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Distribution factors of the epiphytic lichen *Lobaria pulmonaria* (L.) Hoffm. at local and regional spatial scales in the Caucasus: combining species distribution modelling and ecological niche theory

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For the rare epiphytic lichen *Lobaria pulmonaria* (L.) Hoffm., there is a lack of data on ecological niche parameters and distribution factors in the Caucasus, which are necessary to develop an effective system of the species preservation during forest management. The aim of this study was to identify the influence of abiotic, biotic and movement factors on the potential distribution of *Lobaria pulmonaria* in the Caucasus forests, depending on the spatial scale. We combined species distribution modelling and ecological niche theory based on the BAM (Biotic-Abiotic-Movement) concept. A total of 174 occurrence data were retained in the modelling using Maxent ver. 3.4.3 in R. The distribution models of the main lichen phorophytes in the Caucasus (*Pinus sylvestris* L. and *Fagus orientalis* Lipsky) were used as biotic layers in models. The raster of distances from optimal sites, where the probability of the lichen occurrence remained above 0.5, was used as a movement-layer. Different abiotic predictors were significant in the lichen distribution in the Central Caucasus (terrain) and throughout the Caucasus (macroclimate). Interspecific relationships (lichen-phorophyte) were more significant at the local scale. The movement factor contributed most to the local model (80% of the contribution) and limited the lichen distribution to a radius of 20 m in the Central Caucasus and 30 m throughout the Caucasus. Field verification of the local model showed an 85.7% success rate of presence prediction with cutoff values of 0.8. The combination of SDM modelling and ecological niches theory is an effective method for studying the potential localisation and the ecological niches of epiphytic lichens.

Keywords: *Lobaria pulmonaria*, Caucasus Forest, Species Distribution Modelling, Ecological Niche, Biotic-Abiotic-Movement Concept, Spatial Scale

Introduction

The tree lungwort *Lobaria pulmonaria* (L.) Hoffm. is a cosmopolitan epiphytic lichen, widespread in old-growth forests of boreal, oceanic, temperate and mountainous regions (Matwiejuk & Zbyryt 2013, Ignatenko & Tarasova 2018, Ginszt et al. 2022). This large foliose cyanolichen serves as a flagship species that draws attention to lichen preservation (Stoykov 2015, Di Nuzzo et al. 2022, Ginszt et al. 2022). *Lobaria pulmonaria* is mainly confined to intact forests with long ecological continuity and is considered an old-growth forest indicator (Hilmo et al. 2011, Nadyeina et al. 2014, Brunialti et al. 2015, Ivanova 2015, Ignatenko & Tarasova 2018) and an umbrella species (Brunialti et al. 2015, Ivanova 2015, Di Nuzzo et al. 2022, Ginszt et al. 2022). In old-growth forests, *Lobaria pulmonaria* colonises the bark of a wide spectrum of phorophytes, mostly deciduous tree (Matwiejuk & Zbyryt 2013, Stoykov 2015, Ginszt et al. 2022), and *Castanea sativa* Mill. (Nadyeina et al. 2014). It was also recorded on the bark of *Pinus sylvestris* L., *Picea abies* (L.) H. Karst., and *Abies nordmanniana* (Steven) Spach (Hilmo et al. 2011, Urbanavichene & Urbanavichus 2014, Stoykov 2015, Khanov & Pshegusov 2021, Ginszt et al. 2022).

Many authors have highlighted unsustainable silvicultural practices, habitat fragmentation, air pollution and climate change as major threats to the world population of *Lobaria pulmonaria* (Stoykov 2015, Nascimbene et al. 2020, Di Nuzzo et al. 2022, Ginszt et al. 2022). This species, sensitive to anthropogenic influence, is endangered in many European countries and is included in national red lists (Nadyeina et al. 2014, Ignatenko & Tarasova 2018, Ginszt et al. 2022). It is also red-listed in Russia, including many regions of the Caucasus (Istomina 2008). In the Caucasus *Lobaria pulmonaria* seems to be a rare species that occurs mainly on beech (*Fagus orientalis* Lipsky), hornbeam (*Carpinus betulus* L.), linden (*Tilia begoniifolia* Steven), ash (*Fraxinus excelsior* L.), oak (*Quercus* sp.), and maple (*Acer* sp.) (Urbanavichene & Urbanavichus 2014, Gasparyan & Sipman 2020), rarely on fir (*Abies nordmanniana* Spach) and pine (*Pinus sylvestris* L.) (Urbanavichene & Urbanavichus 2014, Khanov & Pshegusov 2021). Although the lungwort lichen distribution patterns are widely studied in European forest landscapes (Di Nuzzo et al. 2022, Ginszt et al. 2022), they have not been sufficiently known in the Caucasus. The forest cover in the region is steadily decreasing (Tembotova et al. 2012), and knowledge of the factors limiting the local and regional distribution of *Lobaria pulmonaria* is therefore essential to develop an effective system of the species preservation during forest management.

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The issue can be addressed by species distribution modelling (SDM) combined with ecological niche theory. SDM, based on statistical processing of ground data (*e.g.*, geographic records of a species) using data obtained from environmental models (geographic layers of climatic and topographic information), is considered an effective method of studying the potential distribution of species (Peterson et al. 2011, Bowen & Stevens 2020). This method identifies the importance of environmental predictors for species distribution by illustrating how the spatial probability of an organism presence depends on variables. Habitats with the highest presence probability are considered most suitable for the target species. Projecting the presence probability over a specific area provides a probability distribution map of species.

Meanwhile, SDM models often consider only abiotic determinants of species distribution and do not include biotic factors (competition, mutualism, predation, etc.), which are known to have a significant influence on species distribution. Accounting for biotic variables in SDM models is possible in the framework of the Biotic-Abiotic-Movement (BAM) concept (Soberón & Peterson 2005, Peterson et al. 2011, Peterson & Soberón 2012). This ecological niche concept considers three groups of factors determining the species distribution, including abiotic predictors (A-factor), biotic determinants (B-factor: interactions between species), and species dispersal capability (M-factor: movement, accessibility of areas – Soberón & Peterson 2005, Peterson et al. 2011). The BAM concept provides for the possibility of studying the effects of the three factors separately (Soberón & Peterson 2005). The A-model is a geographic expression of the fundamental niche of the species, the BA-model is a geographic expression of the realised niche, and the BAM-model represents an occupied distributional area that is closest to the real species distribution (Soberón & Peterson 2005, Peterson et al. 2011). The BAM concept assumes a nested (hierarchical) relationship between the fundamental niche, the realised niche and the occupied distributional area, as well as the possibility of integrating "the geography of other species in single-species models" (Soberón & Peterson 2005, Peterson & Soberón 2012). Accordingly, a hierarchical modelling approach that represents the hierarchy of the conceptual model is appropriate within this framework. The approach includes means to describe hierarchical relationships between model elements, *e.g.*, by embedding some items within others (Maus et al. 2011). Consequently, we first obtained the A-model of *Lobaria pulmonaria* distribution based on abiotic variables only. To integrate the biotic factor into the BA-model, we re-run the model with abiotic and biotic factors. We used previously generated probability distribution maps of the phorophytes (in the range from 0 to 1) as separate biotic covariates (biotic layers – Pshegusov et al. 2022). It is known that epiphytic lichens have to follow their phorophytes, and the dynamic of epiphytic lichen populations is significantly determined by the population dynamic of their phorophyte trees (Ignatenko & Tarasova 2018). In the Central Caucasus, the main lungwort lichen phorophyte is *Pinus sylvestris*, while in the Caucasus region it is *Fagus orientalis* (Khanov & Pshegusov 2021). We therefore used distribution models of *Pinus sylvestris* and *Fagus orientalis* as biotic layers in the local and regional BA-models of *Lobaria pulmonaria*. The main assumption of this method is a limited number of modelled predictor species, while the influence of biotic relationships on the spatial distribution of *Lobaria pulmonaria* may be much more complex.

Movement factor, which determines the dispersal ability of a species, can be formalised through the set of territories accessible to the species (Soberón & Peterson 2005, Peterson & Soberón 2012). At present, there is no unified conceptual approach to the spatial specification of movement factor. As reviewed by Barve et al. (2011), species-accessible areas are typically delineated: (i) within administrative or geographical units with no biologically significant basis; (ii) within biotic areas (regions with a set of species distinct from other regions); and (iii) within territories of historical distribution of species (including those modelled on the characteristics of the species current ecological niches). Accessible areas were also restricted to sites with previously defined climatic classes suitable for the target species (Banerjee et al. 2019) or regions with fossilised species remains (Myers et al. 2015). To consider the movement factor in the BAM-model, we represented the accessibility of areas through the distance from optimal areas (plots with 0.8 threshold of habitat suitability) at which the probability of species occurrence was above 0.5 (Pshegusov et al. 2022). We rerun the model with abiotic variables, biotic factors, and a raster of distances from optimal sites that were calculated from the BA model. The main assumptions of the approach are: (i) areas with an occurrence probability of *Lobaria pulmonaria* above 0.8 (the highest predicted probability of the lungwort lichen) are considered most accessible for the species; (ii) areas with an occurrence probability of lungwort lichen above 0.5 are considered accessible; (iii) the dispersal capacity of *Lobaria pulmonaria* depends on the geographical and ecological accessibility of areas. A somewhat similar approach was applied in the recent study of Soberón & Osorio-Olvera (2023), who estimated region availability using an adjacency matrix. The adjacency matrix represented all cells, eligible or ineligible, that could be reached from eligible cells at a given dispersal parameter (dispersal capacities – Soberón & Osorio-Olvera 2023).

The BA- and BAM-models constructed in this way are a type of nested models that allow us to represent the hierarchical organisation of *Lobaria pulmonaria* ecological niche. Nested models are quite widely used in clinical modelling, but are rarely applied in bioecological modelling (Maus et al. 2011). An example is recent work on incorporating food resource distributions into SDM models of the harpy eagle (Sutton et al. 2023). Using a hierarchical modelling approach, the authors included predictions of food resource raster as separate biotic covariates along with abiotic variables in abiotic-biotic models (Sutton et al. 2023). Perhaps in the future, nested BAM models, which are an example of effective hierarchical modelling, will be used more frequently in bioecological modelling.

As suggested by some authors (Soberón & Peterson 2005, Brooker et al. 2009, Wiens 2011, Peterson & Anamza 2015, Guisan et al. 2017), the importance of abiotic variables and movement factors in species distribution is highest at a regional spatial scale, whereas biotic interactions play a greater role at a local scale. Other authors (Wisz et al. 2013) postulated a major role of biotic factors in the species distribution at regional scale. Thus, species distribution patterns established for large territorial units may not be applicable to explain species distributions at local scales, and the influence of spatial scale on the significance of distribution predictors remains debatable. For lichen species, especially in mountainous areas, there is also a lack of data on the significance of environmental variables in different-scale distribution models. It was suggested that the distribution of small sedentary species such as lichens is influenced by climatic factors mainly at a small spatial scale (Holt et al. 2015, Fos et al. 2017, Ellis & Eaton 2021, Di Nuzzo et al. 2022). Due to its small living space, size and mobility, *Lobaria pulmonaria*, for example, is sensitive to local high light and temperature stress, which strongly affects the surface temperature of the thallus, enhancing water loss (Di Nuzzo et al. 2022). In turn, insufficient hydration reduces turgor pressure, hyphae growth, photosynthetic activity and diaspore number of *Lobaria pulmonaria* (Carlsson & Nilsson 2009, Mikryukov et al. 2010, Di Nuzzo et al. 2022), affecting the reproductive potential and dispersal capability of the species. However, despite the ecological relevance of microclimatic gradients (light levels, humidity, bark pH, etc.), they cannot be mapped at a regional scale to predict species distribution and conservation (Eaton et al. 2018). For SDM purposes, large-scale variables that capture the influence of micro-scale predictors are more appropriate. Such variables are easier to record and map, which increases their value for SDM (Eaton et al. 2018). At the same time, the relevance of the macroclimatic variables in lichen distribution modelling was challenged because of the unclear relationship of lichen ecological performance to coarse-grained macroclimate (Ellis & Eaton 2021). On the other hand, Eaton & Ellis (2012) found that macroclimatic variables such as precipitation and mean annual temperature affect the growth of *Lobaria pulmonaria*. Epiphytic lichens were also shown to prefer regions with more humid climates (Fos et al. 2017). Hence SDM is effective and justified for predicting lichen distribution when macroclimatic data correlate with indicators of the local "ecological success" of species (Eaton et al. 2018, Eaton & Ellis 2012), and distribution models should be supported by knowledge of the lichen functional ecology (Ellis 2019).

The significance of biotic factors may also vary with spatial scale. At the local level, important biotic predictors of *Lobaria pulmonaria* distribution are pH and bark structure (Carlsson & Nilsson 2009, Mikryukov et al. 2010, Ivanova 2015, Ignatenko & Tarasova 2018), trunk diameter (Carlsson & Nilsson 2009, Brunialti et al. 2015, Ivanova 2015), bryophyte coverage (Benesperi et al. 2018), phorophyte age and lifespan (Jüriado et al. 2011). At the landscape level, forest type (species composition), age, area and degree of stand fragmentation are most important for lungwort lichen distribution (Carlsson & Nilsson 2009, Nadyeina et al. 2014, Brunialti et al. 2015, Stoykov 2015, Ignatenko & Tarasova 2018, Di Nuzzo et al. 2022). We hypothesized that in the Caucasus, the relevance of the phorophyte distribution factor in SDM models of *Lobaria pulmonaria* may also vary depending on the spatial scale.

At the regional scale, the study covered the Caucasus, a vast ecoregion (about 390 thousand km^2 between 38° to 47° N and 36° to 50° E) with a combination of lowlands, uplands and high mountain ridges. The prevailing mountainous relief determines the distribution of air masses and altitudinal zonality of climate, and, as a consequence, the great diversity of climate and vegetation types in the Caucasus. The ecoregion comprises a variety of natural complexes from semi-deserts and steppes to alpine meadows and permafrost, including a belt of coniferous and deciduous forests. The Central Caucasus, which was our study area at the local scale, on a relatively small territory (about 20.5 thousand km^2) includes the main natural complexes characteristic of the entire ecoregion. At the same time, this is the most highland part of the Caucasus (from 200 to 5642 m a.s.l.), which may influence the patterns of *L. pulmonaria* distribution.

In this study, we aimed to identify the patterns of influence of abiotic, biotic and movement factors on the potential distribution of *L. pulmonaria* in the Caucasus forests, depending on the spatial scale. We hypothesised that the relative contribution of the different predictors in the lungwort lichen distribution models depends on the scale of the study area. We also wanted to investigate whether species distribution modelling based on the BAM concept is an effective method for studying the ecological niches of epiphytic lichens. Such an understanding is essential as it can be the basis for an effective conservation system not only for *L. pulmonaria*, but also for the main habitats of the lichen, *i.e.*, old-growth forests.

Materials and methods

Study area

The Caucasus territory is divided into several parts based on orography and climate: the Ciscaucasia, the Greater Caucasus (North Caucasus and Transcaucasia), the Lesser Caucasus, the Colchis and Kura-Araks Lowlands, and the Transcaucasian Highland (Fig. 1). The administrative boundaries of the territory include the Russian Federation, Georgia, Azerbaijan, and Armenia. The prevailing climate of the Ciscaucasia is warm continental or Dfa according to the Köppen-Geiger classification (Pshegusov et al. 2022). In most of the Greater Caucasus, the climate is generally warm summer continental (Dfb) from the foothills to the middle mountains and cool summer continental (Dfc) or even alpine (ET) in the highlands. The North-Western Caucasus and the Black Sea coast of Western Transcaucasia also have a humid subtropical (Cfa) and oceanic (Cfb) climate. In the Greater Caucasus as a whole, aridity increases from northwest to southeast. The climate of the Colchis Lowland is humid subtropical and oceanic, similar to that in the northwestern part of the Kura-Araks Lowland. The southeastern part of the Kura-Araks Lowland has a cold semi-arid climate (BSk). In the mountainous areas of the Lesser Caucasus and Transcaucasian Highland, a warm summer continental climate prevails (drier to the southeast). A cold semi-arid climate is prevalent in the southern part of the Transcaucasian Highland (Pshegusov et al. 2022).

The Central Caucasus occupies the most highland areas of the northern slopes in the Greater Caucasus (Fig. 1). The climate of the mountainous areas, as throughout the Caucasus, is cool summer continental (Dfc) and alpine (ET) with increasing dryness and continentality as altitude increases. The average annual precipitation is about 900 mm and mean daily temperature ranges from 12.6 °C in July to -6.7 °C in December (data from Terskol weather station, 2150 m a.s.l.).

The most widespread vegetation belts in the Caucasus are subalpine and alpine meadows and nival heaths. The nival belt is a permafrost zone where vegetation consists of mosses, algae and lichens. The alpine belt includes low-grass meadows and alpine heaths. The subalpine belt features fertile soils and a rich vegetation cover with a predominance of mesophytic meadows. The underlying belt of dark coniferous forests of spruce (*Picea orientalis* [L.] Peterm.) and fir (*Abies nordmanniana*) passes through the humid western and central regions of the Greater and Lesser Caucasus. A belt of deciduous forests of beech (*Fagus orientalis*) with hornbeam (*Carpinus betulus*) extends through the foothills and middle mountains of the entire ecoregion. Only in the Transcaucasian Highland deciduous forests are replaced by oaks (*Quercus robur* L., *Q. iberica* Steven ex M. Bieb., etc.) and juniper (*Juniperus excelsa* M. Bieb., *J. foetidissima* Willd., and *J. oxycedrus* L.) forests. Beech forests in this

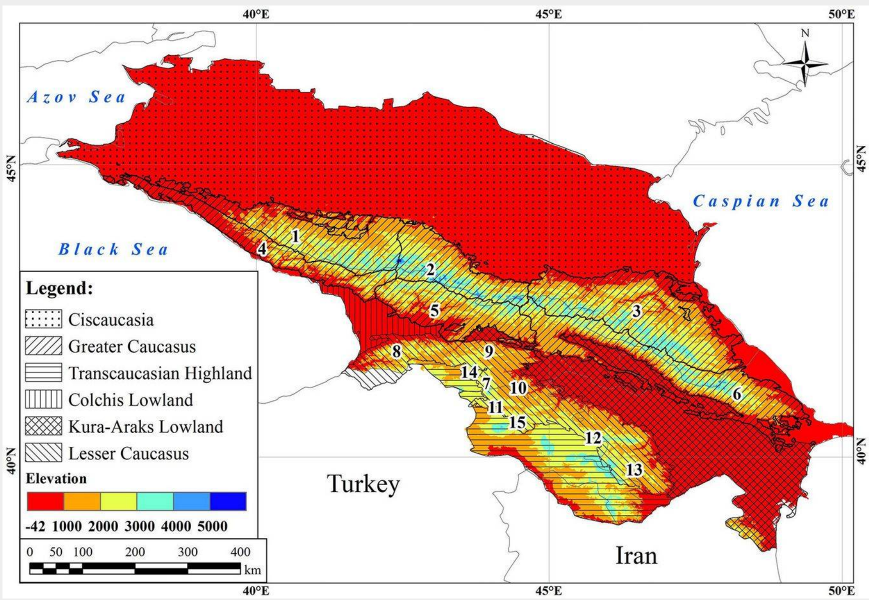


Fig. 1 - The geographic location and orography of the study area. 1 - North-Western Caucasus, 2 - Central Caucasus, 3 - Eastern Caucasus, 4 - Western Transcaucasia, 5 - Central Transcaucasia, 6 - Eastern Transcaucasia, 7 - Javakheti Range, 8 - Meskheti Range, 9 - Trialeti Range, 10 - Somkheti Range, 11 - Bazum Range, 12 - Sevan Range, 13 - Karabakh Range, 14 - Samsari Range, 15 - Tsakhkunyat Range.

Tab. 1 - Results of VIF test used to select noncorrelated environmental variables. Abbreviation, descriptions, and units were based on Title & Bemmels (2018). (*): ENVIREM variables included in the analysis after Variance Inflation Factor (VIF) test.

Variable	Description, units	VIF
PETWettestQuarter *	Mean monthly PET (potential evapotranspiration) of wettest quarter, mm month^{-1}	1.78
EmbergerQ *	Emberger's pluviothermic quotient	1.91
PETColdestQuarter *	Mean monthly PET of coldest quarter, mm month^{-1}	2.06
TRI *	Terrain roughness index	2.24
PETDriestQuarter *	Mean monthly PET of driest quarter, mm month^{-1}	2.37
aridityIndexThornthwaite	Thornthwaite aridity index	4.80
PETWarmestQuarter	Mean monthly PET of warmest quarter, mm month^{-1}	6.37
PETseasonality	Monthly variability in potential evapotranspiration, mm month^{-1}	8.37
minTempWarmestMonth	Minimum temperature of the coldest month, °C×10	9.88
maxTempColdestMonth	Maximum temperature of the coldest month, °C×10	10.57
annualPET	Annual potential evapotranspiration, mm year^{-1}	11.42
thermInd	Compensated thermicity index, °C	11.78
climaticMoistureIndex	A metric of relative wetness and aridity	13.22
growingDegDays5	Sum of mean monthly temperature for months with mean temperature > 5 °C multiplied by number of days	15.63
continentality	Difference between the average temp. of the warmest month and the average temp. of the coldest month, °C	16.48
topoWet	SAGA-GIS topographic wetness index	16.97
growingDegDays0	Sum of mean monthly temperature for months with mean temperature greater than 0 °C multiplied by number of days	17.22
monthCountByTemp10	Number of months with mean temp. > 10 °C	18.34

arid region belong mainly to river floodplains. Pine forests of *Pinus sylvestris* are most widespread in the Greater Caucasus, where they form fragmented stands on the border with subalpine meadows. In the warm humid climate of the Black and Caspian Sea coasts there is a belt of lowland subtropical forests. Semi-deserts form the lower vegetation belts in the relatively arid central and eastern regions of the Caucasus. In the most humid western regions, the lower belt is formed by steppes.

In the Central Caucasus, the belt spectrum includes semi-deserts, steppe meadows and forest-steppes, beech forests, subalpine and alpine meadows, and nival heaths. The beech forest belt is significantly fragmented due to intensive logging during the 20th century (Tembotova et al. 2012, Shkhagapsoev & Kurasheva 2022). Pine forests do not form a vegetation belt, but constitute large undisturbed stands of *Pinus sylvestris* on steep slopes in middle mountains and highlands, mostly within protected areas (Prielbrusye National Park and Kabardino-Balkar High Mountain State Natural Reserve).

Geographic records and environmental variables

The geographic records of *Lobaria pulmonaria* were sourced from the expedition research in 2012-2022 in the Greater and Lesser Caucasus (27 records) and from the Global Biodiversity Information Facility (GBIF 2023 – see Fig. S1 in Supplementary material). Presence points of the species in the Transcaucasian Highland were obtained from the GBIF. A total of 157 species occurrence data from the GBIF (https://doi.org/10.15468/dl.gf6mxy) were used in the analysis. All samples are stored in the herbarium collection of the Tembotov Institute of Ecology of Mountain Territories of the Russian Academy of Science. To address the problem of spatial clustering of geographic records and sampling bias, we applied spatial thinning. This popular correction method, based on the removal of presence points, provides an occurrence dataset from which efficient SDM models can be constructed (Aiello-Lammens et al. 2015, Sillero et al. 2021). Accordingly, the species occurrence data for the regional SDM model, were checked for duplicates and spatially rarefied to one record per 1 km^2 grid cell using the "clean duplicate" function of the R package "ntbox" (Osorio-Olvera et al. 2020). A total of 174 species occurrence data were retained in the analysis after spatial thinning. The local SDM model (Central Caucasus) was built from 32 geographic records with density and location that did not suggest the necessity for spatial thinning.

We used 16 climatic and two topographic variables from the ENVIronmental Rasters for Ecological Modeling, *i.e.*, the ENVIREM dataset (Title & Bemmels 2018, ENVIREM 2023 – Tab. 1). A number of ENVIREM variables (potential evapotranspiration of different quarters, annual potential evapotranspiration, Emberger's pluviothermic quotient, Thornthwaite aridity index, monthly variability in potential evapotranspiration) based on the evapotranspiration, which is directly linked to physiological and ecological processes in vegetation cover (Title & Bemmels 2018). These variables, therefore, are effective for predicting the distribution of biological objects (Adhikari et al. 2019, Tytar 2021). Second, in mountainous areas, many direct environmental predictors (temperature, precipitation, evapotranspiration, and slope steepness) vary consistently with altitude, leading to an increase in their correlation. However, some ENVIREM variables combine direct predictors such as temperature and potential evapotranspiration (Emberger's pluviothermic quotient), precipitation and potential evapotranspiration (Thornthwaite aridity index), slope height and steepness (terrain roughness index), slope steepness and moisture (topographic wetness index). Their use, in our opinion, avoids the application of highly correlated direct variables that have consistent variability along an altitude gradient in mountains. To prevent model overfitting, we used the VIF (Variance Inflation Factor) test in R to select uncorrelated environmental layers (VIF threshold ≤ 3), also excluding latent correlations. As a result, five climatic and topographic variables were involved in the analysis (Tab. 1).

To build BA-models of *Lobaria pulmonaria*, we re-modeled the spatial distribution of lungwort lichen using the abiotic environmental variables and previously obtained BAM-models of *Pinus sylvestris* and *Fagus orientalis* (Pshegusov et al. 2022) as biotic layers. This method is consistent with the correlative approach to ecological niche modeling, which involves incorporating the geography of other species into single-species models (Soberón & Peterson 2005). Movement factor in BAM-models characterizes a species dispersal capacity or accessible areas (Soberón & Peterson 2005, Peterson et al. 2011, Peterson & Soberón 2012). Geographically, the movement factor indicates "the regions that are accessible to dispersal by the species from some original area over a relevant period of time" (Soberón & Peterson 2005, Peterson & Soberón 2012). At present, there is no unified framework for the geographic specification of these regions. In our study, the movement factor indicated the part of the Caucasus that was most accessible to *Lobaria pulmonaria* at regional and local scales. Sites with a species occurrence probability of 0.8-1 in the BA-models were considered optimal areas. The raster of distances from optimal sites, where the probability of the lungwort lichen occurrence remained above 0.5, was used as a movement-layer in the BAM-models of *Lobaria pulmonaria*.

For the regional SDM model, ready-to-use environmental layers were downloaded (ENVIREM 2023) with a resolution of 1 km per pixel. For the local model, environmental layers (except TRI values) were downscaled in resolution to 30 m per pixel by the cubic spline interpolation (Dodgson 1992) and cropped by the mask of the Central Caucasus in the R "dismo" package (Hijmans et al. 2017). The basic assumption of this method is that when the resolution of the environmental layers is downscaled to 30 m per pixel by cubic spline interpolation, the amount of information also increases. The TRI values for the local model were calculated in the R package "spatialEco" (SpatialEco 2023) using data from the Shuttle Radar Topography Mission (SRTM 2023) digital elevation model.

Maxent model development and evaluation

We used the Maxent software ver. 3.4.3 (Phillips et al. 2017) in the R "dismo" package (Hijmans et al. 2017) as an efficient modelling method based on presence-only data (Phillips & Dudík 2008). Optimal model parameters were determined in the R "ENMeval" package (Muscarella et al. 2014). We applied 10,000 background samples and feature types L, Q, H, LQ, and LQH. Regularization multiplier ranged from 0.5 to 2 in increments of 0.5 for local models and from 0.5 to 5 in increments 0.5 for regional models. A total of 20 local and 50 regional models were generated. We used the Akaike's information criterion corrected (AICc), the difference between the AICc and its minimum value (ΔAICc), the continuous Boyce index (CBI), and the area under receiver operating characteristic curve AUC from the training data (AUCtrain) to select the models with optimal combinations of regularization multiplier and feature types (Tab. 2). We preferred models with the lowest AICc, ΔAICc, BIC and highest CBI values, which balance model complexity and accuracy/goodness-of-fit (Boyce et al. 2002, Burnham & Anderson 2002). The higher the AUCtrain values, the better the specificity and sensitivity of model in distinguishing occurrence data from random (background) data (Fielding & Bell 1997). For the resulting A-, BA- and BAM-models of *Lobaria pulmonaria*, we applied a five-fold cross-validation, using 20% of occurrence data as test samples and 80% as training samples (Phillips & Dudík 2008). Accordingly, the AUC values of models were averaged over five replicates.

There is no optimal method for determining the habitat suitability threshold and various thresholds values were used in Maxent modelling (Liu et al. 2013). In this study, we applied a fixed high habitat suitability threshold of 0.8 for optimal localities (Buhl-Mortensen et al. 2019), which reduces the risk of false positives, and a habitat suitability threshold of 0.5 for potentially suitable localities.

The significance of environmental predictors in *Lobaria pulmonaria* distribution was analyzed using percentage contribution (PC, %) and permutation importance (PI, %)

Tab. 2 - Parameters and evaluation of optimal Maxent models of *Lobaria pulmonaria* distribution in the Caucasus at local and regional spatial scales. AICc: Akaike's information criterion corrected; AUC: area under the curve; CBI: continuous Boyce index; RM: regularization multiplier.

Spatial scale	Model	AICc	ΔAICc	CBI	AUCtrain	Feature type	RM
Local	A-Model	205.6	25.7	0.95	0.98	LQH	0.5
	BA-Model	195.14	0.00	0.82	0.99	LQH	1.5
	BAM-Model	190.4	0.00	1.00	0.99	L	0.5
Regional	A-Model	2638.6	17.40	0.99	0.97	LQH	0.5
	BA-Model	2613.8	6.25	0.99	0.97	LQH	0.5
	BAM-Model	2538.6	3.48	1.00	0.98	LQH	0.5

Tab. 3 - Contribution of environmental variables to the Maxent distribution models of *Lobaria pulmonaria* in the Caucasus. PC (percentage contribution): variable contribution in the models; PI (permutation importance): the permutation coefficient. Optimal values: optimal values of variables (0.8 thresholds of habitat suitability) from the response curves. Species occurrence: probability of tree species occurrence in sites with 0.8 habitat suitability threshold for *Lobaria pulmonaria*.

Spatial scale	Environmental variable	A-Model			BA-Model			BAM-Model		
		PC, %	PI, %	Optimal values	PC, %	PI, %	Optimal values	PC, %	PI, %	Optimal values
Local	TRI	49.9	21.4	200-580	8	18.2	200-580	0.1	0.4	200-650
	PETDriestQuarter, mm month^{-1}	24.2	15.5	20-25	1.8	0.7	20-25	0	0	20-25
	embergerQ	21.6	59.8	115-140	8.7	20.3	115-140	0.8	0.5	115-140
	PETColdestQuarter, mm month^{-1}	2.1	1.8	15-17	1.6	4.6	15-17	0.2	0.2	15-17
	PETWettestQuarter, mm month^{-1}	1.2	1.4	80-115	0.3	1.7	80-115	0	0.1	80-115
	Pinus sylvestris occurrence	-	-	-	70.7	42.1	0.8-1	17.6	1.1	0.8-1
	Fagus orientalis occurrence	-	-	-	8.7	10.3	0-0.1	1.3	0	0-0.1
	Movement factor, km	-	-	-	-	-	-	79.9	97.6	0.02
	AUC ± SD	0.96 ± 0.08			0.90 ± 0.18			0.94 ± 0.11		
Regional	embergerQ	59.4	48.2	100-150	34.7	33.8	100-150	3.2	11	100-150
	TRI	17.5	10.9	100-200	0.3	1.4	100-200	0.5	2.1	100-200
	PETDriestQuarter, mm month^{-1}	14.3	18.7	20-40	12.1	18.2	20-40	2.1	17	20-40
	PETWettestQuarter, mm month^{-1}	8	20.2	110-130	3.4	3.9	110-130	1.5	6.5	110-130
	PETColdestQuarter, mm month^{-1}	0.9	2	18-20	0	0	18-20	0.5	2.1	18-20
	Fagus orientalis occurrence	-	-	-	35.1	21.7	0.7-1	28	13.3	0.7-1
	Pinus sylvestris occurrence	-	-	-	14.5	21	0.8-1	8.6	1.5	0.8-1
	Movement factor, km	-	-	-	-	-	-	55.6	46.7	0.03
	AUC ± SD	0.95 ± 0.01			0.96 ± 0.01			0.96 ± 0.01		

(Phillips et al. 2017). We also analysed the optimal values of variables from the response curves, which demonstrate the relationship between predictors and the probability of optimal (0.8 thresholds of habitat suitability) conditions.

After model development and evaluation, we conducted field verification of the results. Points for field verification were randomly generated using the "randomPoints" function of the R package "dismo" (Hijmans et al. 2017). The presence points were exluded from background and the predicted probabilities were used as probability weights. A total of 49 locations were surveyed in the Central Caucasus with predicted probability values ranging from 0.07 to 0.98.

Visualisation and assessment of ecological niche overlap

We used the KDE (Kernel density estimation) method of Blonder et al. (2014) to visualise ecological niches (Hutchinson hypervolumes) as agglomerations of points in an *n*-dimensional space of environmental variables (biologically important independent axes), where the points represent acceptable values of these variables. The KDE method is conceptually simple, requires no absence data and is suitable for SDM modelling (Blonder et al. 2014). It is particularly effective in studying the realised ecological niches of species (Qiao et al. 2017). In our study, the lungwort lichen ecological niches were visualised in the orthogonal space of PCA (Principal Component Analysis) axes that integrated the ENVIREM variables selected by the VIF test. We used the the "FactoMineR" package in R (Lê et al. 2008) for principal component analysis and the "factoextra" (Kassambara & Mundt 2019) and "ggplot2" (Wickham 2009) packages in R for axis extraction and visualisation.

Results

BAM-models of Lobaria pulmonaria distribution

AUC values of the A-models as well as the BA- and BAM-models of *Lobaria pulmonaria* indicated their good predictive success (Tab. 3). The main abiotic predictor for the species distribution in the Central Caucasus was the Terrain roughness index (TRI), which quantifies the local vertical orographic heterogeneity of landscapes (Riley et al. 1999 – Tab. 3). Optimal TRI values (0.8 thresholds of habitat suitability) at the local scale ranged from intermediately rugged (162-239) to highly rugged (498-958) mountain slopes as classified by Riley et al. (1999). In terms of percentage contribution, PETDriestQuarter and embergerQ contributed less to the local A-model. According to the optimal values of these parameters (Emberger 1955, Daget et al. 1988), the lichen occurred mostly in humid areas of the Central Caucasus. At the regional scale, the main environmental predictor was embergerQ, which characterizes humidity and temperature of climate with increasing values for wetter conditions (Emberger 1955, Daget et al. 1988 – Tab. 3). In the Caucasus region, *Lobaria pulmonaria* also preferred humid areas with embergerQ of at least 100. At the same time, the optimal habitats of the lungwort lichen were more gentle slopes, ranging from nearly level (81-116) to intermediately rugged (162-239) according to Riley et al. (1999). The percentage contribution of TRI in the regional A-model was only 17.5%.

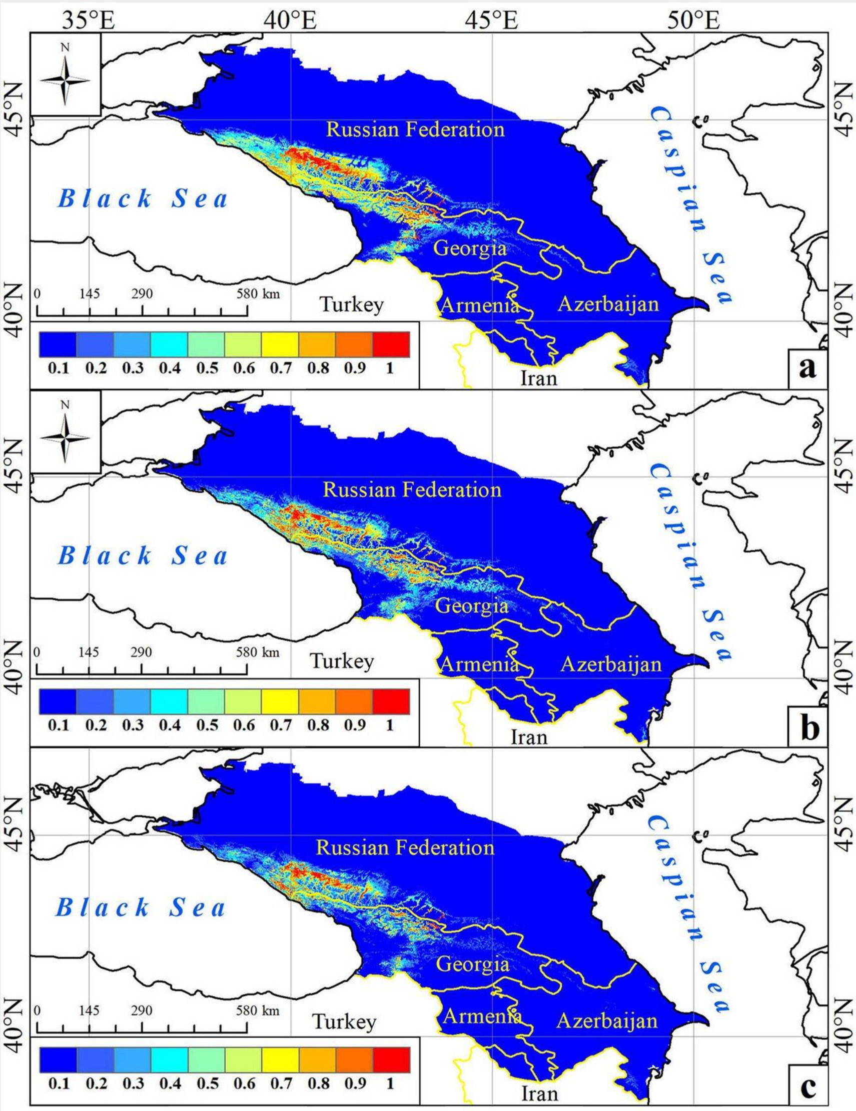
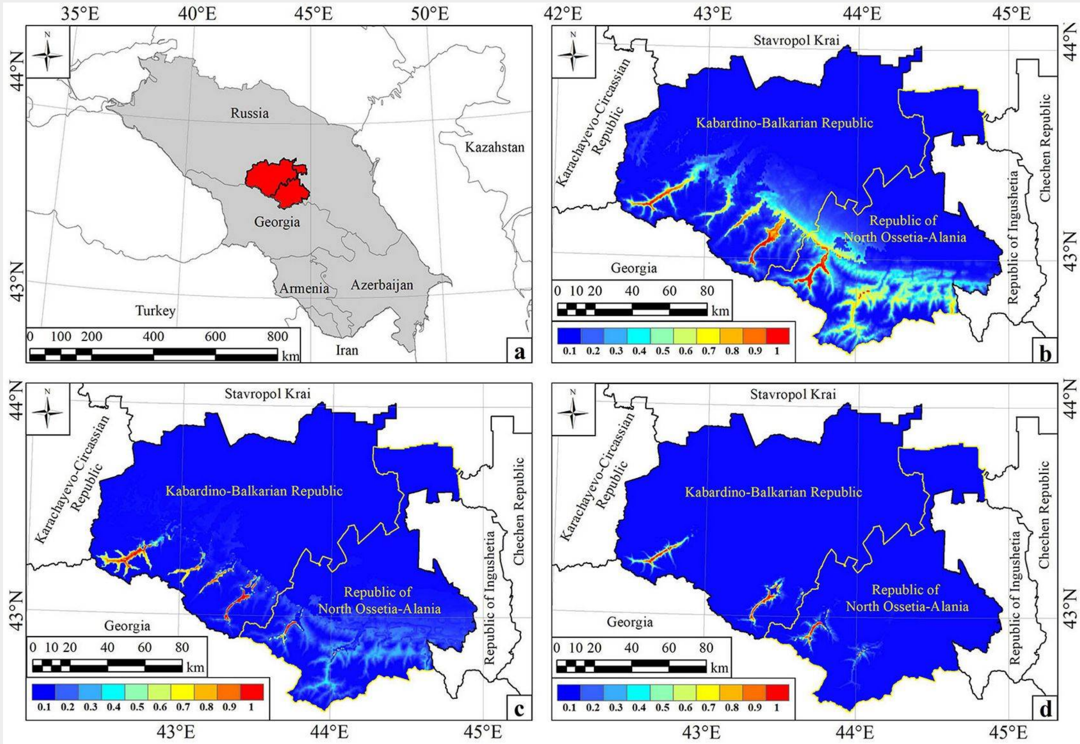


Fig. 2 - Distribution maps of *Lobaria pulmonaria* potential habitats in the Caucasus: A-Model (a), BA-Model (b) and BAM-Model (c). 0-1 is the probability of the species occurrence in the Maxent standard palette colour gradations. Distribution maps were obtained by converting the Maxent output file into a netCDF file with visualisation in PanoplyWin (PanoplyWin 2021).

Fig. 3 - Distribution maps of *Lobaria pulmonaria* potential habitats in the Central Caucasus. The geographic location of the Central Caucasus (a); A-Model (b), BA-Model (c) and BAM-Model (d) of the lichen distribution.



The mapped regional A-model illustrated the concentration of the lichen optimal habitats in the wettest areas of the Caucasus, specifically in the middle mountains and highlands of the North-Western Caucasus, the Western and Central Transcaucasia and the north-western ridges of the Lesser Caucasus (Fig. 2b). The Colchis and Kura-Araks Lowlands, the Ciscaucasian plains as well as the mountainous areas with a dry continental climate (Eastern Caucasus, Transcaucasian Highland, and most of the Lesser Caucasus) had the least suitable abiotic conditions for *Lobaria pulmonaria*. Optimal areas in the Central Caucasus with a relatively dry continental climate were limited to the valleys of large rivers (Fig. 3b).

In the BA-models, the most significant environmental predictors of the lichen distribution were biotic variables (phorophyte occurrence), which masked the effects of abiotic factors, particularly at the local scale (Tab. 3). Climate type (embergerQ) remained an important habitat characteristic of the species at the regional scale. In the Central Caucasus, habitats were considered optimal for *Lobaria pulmonaria* if the probability of *Pinus sylvestris* occurrence at the sites was 0.8-1.0. *Fagus orientalis* occurrence was more important for the lichen distribution at the regional scale. The optimal habitats of the lungwort lichen were those with a probability of beech forest occurrence of 0.7-1.0.

Comparing A- and BA-models, the biotic factor reduced the area of suitable and optimal lungwort lichen habitats by 3.0-3.3 times at the local scale and by 1.3-1.8 times at the regional scale (Tab. 4). In the Central Caucasus, *Lobaria pulmonaria* habitats were mostly predicted in the Kabardino-Balkarian Republic, where the main pure pine stands of the Caucasus region are concentrated (Fig. 3c). In the Caucasus region, areas of the potential lichen habitats decreased evenly throughout the entire predicted range (Fig. 2b). The lesser reduction in the lungwort lichen range in the regional BA-model was probably due to the remaining influence of the macroclimatic embergerQ factor.

Movement factor was the most significant environmental predictor of *Lobaria pulmonaria* distribution in the BAM-models (Tab. 3). However, the percentage contribution of *Fagus orientalis* occurrence in the regional BAM-model was not much less

Tab. 4 - Areas of acceptable and optimal habitats of *Lobaria pulmonaria* in the Caucasus by the Maxent distribution models.

Spatial scale	Model	Local	Regional
Acceptable areas, thousand km^2	A-Model	0.76	25.34
	BA-Model	0.23	19.28
	BAM-Model	0.06	14.83
Optimal areas, thousand km^2	A-Model	0.06	7.3
	BA-Model	0.02	3.94
	BAM-Model	0.01	2.32

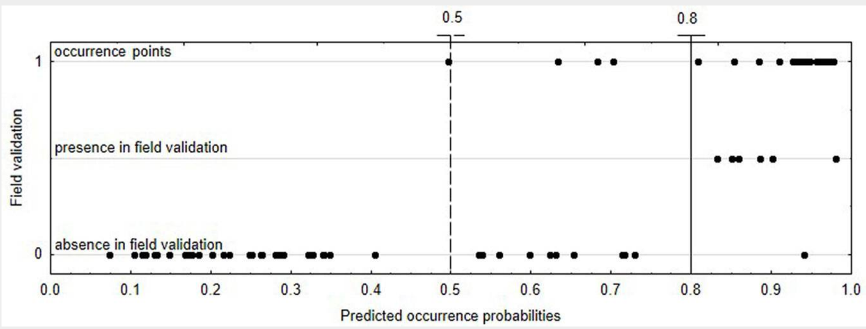


Fig. 4 - Results of field verification of *Lobaria pulmonaria* SDM model in the Central Caucasus. Dotted and solid lines indicate cut-offs at predicted occurrence probabilities of 0.5 and 0.8, respectively (n = 49 localities).

Tab. 5 - Results of a principal component analysis (Varimax normalized) of environmental variables in *Lobaria pulmonaria* occurrence points from the Caucasus. (*): Factor loadings > 0.7.

Environmental variables	Factor 1	Factor 2	Factor 3	Factor 4
embergerQ	-0.31	0.04	0.86*	-0.18
Fagus orientalis occurrence	0.05	0.01	0.81*	0.51
PETColdestQuarter, mm $month^{-1}$	-0.66	-0.10	0.57	0.29
PETDriestQuarter, mm $month^{-1}$	0.97*	-0.06	-0.10	0.12
Pinus sylvestris occurrence	0.07	0.99*	0.02	-0.15
TRI	-0.23	0.18	-0.06	0.91*
Eigenvalue	2.71	1.25	0.91	0.67
Explained variance, %	45.11	20.79	15.17	11.12

than that in the BA-model. The distance of suitable areas from the optimal lichen habitats was only 20 m in the Central Caucasus and 30 m within the Caucasus region. Twenty-metre accessibility of suitable areas reduced the potential range of *Lobaria pulmonaria* in the Central Caucasus by 3.8 times (suitable areas) and 2.5 times (optimal areas) compared to BA-models (Tab. 4, Fig. 3d). The area of species potential habitat at the regional scale decreased only by 1.3 times (suitable areas) and 1.7 times (optimal areas – Tab. 4, Fig. 2c).

Most of the occurrence points used for local model construction were within sites with a high (above 0.8) predicted probability of *Lobaria pulmonaria* occurrence (Fig. 4). Of the 49 locations visited during the field verification in the Central Caucasus, seven points had predicted occurrence probabilities above 0.8. Of these, *Lobaria pulmonaria* presence was confirmed at six locations (presence in field validation – Fig. 4), which accounted for 85.7% of correct predictions. The absence of the species was observed in 43 locations (absence in field validation). Only 11 of them had relatively high (0.5-0.8, 10 locations) and high (above 0.8, one location) predicted probability of occurrence (false positives). The remaining 33 locations with confirmed absence of the lungwort lichen had low, up to 0.5, predicted occurrence probabilities (Fig. 4).

Differentiation of the lungwort lichen ecological niches at local and regional scales

The PCA analysis revealed four main complex factors with a cumulative variation of about 92% in environmental variables (Tab. 5). The climate predictor PETDriestQuarter

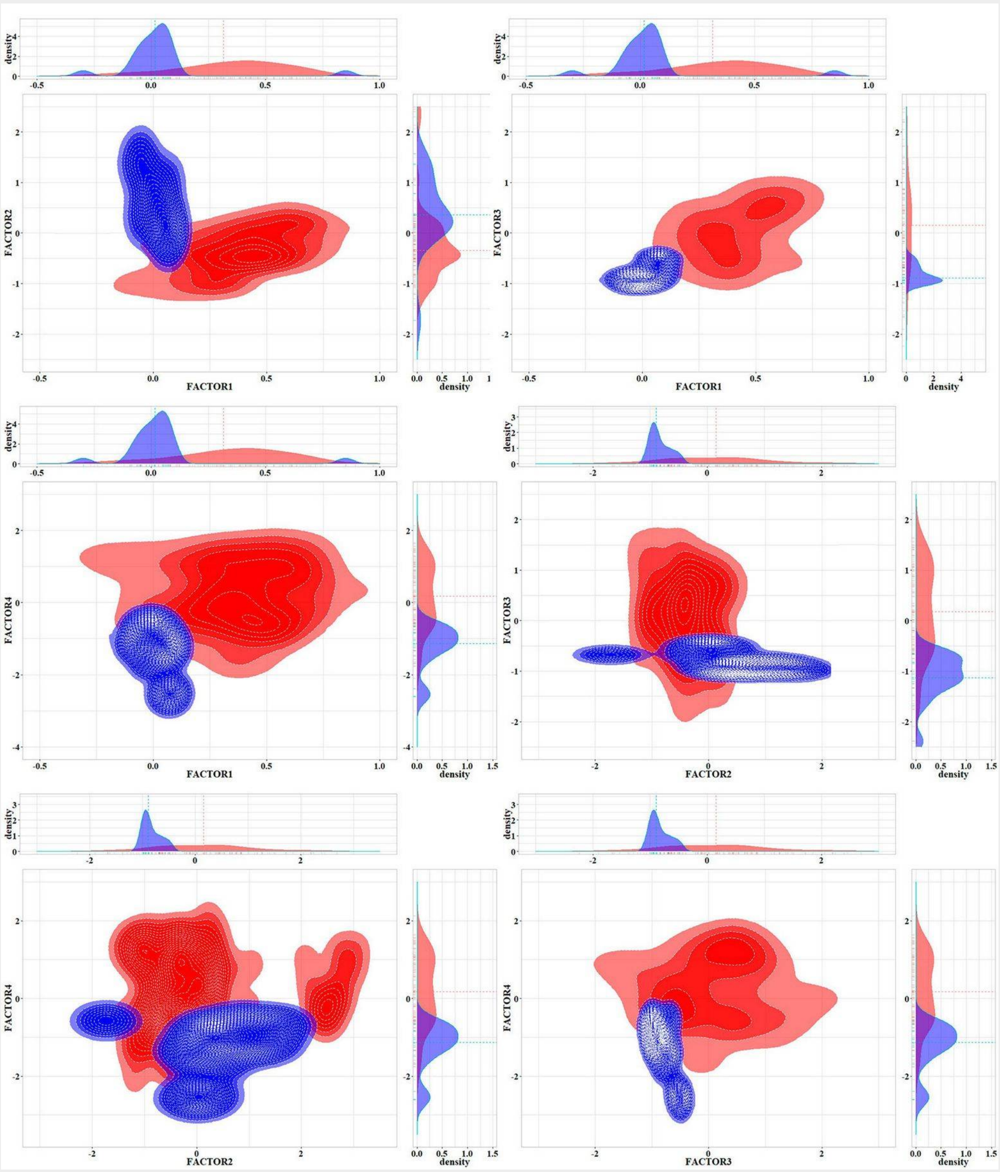


Fig. 5 - Visualization of *Lobaria pulmonaria* ecological niches at the local (blue) and regional (red) spatial scales in the orthogonal space of PCA axes.

mostly formed the first main axis of the PCA (about 45% of variable variance). *Pinus sylvestris* occurrence had the greatest factor loading on the second PCA axis. The two correlated variables of the third PCA factor were embergerQ and *Fagus orientalis* occurrence. The fourth PCA axis was formed by a single orographic variable TRI. Visualisation of the lungwort lichen ecological niches at local and regional spatial scales using the KDE method showed their significant differentiation along all four PCA axes (Fig. 5).

Discussion

Our approach to identifying the distribution factors of the rare epiphytic lichen *Lobaria pulmonaria* in the Caucasus forests was based on the use of species distribution modelling and ecological niche theory. Such an approach allowed us not only to reveal the main environmental predictors and to map the lichen possible distribution, but also to assume a significant influence of spatial scale of research on the modelling results. In contrast to conventional SDM studies, we based our models on the BAM concept (Soberón & Peterson 2005, Peterson et al. 2011, Peterson & Soberón 2012) and considered not only abiotic factors, but also interspecific interactions (occurrence of phorophyte species) and movement factor (accessibility of areas).

Main predictors of Lobaria pulmonaria distribution

Considering that the distribution of epiphytic lichens strongly depends on the localization of their phorophytes, the TRI values in the optimal localities of *Lobaria pulmonaria* probably characterised the orographic distribution of its main epiphytes. Pine forests, which are the main phorophyte of the lungwort lichen in the Central Caucasus, grows on steeper slopes (up to highly rugged) than beech forests, which are the main lichen phorophytes in the Caucasus ecoregion and grow mainly from nearly level to intermediately rugged slopes (Pshegusov et al. 2022). Accordingly, the optimal habitats for *Lobaria pulmonaria* at the local scale were mountain slopes from intermittently rugged to highly rugged, while at the regional scale the optimal slopes ranged from nearly level to intermediately rugged (Tab. 3).

The significance of embergerQ and PETDriestQuarter in *Lobaria* distribution models is consistent with previous studies, which showed the important role of climatic factors in physiological processes and distribution of the lichen. Being macroclimatic large-scale parameters, embergerQ and PETDriestQuarter characterize climate temperature and humidity. Fos et al. (2017) emphasized the relationship of *Lobaria pulmonaria* distribution with climate humidity in the Iberian Peninsula. As in the Caucasus ecoregion, the species mainly occurred in the northern and western parts of the peninsula with a wetter climate (Fos et al. 2017). The bioclimatic models of Eaton & Ellis (2012) demonstrated that a macroclimatic variable such as precipitation positively affects the *Lobaria pulmonaria* growth rate in North America. Considering that there is a positive relationship between thallus size and the number of the diaspores (Carlsson & Nilsson 2009, Mikryukov et al. 2010), precipitation also affects the distribution of lungwort lichen. At the local scale, this factor influences the microclimatic characteristics of habitat humidity, which in turn determine indicators of *Lobaria pulmonaria* distribution efficiency such as soredia maturation, germination and attachment to the substrate (Carlsson & Nilsson 2009, Mikryukov et al. 2010).

Due to the complex interactions of epiphytic lichens with phorophyte species, tree parameters and forest stand characteristics, the analysis of abiotic predictors of *Lobaria pulmonaria* distribution alone is insufficient. At the local scale, the probability of the lichen occurrence was highest (80-100%) in areas optimal for pine forests (Tab. 3). In fact, the lungwort lichen localities in the Central Caucasus were strictly confined to pine forests (Khanov & Pshegusov 2021). In beech stands of the Central Caucasus with a predicted probability of the lichen occurrence of only 10% (Tab. 3), we did not find *Lobaria pulmonaria* despite long-term careful field investigations. In contrast, the spatial localisation of beech forests was a significant predictor of the lichen distribution at the region scale (Tab. 3). The overlapping ranges of *Lobaria pulmonaria* (Fig. 2) and *Fagus orientalis* (Pshegusov et al. 2022) occurred mainly in the western and central parts of the Greater and Lesser Caucasus. This observation supports previous studies that in the Mediterranean region, the lungwort lichen was mainly distributed in humid oceanic areas also optimal for broadleaved forests (Fos et al. 2017). The fragmented more arid eastern part of beech range (Eastern Caucasus and Transcaucasia, south-eastern Lesser Caucasus and Transcaucasian Highland) also was least suitable for the lichen. However, the eastern range of *Fagus orientalis* (Pshegusov et al. 2022) still included some areas unsuitable for *Lobaria pulmonaria* populations. Although the beech forest distribution contributed greatly to the regional BA-model (percentage contribution about 35%), the climatic parameter embergerQ remained equally important (Tab. 3). Therefore, the predicted absence of lungwort lichen in beech forests of the Eastern Caucasus and Transcaucasia, south-eastern Lesser Caucasus and Transcaucasian Highland was most probably caused by unsuitable climatic conditions, which were as important for the lichen distribution as the biotic factor.

It is commonly known that *Lobaria pulmonaria* usually colonised old trees with a large trunk diameter (Carlsson & Nilsson 2009, Brunialti et al. 2015, Ivanova 2015). At the landscape level, the lungwort lichen populations did best in undisturbed old-growth forests with a large area and low fragmentation (Carlsson & Nilsson 2009, Nadyeina et al. 2014, Brunialti et al. 2015, Ignatenko & Tarasova 2018). Moreover, fertile populations of *Lobaria pulmonaria* were most commonly found in low canopy forests or within "gaps" in the canopy layer (Mikryukov et al. 2010, Nadyeina et al. 2014, Ivanova 2015). In dense forests, the lichen preferred the upper parts of tree trunks if there was sufficient humidity (Nadyeina et al. 2014). Based on the above, we hypothesised that the absence of *Lobaria pulmonaria* in beech forests of the Central Caucasus was probably due, firstly, to unsuitable microclimatic conditions for the species. In this area, the main beech forest type is dense stands (canopy density of 0.8-0.9) with insolation and moisture deficit in the understorey (Tembotova et al. 2012, Shkhagapsoev & Kurasheva 2022). Secondly, intensive clear-cutting of beech forests in the Kabardino-Balkarian Republic alone decreased their area by 53.4% between 1957 and 2007 (Tembotova et al. 2012, Shkhagapsoev & Kurasheva 2022). Fragmentation and extensive loss of old-growth forests has probably reduced the suitability of beech stands for *Lobaria pulmonaria* in the Central Caucasus.

The moisture availability in the undergrowth of pine forests in the Central Caucasus varies considerably according to their type. Slope pine forests with rhododendron (*Rhododendron caucasicum* Pall.) in the undergrowth, as well as valley pine green-moss and bilberry (*Vaccinium myrtillus* L.) forests have a relatively humid microclimate (Shkhagapsoev & Kurasheva 2022). Canopy density of such forests rarely exceeds 0.6-0.8. The pine forests of the Central Caucasus are generally distributed on steep slopes in the middle mountains and highlands, which make logging and skidding difficult. The last incidents of intensive destruction of mountain pine forests in Kabardino-Balkaria occurred in the late 1910s, during the civil war, then the forests were protected (Shkhagapsoev & Kurasheva 2022). Thus, sufficient insolation, humidity and extent of pine forests, their relative undisturbedness and the presence of old-growth stands probably explain the occurrence of *Lobaria pulmonaria* in pine forests of the Central Caucasus.

According to the BAM-models, the most important predictor of *Lobaria pulmonaria* distribution at the local and regional scales was the dispersal capability of the species (accessibility of areas), which was only 20 m in the Central Caucasus and 30 m throughout the Caucasus (Tab. 3). This observation supports previous studies that dispersal capability mainly limited the lungwort lichen local distribution in southern Sweden (Ockinger et al. 2005). The established average dispersal distance of vegetative diaspores of the species was 15-30 m (Ockinger et al. 2005, Mikryukov et al. 2010, Jüriado et al. 2011). At the same time, vegetative reproduction by thallus fragments, soredia and/or isidia dominates the lichen life cycle (Matwiejuk & Zbyryt 2013, Brunialti et al. 2015). Vegetative diaspores are spread by wind, snails, insects (Rys 2005) and have a low survival rate (Mikryukov et al. 2010). Sexual reproduction by small ascospores ensures dispersal of *Lobaria pulmonaria* over hundreds of metres, but occurs rarely even in optimal habitats of the species (Carlsson & Nilsson 2009, Brunialti et al. 2015, Ivanova 2015). According to Carlsson & Nilsson (2009), sexual reproduction of the lungwort lichen does not occur if the entire lichen population comprises a single genotype.

Overlap of the lungwort lichen ecological niches at local and regional scales

KDE methods revealed a significant differentiation of *Lobaria pulmonaria* ecological niches formed at the local and regional spatial scales (Fig. 5). The niche divergence by Factor 2 (*Pinus sylvestris* occurrence) and by Factor 3 (embergerQ and *Fagus orientalis* occurrence) is probably related to different substrate preferences of the lichen, *i.e.*, pine forests in the Central Caucasus and beech forests throughout the Caucasus. The localisation of phorophytes also probably determines the niche divergence by orographic Factor 4 (TRI). Pine forests of the Caucasus are distributed on steep slopes in the middle mountains and highlands, while beech stands occur mainly on gentler slopes in the lowlands and middle mountains.

Thus, the spatial localisation patterns and ecological niche parameters of *Lobaria pulmonaria* strongly depended on the scale of the analysed area. According to the theoretical framework of the BAM-diagram (Soberón & Peterson 2005, Barve et al. 2011, Peterson & Anamza 2015), in large-scale studies at a continental or regional level, the importance of bioclimatic variables and the movement factor in species distribution should be particularly high; in local studies interspecific interactions become more important. In this study, we confirmed that the importance of bioclimatic variables in the spatial distribution of biological objects is higher in large-scale studies, while interspecific interactions are more significant in local studies. On the other hand, the contribution of the movement factor to the local BAM-model of *Lobaria pulmonaria* distribution reached 80%, which contradicts the theory on the relative insignificance of area accessibility in local studies (Soberón & Peterson 2005, Barve et al. 2011, Peterson & Anamza 2015). In our opinion, these contradictions were related to the specificity of research in the mountains, where species dispersal is primarily hampered by the factor of geographical isolation, appearing first of all at the local scale.

Conclusions

Spatial scale affected the potential localisation and ecological niche of the epiphytic lichen *Lobaria pulmonaria*. Therefore, the patterns of the lichen spatial distribution at the regional scale are not applicable to explain the species distribution at the local scale. Different abiotic predictors determined the potential lichen distribution in the Central Caucasus (terrain) and throughout the Caucasus (macroclimate). The influence of interspecific relationships (lichen-phorophyte) was more important at the local scale, whereas the regional model retained a significant macroclimate contribution. In the Central Caucasus, the highest probability of the lungwort lichen occurrence (80-100%) was predicted in valley pine forests. In the Caucasus region, the lichen occurrence was most probable in humid beech forests (70-100%) of the North-Western Caucasus, the Western and Central Transcaucasia and the north-western ridges of the Lesser Caucasus. Due to the strong dependence of *Lobaria pulmonaria* distribution on the biotic factor (suitable phorophytes), protection of pine and beech forests in the Caucasus is necessary to preserve the species. According to the final BAM-models, the most significant predictor of the lichen spatial distribution was the movement factor (accessibility of areas), which limited species dispersal from optimal habitats within a radius of 20 m in the Central Caucasus and 30 m through the Caucasus.

The resulting BAM-models had a high predictive accuracy in accordance with the AUC values. Field verification of the local BAM-model showed that using a cut-off value of 0.8, the presence prediction success rate was 85.7%. We identified six new occurrences of *Lobaria pulmonaria* at predicted locations in the Central Caucasus. Therefore, in our opinion, the combination of SDM modelling and ecological niches theory based on the BAM concept is an effective method for studying the potential localisation and the ecological niches of epiphytic lichens.

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Author contributions

RP and VCh planned the study. ZKh carried out the data collection, wrote the first draft. RP performed the statistical analysis and designed the figures. VCh contributed to data analysis, reviewed and edited the manuscript.

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Supplementary Material

Fig. S1 - *Lobaria pulmonaria* occurrence points in the Caucasus.

Link: Pshegusov_4406@suppl001.pdf