sites, and the moss *Neckera pennata* in 145 sites (Table 1).

The collected lichen samples were determined in the laboratory by standard lichenological methods (Golubkova 1996a 1996b; Muchnik et al. 2011) using a binocular and a set of chemicals. Samples of *Bryoria* spp. were confirmed basing of the analysis of secondary metabolites by thin layer chromatography (TLC) at the laboratory of lichenology and bryology of the BIN RAS.

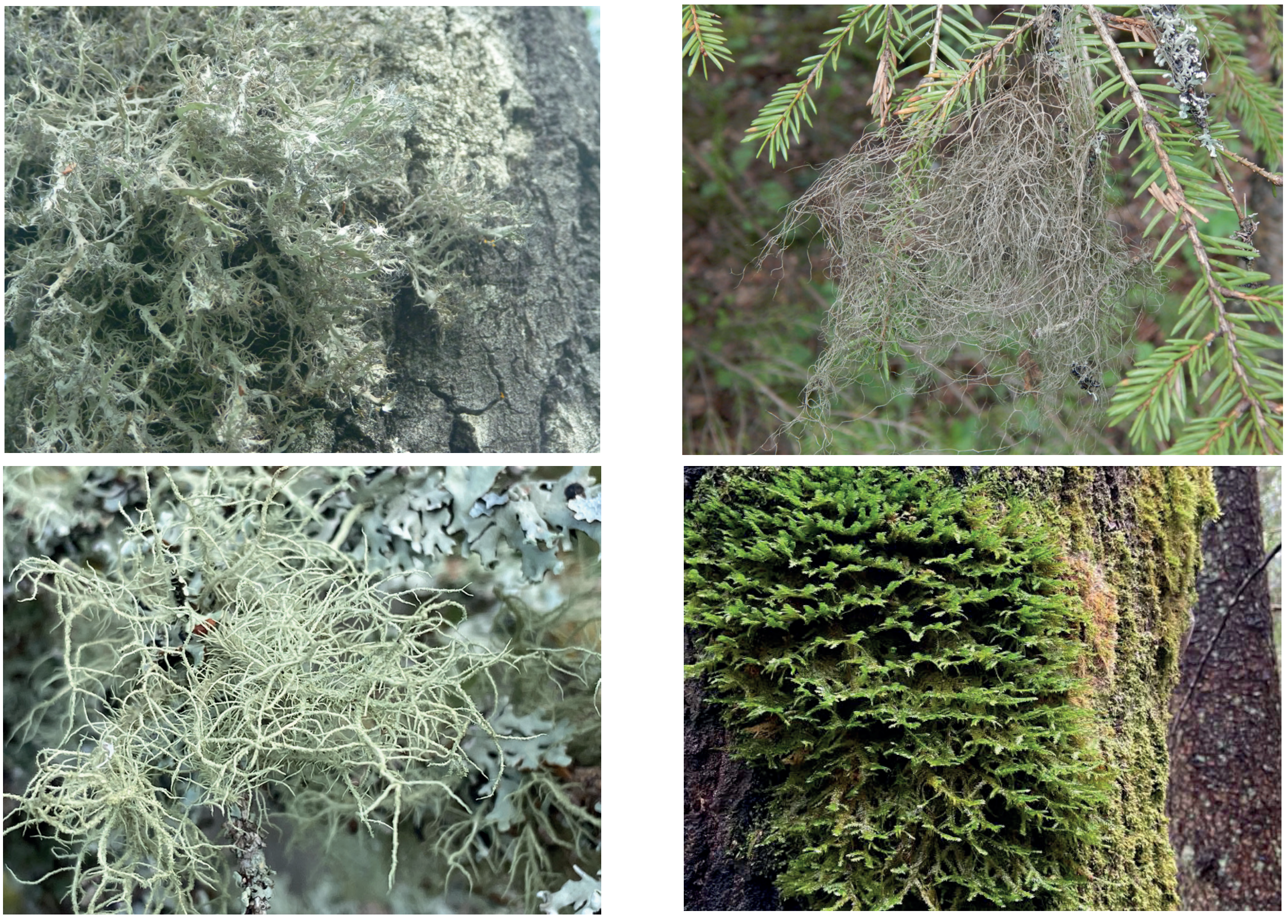

Fig. 3. Photo of the red-listed epiphytic species. a – *Anaptychia ciliaris*, b – *Bryoria* spp., c – *Usnea* spp., d – *Neckera pennata (photo E.G. Suslova)*

Table 1. Numbers of records of the studied species (n)

n	Species	Species code
27	*Anaptychia ciliaris*	An cil
247	*Bryoria fuscescens*	Br fus
45	*Bryoria implexa*	Br imp
145	*Neckera pennata*	N pen
125	*Usnea dasopoga*	Us das
24	*Usnea glabrescens*	Us gla
202	*Usnea hirta*	Us hir
60	*Usnea subfloridana*	Us sub

Data analysis

The influence of principal environmental factors explaining the uneven distribution of cryptogamic epiphytic species was analyzed at different spatial levels, namely regional, coenotic, and biotopic. A hypothesis for the uniform distribution of species within the indicated spatial units was evaluated using the frequency analysis (observed frequencies were compared with expected uniform ones) according to the Chi-Square statistics (Statistica 12), taking into account critical values for probability level (0.05) and degrees of freedom.

Region level

The distribution of studied rare species was investigated over the entire geographic space of the Moscow region within the boundaries of seven PgPs (Figure 1).

To assess the influence of environmental factors, the correlation between species distribution and climatic characteristics was spatially analyzed using the Worldclim database with the spatial resolution of 1x1 km (Fick and Hijmans 2017). The autocorrelation analysis was applied to select the least correlated predictor variables (correlation level not more than 0.5) from a complete set of 48 monthly climatic characteristics; these are January temperature ($T_{avg\ jan}$), March temperature ($T_{avg\ march}$), May temperature ($T_{avg\ may}$), March precipitation ($P_{avg\ march}$), and April precipitation ($P_{avg\ april}$).

The NDWI spectral index (Normalized difference water index) (McFeeters 1996) was used as an ***indicator of environmental moisture*** (vegetation and soil). The index is calculated based on the cloudless Sentinel-2 multispectral mosaic compiled from images of June 18 and 20 2021.

$$NDWI = \frac{B03 - B08}{B03 + B08}$$

The ***anthropogenic impact*** factor was estimated using remote information on the nighttime brightness of the Earth's surface according to the VIIRS satellite data (VNP46A3/VJ146A3 Monthly and VNP46A4/VJ146A4 Yearly Moonlight-adjusted Nighttime Lights (NTL) Product) (Wang et al., n.d.). The nighttime brightness correlates well with the consumption of primary energy resources at the regional level (Tronin et al. 2014). It is assumed that Nighttime lights mark a number of anthropogenic pressure parameters, such as population density, recreational load, and atmospheric pollution. The following independent variables have been used:

- night illumination ($W{\cdot}cm^{-2}{\cdot}sr^{-1}$),
- distance to objects with illumination over 100 $W{\cdot}cm^{-2}{\cdot}sr^{-1}$,
- azimuth to the same objects with illumination over 100 $W{\cdot}cm^{-2}{\cdot}sr^{-1}$,
- distance and azimuth to the center of Moscow.

After excluding correlated variables, we chose from the above-listed three types of data, i.e. climate, NDWI, and nighttime luminosity, the variables that differentiate the studied rare species based on F-statistics (ANOVA). The multiple linear regression method (Statistica 12) was used to evaluate the most significant factors governing the occurrence and abundance of different species; the points where the species are absent were also taken into account.

Community level

The frequency analysis was applied to study the allocation of the studied rare species within various types of forests; 33 types of communities identified on the basis of the previously developed ecological-coenotic approach (Chernenkova et al. 2020) were analyzed. The type of community was determined according to the canopy composition (vertical column) and ground layers of vegetation, i.e. herb and moss layers (Table 2). The presence of species within four non-forest habitat types (Small leaf scrub, Cuts, Meadows and Open marshy habitat) was also taken into account.

Table 2. Forest community types

Tree layer	Ground layers								
	Dwarf shrubs–small herb–green moss	Small herb	Small herb–broad herb	Broad herb	Moist herb –broad herb	Grass-marsh	Meadow herb	Dwarf shrubs–herbal-sphagnum	Non-forest land cover types
Spruce	1	2	3	4					
Spruce – aspen/ birch	5	6	7	8					
Pine – spruce	9	10	11	12					
Pine	13	14	15	16			17	18	
Oak - spruce				19					
Broad leaf – spruce				20					
Linden				21					
Birch		22	23	24	25	26	27	28	
Aspen				29	30				
Grey alder					31				
Black alder					32	33			
Small leaf scrub									34
Cuts									35
Meadows									36
Open marshy habitats									37

Biotope level

Distribution of the studied rare species was assessed based on the frequency analysis within five main biotope types:

1 – forests of fresh habitats (mesotrophic forests) are groups of plant communities of sufficiently drained habitats with predominance of mesophytes. They are small herb, small herb–broad herb, broad herb spruce, and broad leaf–spruce, spruce–pine, and pine dwarf shrubs–small herb–green moss and spruce–aspen/birch forests. The shrubs, such as *Corylus avellana*, and *Lonicera xylosteum*, often form a well-defined layer. *Oxalis acetosella, Lamium galeobdolon, Carex pilosa, Asarum europaeum, Luzula pilosa, Vaccinium myrtillus*, etc. are typical plant species of the herb-shrub layer.

2 – forests of humid habitats (humid forests) are spruce, pine–spruce, pine, spruce–aspen/birch and small-leaved (aspen/birch/alder) moist herb–broad herb and fern–moist herb forests of shallow flat depressions with a water confining stratum. *Polytrichum commune* and *Sphagnum* spp. mosses are present in such coniferous forests in addition to *Bryidae* green mosses and *Vaccinium myrtillus* is abundant. The herb layer of small-leaved, aspen and alder, forests is dominated or co-dominated by hygromezophyte species (*Athyrium filix femina, Deschampsia cespitosa, Cirsium heterophillum, Crepis paludosa*) and some hygrophytes (*Filipendula ulmaria*).

3 – wetlands and peatlands with pine, birch, spruce undergrowth with *Carex* spp., *Sphagnum* spp., *Eriophorum vaginatum* and dwarf shrubs.

4 – opening in the forest, forest edge, clearing, road (marks the degree of illumination).

5 – local swampy depression, forest on the outskirts of a swamp, watercourse bed (marks the degree of moisture). This group of biotope types is represented by swamp *Polytrichaceae* moss, herbal-sphagnum and grass–marsh coniferous, coniferous–small-leaved and small-leaved forests of waterlogged depressions and the margins of wetland forests on the border with marshes, as well as forest-marsh complexes with alternation of willow-birch wetlands and wetlands with spruce, pine and grey or black alder. Floodplain coniferous-small-leaved and small-leaved moist herb and grass-marsh forests of small rivers and streams with spruce, black or grey alder, with *Padus avium*, and tree and shrub willows are also included in this type. Such habitats are found on the slopes and bottoms of forest ravines.

RESULTS

Region level

The frequency of records of the studied rare species under study varied considerably. *Anaptychia ciliaris, Bryoria implexa, Usnea subfloridana,* and *U. glabrescens* were the rarest among the listed lichen species (Table 1). Species abundance on the area of 1 km^2 also varied greatly in the range of 1.3 to 1.8 points. Such species of epiphytic lichens as *Anaptychia ciliaris, Bryoria fuscescens, Usnea dasopoga, U. hirta* and *U. subfloridana* in most cases form isolated groups with the abundance of more than 1.6 points. The rare and sporadic presence, or occasional in small groups, is characteristic of *Bryoria implexa, Usnea glabrescens* and *Neckera pennata* species (Fig. 4).

The distribution of species within the study area is extremely uneven (Fig. 1, 5). The overwhelming number of records was in the western and northern sectors, i.e. within

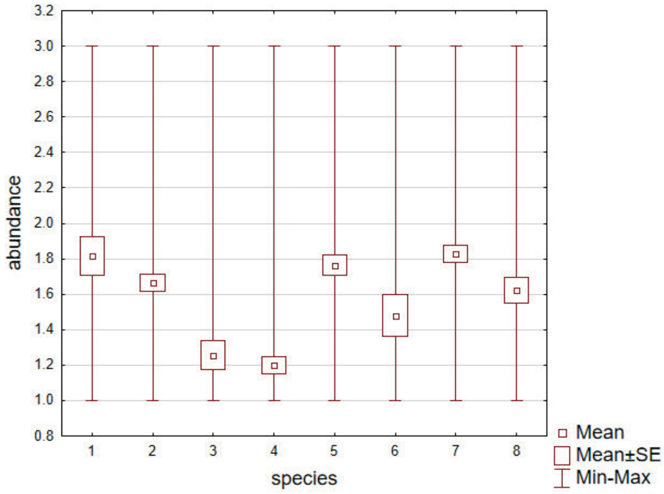

Fig. 4. Variations in the abundance of the studied rare species according to a three-point scale. The species codes are given in Table 1

#1-3 PgPs, very small number of occurrences in #4 and 5, and the absence in #6 and 7, which are characterized by increased mean annual temperatures and less precipitation (Fig. 2). Many habitats suitable for the studied rare species but lacking them totally (0-points) were recorded in the south and southeast sectors of the region (Fig. 1).

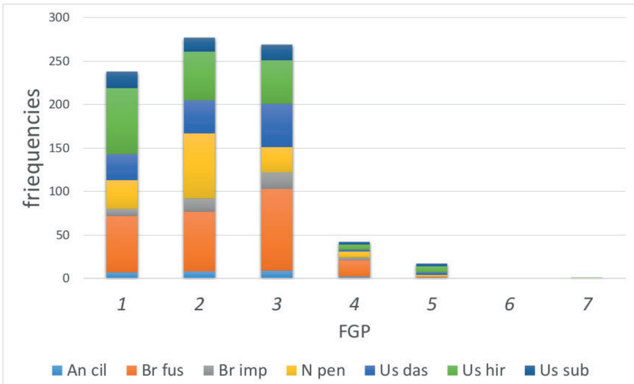

Fig. 5. Distribution of rare species within PgPs: 1 – Verkhnevolzhskaya, 2 – Moskovskaya, 3 – Smolenskaya, 4 – Moskvoretsko-Okskaya, 5 – Mescherskaya, 6 – Zaokskaya и 7 – Srednerusskaya (Annenskaya et al. 1997)

Specific distribution of particular studied rare species was noted (Fig. 5, Table 3). Thus, *Usnea hirta* and *U. subfloridana* are limited to the Verkhnevolzhskaya, Moskovskaya and Smolenskaya provinces (#1–3). Bryoria implexa is more common in the west of the region, i.e. in the Smolenskaya and Moskovskaya provinces (#2,3); *B. fuscescens* and *Usnea dasopoga* – in the Moskovskaya province (#2), and *Neckera pennata* in the Smolenskaya province (#3). Thus, a significant correlation was confirmed for almost all species, mainly with three PgPs (#1,2 and/or 3). Singular records of *Bryoria* and *Usnea* species in the SE part (the broad-leaved forests zone) were due to the absence of natural forest stands, where the studied species could be found. *Bryoria fuscescens* and *Usnea dasopoga* lichens were rarely recorded on isolated old birches.

To understand the nature of epiphyte distribution trends, independent climate variables with significant inter-group differences (ANOVA) were analyzed. As a result, we obtained significant climatic characteristics at the sites where epiphytic organisms were recorded, in addition to the average values of $T_{avg\ jan}$, $T_{avg\ july}$, Annual precipitation, and Precipitation of warmest month within PgPs. Such variables include temperatures in March ($T_{avg\ march}$) and May ($T_{avg\ may}$), and precipitation in March ($P_{avg\ march}$) and April ($P_{avg\ april}$) (Table 4).

Table 3. Results of frequency analysis of species distribution within PgPs

Species	χ^2	*p*	*df*	Class_number
Anaptychia ciliaris	9.851852	0.043001	4	1, 2, 3
Bryoria fuscescens	118.6129	0.00000	4	3
Bryoria implexa	13.57778	0.00354	3	2, 3
Neckera pennata	114.5479	0.00000	4	2
Usnea dasopoga	74.43902	0.00000	4	3
Usnea glabrescens	6.608696	0.036724	2	3
Usnea hirta	155.9796	0.00000	5	1, 2, 3
Usnea subfloridana	22.27119	0.000177	4	1, 2, 3

Table 4. Environment Variables (F-test, ANOVA)

	F	*df*	*p*
Climate Variables			
$T_{avg\ march}$	2.7784	7	0.0073
$T_{avg\ may}$	2.1190	7	0.0393
$P_{avg\ march}$	4.6633	7	0.00004
Pavg april	2.8001	7	0.0069
Water index			
NDWI	7.3821	7	0.00000
Anthropogenic pressure			
azim_0km	3.5788	7	0.0008
azim_light_100	2.4126	7	0.0189
dist_0km	3.4047	7	0.0014

To identify the importance of environmental moisture for epiphytic species, the values of the NDWI humidity index were involved in the analysis. The distribution of epiphytic organisms showed a significantly high level of correlation with the humidity index (Table 4).

Among the factors of anthropogenic pressure, the intergroup differences were revealed for azimuth to the center of Moscow (azim_0km), azimuth to objects with illumination over 100 W•cm^{-2}•sr^{-1} (azim_light_100) and distance to the center of Moscow (dist_0km) (Table 4).

It is interesting, that no trend of recording rare species of epiphytic organisms within the existing network of NPA has been established. Moreover, Bryoria fuscescens was often recorded outside the boundaries of protected areas (Table 5).

Community level

When considering the total number of species records in different types of communities, in more than 70% of cases

Table 5. Results of frequency analysis of the NPA

Species	χ^2	*p*	*df*	Class_number
Anaptychia ciliaris	1.81481	0.177933	1	
Bryoria fuscescens	10.8160	0.001006	1	0 outside NPA
Bryoria implexa	1.08889	0.296718	1	
Neckera pennata	2.45578	0.117094	1	
Usnea dasopoga	0.968	0.325180	1	
Usnea glabrescens	1	0.317311	1	
Usnea hirta	0.32	0.571608	1	
Usnea subfloridana	0.26667	0.605577	1	

the preference is for spruce, pine and birch communities with a diverse composition of the ground layer, from boreal, subnemoral and nemoral to mesotrophic and oligotrophic types of community (Fig. 6).

At the same time, it is noticeable that certain types of epiphytic lichens are significantly more common in a limited range of forest types with highly humid habitat conditions. For example, *Anaptychia ciliaris, Bryoria fuscescens* and *Usnea dasopoga* are often found in birch grass-marsh forests (#26). *Bryoria fuscescens* and *Usnea dasopoga* are also characteristic of spruce small herb–broad herb forests (#3). *Usnea hirta* mostly grows in the peatlands with pine or birch (#18,28). The *Neckera pennata* epiphytic moss is most found in small herb–broad herb or broad herb spruce forests (#3,4) (Table 6).

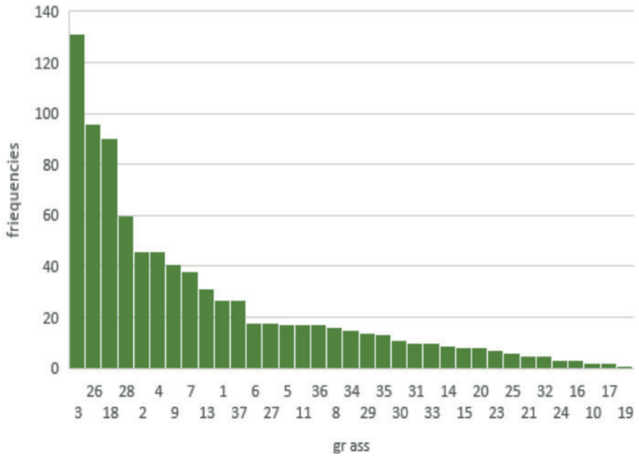

Fig. 6. Distribution of indicator species within different types of communities. Group numbers of community types are given in Table 2

Thus, the hypothesis for the uniform distribution of species in different types of communities was not confirmed in most cases. *Usnea glabrescens, Bryoria implexa* and *Usnea subfloridana* are not limited in their distribution to certain types of communities.

Biotope level

At the lowest spatial level (biotopes), all species of *Bryoria* genus and *Usnea dasopoga* are limited to humid forests (#2) and *U. hirta* to swamp forests (#3), while *Neckera pennata* grows in the least humid forest types of biotopes (mesotrophic forests) (#1). *U. subfloridana* was recorded evenly in all biotopes except for #5, where only one record was made (Fig. 7, Table 7).

Mesotrophic and humid forest biotopes (#1,2) rank first in the total number of records. This is obviously explained by a large area of these types of sites. The margins of peatlands and wetlands (#3) with spruce undergrowth are quite rich in epiphytic lichens; spruce branches host large numbers of *Usnea* spp. and *Bryoria* spp. *Anaptychia ciliaris* and *Neckera pennata* are absent from these sites.

The formation of biotope #4 can be logically assessed as a result of anthropogenic disturbance caused by the local forest cutting and creating ecotone conditions. Favorable conditions for the development of many epiphytic lichens, which urgently need sufficient light, are created within dampish and swampy forest edges, and also swampy glades, clearings, and power lines. Narrow forest roads and rather narrow clearings usually have higher numbers of individuals and species of *Usnea* spp. and *Bryoria* spp., which receive sufficient moisture and light there. Rarer occurrence of epiphytic species was observed at the edges of watershed forests and upland meadows, where epiphytic organisms are exposed to the desiccation factor because of excessive light and wind. Only *Usnea hirta* and *U. dasopoga* were sporadically recorded within such edges in the lower part of the trunks of old birches.

Despite favorable microclimate in habitats (#5), where both soil and atmospheric air are more humid, the frequency of occurrence of epiphytic lichens and mosses is low.

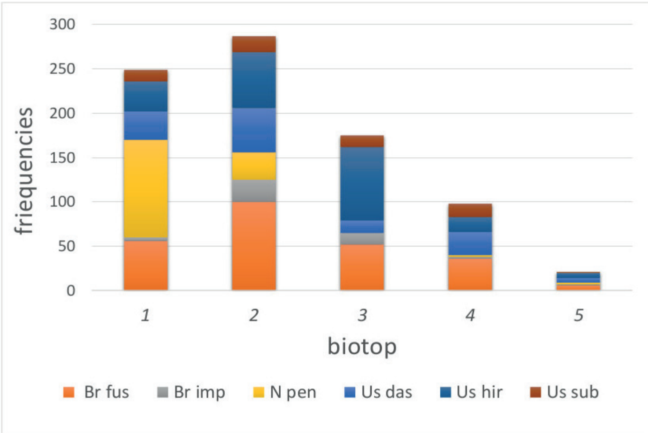

Fig. 7. Distribution of studied rare species in different types of biotopes

1 – fresh forest (mesotrophic forest), 2 – wet forest (humid forest), 3 – wetlands and peatlands, 4 – opening in the forest, forest edge, clearing, road (marks the degree of illumination), 5 – local swampy depression, outskirts of a swamp, watercourse bed (marks the degree of moisture).

Table 6. Results of frequency analysis within types of communities

Species	χ^2	*p*	*df*	Class number
Anaptychia ciliaris	54.63704	0.00000	7	26
Bryoria fuscescens	**341.408**	0.00000	26	3, 26
Bryoria implexa	25.51111	0.111482	18	
Neckera pennata	**217.6207**	0.00000	19	3, 4
Usnea dasopoga	133.2205	0.00000	23	3, 26
Usnea glabrescens	10.88	0.539231	12	
Usnea hirta	**373.7241**	0.00000	24	18, 28
Usnea subfloridana	28.93333	0.146786	22	

Table 7. Results of frequency analysis within biotopes

Species	χ^2	*p*	*df*	Class_number
Anaptychia ciliaris	8.222222	0.01639	2	2, 4
Bryoria fuscescens	93.44	0.00000	4	2
Bryoria implexa	45.55556	0.00000	4	2
Neckera pennata	215.5241	0.00000	3	1
Usnea dasopoga	7.05512	0.00000	4	2
Usnea glabrescens	9.4	0.024421	3	1, 2
Usnea hirta	100.9163	0.00000	4	3
Usnea subfloridana	14	0.007296	4	all except 5

Distribution of all epiphytes, except *Usnea glabrescens,* demonstrates that they are limited to a certain tree species (substrate type). Most of the studied rare species are found on the trunks and branches of spruce, and *Anaptychia ciliaris* and *Neckera pennata* prefer the trunks of old aspens 45-50 cm in diameter. Other tree species host far fewer studed epiphytic lichens and mosses (Table 8)

Discussion

The study focuses on identifying patterns in the distribution of rare epiphytic cryptogamic organisms within the territory of the Moscow region, the area of active development in recent decades. Variability in the distribution of different types of epiphytic lichens and mosses is well marked by the environmental features that correspond well to the original and published data.

4.1. Regional level

It is shown that distribution of the studied species within the territory of the Moscow region is extremely uneven and is clearly subject to natural patterns (Fig. 1, 5). It was revealed that the vast majority of records were in the western and northern sectors of the region, within the broad-leaved–coniferous forest zone, while the 0-point predominately concentrate in the southern and eastern sector, i.e. the area of broad-leaved forests. Based on the χ^2 criterion, a statistical correlation with three types of landscapes (#1–3) was confirmed, which have the lower temperatures of the coldest and warmest months and the maximum mean annual precipitation (Fig. 2). At the same time, one cannot deny the warming effect of the urban climate of the city of Moscow within landscape province #4, particularly in terms of the January temperature pattern, which was discussed in other publications (Varentsov et al. 2017). The fact of climate controlled distribution of lichens has been noted in other works (Cardós et al. 2017; Ellis 2019).

The analysis of 48 climate variables from the Worldclim database (Fick and Hijmans 2017) showed that distribution of the studied rare species is significantly determined by temperature and precipitation. The use of NDWI values for the summer period made it possible to link the points of species records with increased moisture content in habitats. This is another fact emphasizing the importance of the indicator, which during dry periods limits the existence of epiphytic organisms in the temperate zone (Hauck et al. 2013).

What is the **role of anthropogenic factor** in the distribution of epiphytic organisms within the forests of the region? A hypothesis for the principal importance of such indicators as the distance and direction from large urbanized systems, which determine the degree of air pollution, was confirmed. By applying the linear regression method, it was shown that the distribution and abundance of studied rare species is largely effected by the factor azim_0km - (direction to the city of Moscow); the factor showed the maximum coefficients of determination R2 for almost all species (Table 8). Obviously, the atmospheric transport of pollutants is determined by the prevailing SW winds in the region ("Weather in Moscow by months," n.d.), which results in the predominant distribution of epiphytes in the W, N, and N-W sectors of the region, in the "shadow" of the city of Moscow (Fig. 1). The factor of pollutant transfer from other large urban settlements (azim_osv_100) is no less significant. It was calculated using the original technique for assessing the level of anthropogenic pressure

Table 8. Results of frequency analysis in terms of substrate (tree species)

Species	χ^2	*p*	*df*	Tree species
Anaptychia ciliaris	16.33333	0.000053	1	*Populus tremula*
Bryoria fuscescens	1337.419	0.000000	8	*Picea abies*
Bryoria implexa	79.57143	0.000000	3	*Picea abies*
Neckera pennata	539.0884	0.000000	4	*Populus tremula*
Usnea dasopoga	550.1791	0.000000	9	*Picea abies*
Usnea glabrescens	10.96296	0.026985	4	
Usnea hirta	533.751	0.000000	7	*Picea abies*
Usnea subfloridana	114.8485	0.000000	7	*Picea abies*

through the night illumination index of large urban objects (Tronin et al. 2014). The proximity to the center of Moscow (dist_0km) showed lower coefficients of determination, which could be explained by specific features of species distribution due to natural factors in accordance with pronounced zoning (Petrov 1968; Kurnaev 1973).

The studied rare species are different in the response of their distribution to environmental factors. The results of the multiple linear regression analysis showed that the influence of a combination of factors at the regional level was most pronounced for *Usnea hirta* (R2=0.549), *Usnea dasopoga* (R2=0.453) and *Neckera pennata* (R2=0.428), while for other species the R2 determination value was less, from 0.323 to 0.131 (p=0.005) (Table 8).

As for particular variables, the highest values of the coefficient of determination were for *Anaptychia ciliaris* and *Neckera pennata* by dist_0km, which characterizes the distance to the center of Moscow (Table 8). Unlike other species, the moss *Neckera pennata* demonstrated the negative correlation with the effect of the variable dist_0km, and positive one with azim_0km, which could result from the substrate eutrophication due to the deposition of nitrogen compounds from the atmosphere near Moscow (Averkieva and Priputina 2011; Bednova 2017). Sporadic records of *Neckera pennata* are known even from several old parks in Moscow and the Moscow region (oral communication by E.G. Suslova). A high negative correlation with the azim_0km variable is characteristic of the distribution of epiphytic lichens *Anaptychia ciliari* and *Usnea* spp., indicating higher sensitivity of these lichen species to excessive levels of pollutants in the atmosphere in full compliance with the literature data (Carreras et al. 1998; Giordani et al. 2002; Otniukova and Sekretenko 2008). Generally low number of *Anaptychia ciliaris* and *Usnea subfloridana* records (Table 1) is obviously associated with high negative value of azim_0km, which confirms the transfer of suspended particles, carbon monoxide, nitrogen oxide and dioxide from the city of Moscow.

The temperatures of March and May, as well as the amount of precipitation in March, were significant for almost all types of rare epiphytic organisms.

The conservation significance of SPNAs for creating a favorable habitat for the studied rare species was not confirmed (Table 5). This suggests that under the current state of forest cover in the region the location within a SNPA is not so important in the distribution of species.

Community level

When analyzing the confinement of species to certain forest types, a stable correlation was found between the distribution of studied rare species and coniferous and small-leaved communities. It is quite obviously due to the distribution of coniferous forests in accordance with pronounced zoning (Kurnaev 1973; Petrov 1968). The connection between species and community types has rather different values. Thus, the highest value of χ^2=373.7241 was recorded for *Usnea hirta,* which is closely associated with the swamp type of dwarf shrubs–herbal-sphagnum communities (#18,28). The location of *Bryoria fuscescens* within nemoral spruce forests and birch forests of the grass-marsh group (#3,26) is confirmed by χ2=341.408. The distribution of *Neckera pennata* in the nemoral spruce communities (#3,4) is confirmed by the high correlation coefficient χ^2=217.6207 (Table 6). Low χ^2 values and no significant correlation with forest types are characteristic of *Bryoria implexa, Usnea glabrescens*, and *U. subfloridana*. It is quite obvious that in such case the conditions of biotopes within the considered types of communities are the most significant.

Biotope level

Considering a more detailed biotope level, we see that 80% of the records of epiphytic organisms are limited to three categories of humid habitat biotopes (#1–3). The critical importance of humidity and light for poikilohydric organisms has been repeatedly emphasized in other studies (Campbell and Coxson 2001; Nash 1996).

Lower number of the records of the studied rare species in biotope #4 (opening in the forest, forest edge, clearing, road) is directly related to anthropogenic disturbance and formation of the edge effect (Saunders et al. 1991). However,

Table 9. Results of multiple linear regression analysis of species distribution based on spatial environment factors (with due account of 0-points)

Environment factors	Anaptychia ciliaris	Bryoria fuscescens	Bryoria implexa	Neckera pennata	Usnea dasopoga	Usnea glabrescens	Usnea hirta	Usnea subfloridana
a	5.895	11.447	3.964	2.709	7.829	5.621	12.713	5.276
azim_osv_100	0.07	**0.154**	-0.01	0.038	**0.089**	0.079	0.006	0.032
dist_0km	**0.379**	**-0.18**	**0.149**	**-0.53**	**0.205**	**0.183**	**0.291**	**0.223**
azim_0km	**-0.57**	-0.2	**-0.33**	**0.3**	**-0.54**	**-0.43**	**-0.54**	**-0.56**
NDWI	-0.03	0.071	-0.06	**0.083**	-0.05	-0.05	**-0.08**	-0.02
$T_{avg\ march}$	**-0.27**	-0.05	**-0.21**	**-0.15**	**-0.22**	**-0.32**	**-0.27**	**-0.24**
$T_{avg\ may}$	**-0.27**	-0.13	**-0.36**	**-0.23**	**-0.31**	**-0.33**	**-0.41**	**-0.22**
$P_{avg\ march}$	**-0.18**	**-0.21**	**-0.17**	-0.01	**-0.17**	**-0.28**	**-0.17**	**-0.19**
$P_{avg\ april}$	-0.11	-0.15	0.113	-0.03	0.049	-0.03	-0.04	0.026
p	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
R2	0.289	0.131	0.323	0.428	0.453	0.222	0.549	0.316

a – intercept, *p* – p-level, *R2* – coefficient of determination on the one hand, narrow forest roads and rather narrow clearings with additional illumination have higher numbers of individuals and species of *Usnea* spp. and *Bryoria* spp. On the other hand, the number of species is noticeably lower at the edges of watershed forests and upland meadows, where epiphytic organisms are exposed to the desiccation factor because of excessive light and wind. Similar data on the negative impact of undesirable gradients of light, humidity and wind at the edge of forest stands, where different microclimatic environmental conditions are formed, have been obtained in other studies (Esseen 2006; Hilmo and Holien 2002). The negative impact of linear cuts in managed forests has been analyzed in detail in relation to the distribution of epiphytic lichens *Bryoria* spp., *Usnea* spp. and *Evernia mesomorpha* (Boudreault et al. 2008).

In our study, the distribution of *Neckera pennata* in mesotrophic forest (#1) is confirmed by the highest correlation coefficient χ^2= 215.5241. Other species also have significant coupling coefficients. *Usnea glabrescens* is an exception, its distribution is not limited to any particular biotope type. It is a very rare species, and the validity of the sample is insufficient (Table 7). To clarify, it is desirable to increase the sample of records of the species in the future.

A large number of publications analyze the distribution and diversity of epiphytic cryptogamic organisms on different tree species (Nascimbene et al. 2009; Sales et al. 2016; Spier et al. 2010; Thor et al. 2010; Wirth 1995). In our study, a significant correlation of the habitats of the studied species with two tree species, i.e. spruce and aspen, was confirmed. It is important that the degree of connection with the substrate (tree species) is the closest in comparison with other biotic characteristics. Thus, the distribution of *Bryoria fuscescens* on spruce branches is confirmed with χ^2=1337.419, *Usnea dasopoga* with χ^2= 550.1791, *Usnea hirta* with χ^2=533.751. Location of *Neckera pennata* on mineral-rich, rather simple, cracked bark, mainly on old, free-standing aspen trunks, is confirmed with χ^2=539.0884. A small number of *Usnea glabrescens* records also did not allow establishing a reliable relationship with the tree species.

CONCLUSION

Epiphytes model the diversity of forest communities and fulfill certain ecosystem functions, despite their minor contribution to production processes in the temperate zone. The study is devoted to the patterns of distribution of rare epiphytic species at the border of the broad-leaved–coniferous forest zone. Identification of the limiting factors of the natural environment for such organisms at different spatial levels is a key to detailing natural boundaries over large geographic areas, and the ecological well-being of forests at the level of individual communities and biotopes. At the regional level we recorded edge effects on studied rare species at the gradient of climatic conditions and the transition of the broad-leaved-coniferous forest zone into the broad-leaved one. The distribution of studied rare species is synergistically superimposed by the influence of atmospheric transport of pollutants from the city of Moscow. The warming effect from Moscow remains possible but needs to be confirmed in the future. In general, the state and habitat feature of most forests outside the SPNA of the Moscow region do not differ significantly from those within the protected areas. This is confirmed by the absence of dependence of the studied rare species distribution on the areas with protection status.

Local ecological and coenotic conditions influencing light, temperature and humidity regimes are among the principal factors in the distribution of the rare species of epiphytic organisms at the level of habitats. Edge effects as represented by the decreasing number of species records are characteristic of the forest borders near major roads, as well as at the edge of watershed forests and upland meadows.

The narrow ecological compliance of epiphytic cryptogamous species and their sensitivity to air pollution make them good indicators of the environmental quality within anthropogenic landscapes. Subsequently, this will help in the best way determine the optimal conditions contributing to biodiversity conservation in forests near large metropolitan areas and optimization of optimal habitat diversity.

Funding

This study was conducted in the framework of the Institute of Geography RAS (№ 0148-2019-0007) and Severtsov Institute of Ecology and Evolution RAS.

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