An old-growth forest at the Caspian Sea coast is similar in epiphytic lichens to lowland deciduous forests in Central Europe

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We have recorded 138 species (125 of them epiphytic/epixylic) in a single preserved lowland forest in Dagestan (Russia), "Samurski" forest at the west coast of the Caspian Sea. Within its 2,000 hectares, some remnants of old-growth forests persist, dominated by *Acer campestre*, *Carpinus betulus* and *Quercus robur*. This mix of tree species is typical of many lowland deciduous forests in Central Europe, and we found that the lichen flora of Samurski also has much in common with those forests, but less in common with other types of Central European forests. Comparison with geographically closer lowland forests in Azerbaijan, Russia and Iran is impossible due to a lack of data. Using Detrended Correspondence Analysis, we defined a group of species diagnostic for temperate lowland deciduous forests; it includes about 20 species recorded in Samurski, most of which are crustose and usually with *Trentepohlia* as photobiont. In contrast to Central European lowland deciduous forests, the lichen flora of Samurski includes several species known mainly from the oceanic western Caucasus and Western Europe. To enable comparison with "fixed-area" lichen inventories, we have obtained a separate list of 82 lichen species from a detailed survey of a 1 ha plot in one of the best-preserved forest spots in Samurski.

Fifty-nine species in 17 genera (*Arthothelium*, *Bactrospora*, *Bryostigma*, *Catinaria*, *Coniocarpon*, *Cresporhaphis*, *Dendrographa*, *Enchylium*, *Enterographa*, *Inoderma*, *Lecanographa*, *Lepraria*, *Pachnolepia*, *Peridiothelia*, *Sclerophora*, *Xanthoriicola*, *Zwackhia*) are new to Dagestan. *Agonimia flabelliformis*, *Arthonia exilis*, *Bacidina auerswaldii*, *Cresporhaphis wienkampii*, *Caloplaca raesaenenii*, *C. tominii*, *Candelariella superdistans* and *Verrucaria umbrinula* are new to the Greater Caucasus. *Agonimia borysthenica*, *Bacidina adastra* and *Lecanographa lyncea* are new to Russia. *Candelariella superdistans* is new to Asia.

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Es werden 138 Arten (davon 125 epiphytisch/epixyl) in einem einzelnen erhalten gebliebenen Tieflandswald, dem Wald "Samurski" in Dagestan (Russland) an der Westküste des Kaspischen Meeres nachgewiesen. In dem 2000 Hektar umfassenden Gebiet haben einige Reste von alten Waldstandorten überdauert. Sie sind dominiert von *Acer campestre*, *Carpinus betulus* und *Quercus robur*. Diese Baumartenzusammensetzung ist typisch für viele Tieflagenwälder in Mitteleuropa, und auch mit deren Flechtenflora hat der Wald "Samurski" vieles gemein. Die Gemeinsamkeiten mit der Flechtenflora anderer mitteleuropäischer Waldtypen sind geringer. Der Vergleich mit geographisch näher gelegenen Tieflagenwäldern in Aserbaidschan, Russland und dem Iran ist mangels Daten nicht möglich. Mittels Detrended Correspondence Analysis definieren wir eine Gruppe diagnostischer Arten für Tieflagenwälder, bestehend aus ca. 20 Arten aus dem Samurski-Wald, überwiegend Krustenflechten, die meisten mit *Trentepohlia*-Photobiont. Im Unterschied zu mitteleuropäischen Tieflagenwäldern enthält die Flechtenflora von "Samurski" eine Reihe von Arten, die sonst im ozeanischen Westkaukasus und in Westeuropa zu finden sind. Um den Vergleich mit Untersuchungen auf standardisierten Flächengrößen zu ermöglichen, wurde eine 1 ha große Fläche in einem der am besten erhaltenen Waldbereiche des Gebietes detailliert untersucht; dort wurden 82 Arten nachgewiesen.

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59 Arten in 17 Gattungen (*Arthothelium*, *Bactrospora*, *Bryostigma*, *Catinaria*, *Coniocarpon*, *Cresporhaphis*, *Dendrographa*, *Enchylium*, *Enterographa*, *Inoderma*, *Lecanographa*, *Lepraria*, *Pachnolepia*, *Peridiothelia*, *Sclerophora*, *Xanthoriicola*, *Zwackhia*) sind neu für Dagestan. *Agonimia flabelliformis*, *Arthonia exilis*, *Bacidina auerswaldii*, *Cresporhaphis wienkampii*, *Caloplaca raesaenenii*, *C. tominii*, *Candelariella superdistans* und *Verrucaria umbrinula* sind neu für den Großen Kaukasus. *Agonimia borysthenica*, *Bacidina adastra* und *Lecanographa lyncea* sind neu für Russland. *Candelariella superdistans* ist neu für Asien.

Key words: Dagestan, forest protection, Hyrcanian, inventory, lichen diversity, lowland forest indicator, Russia.

Introduction

Surveys of various organisms in old-growth forests are important for forest quality assessment and forest protection, and epiphytic lichens are among the most reliable indicators of forest-continuity and forest quality (Johansson & Gustafsson 2001, Paillet et al. 2010). The lack of data about lichen diversity in remnants of lowland deciduous old-growth forests in Russia (Urbanavichus, unpublished) is thus a gap that needs to be filled.

We first provide data on lowland deciduous forest lichen diversity in Russia from a protected area "Samurski" that includes several square kilometres of lowland forest in Dagestan, including old-growth forest remnants. It is situated in the southernmost part of Russia, at the Caspian Sea coast and at the border with Azerbaijan. It is the only well-preserved lowland forest along the Caspian Sea in Russia: more northern territories of Dagestan are drier and covered by cultural steppe or spots of degraded or secondary tree vegetation. Samurski is, however, adjacent to a larger forested area in northern Azerbaijan that may have a similar character (lichen diversity data are absent from this area). Humid Hyrcanian forests (annual rainfall to 2,000 mm) further south in Azerbaijan and those in northern Iran are distinct and have quite different tree species, e.g. *Acer velutinum* Boiss., *Albizia julibrissin* Durazz., *Gleditsia caspica* Desf., *Parrotia persica* (DC.) C.A.Mey., *Pterocarya pterocarpa* (Michx.) Kunth ex I.Iljinsk., *Quercus castaneifolia* C.A.Mey., and *Zelkova carpinifolia* (Pall.) K.Koch (Akhani et al., 2010). Although relevant lichen inventories are missing for Hyrcanian forests, their lichen flora has definitely a more oceanic character in comparison with the much dryer Samurski: it contains some epiphyllous lichens (Novruzov & Alverdieva 2014, Barkhalov 1975) which are absent from Samurski forest. In this context, Samurski and woodlands in its Azerbaijan vicinity represent a remote group of forests dominated by *Acer campestre*, *Carpinus betulus* and *Quercus robur* (more information in "locality description"). We have not been able to locate the nearest lowland old-growth forests of similar tree species composition, but they are probably hundreds of kilometers distant. Some lowland forest types in Central Europe have very similar tree species composition with identical tree dominants (e.g. Vondrák et al. 2016). Those forests are more than 2,000 km distant from Samurski.

Our primary aim was to perform a lichen inventory of the Samurski forest. As a secondary aim, we compare epiphytic lichen composition of Samurski with various Central European forest types to assess whether, and to what extent, the forest type and tree species composition may determine lichen diversity; i.e. we consider whether those Central European forests dominated by *Acer campestre*, *Carpinus betulus* and *Quercus robur* have a lichen flora similar to Samurski.

Study area

The surveyed forest "Samurski" is located in the south-east of Dagestan, at the border with Azerbaijan, in the delta of the Samur river; it covers an area of c. 2,000 ha and it is part of a State Nature Sanctuary (also called Samurski) of federal importance with a total area of 11,200 ha. Altitude of the Samurski forest ranges between -25 to 35 m asl. Its climate is warm temperate; average annual temperature is 12.6 °C (1.4 °C in January, 24.5 °C in August, the latter being the warmest month). Average annual rainfall is low (400 mm), but the humidity is high due to the vicinity of the Caspian Sea, a dense river system and high groundwater level; average relative air humidity is 78 % (GADJIEVA & SOLOVYEV 1996).

Forest types in Samurski

Core forests with dense tree cover are dominated by *Acer campestre* L., *Carpinus betulus* L. and *Quercus robur* L. *Ulmus campestris* L. and various shrubs (*Cornus mas* L., *Crataegus* spp., *Euonymus europaea* L., *E. verrucosa* Scop., *Mespilus germanica* L., *Prunus caspica* Kov. et Ekim., *Rosa* spp. and *Swida australis* (C.A.Mey.) Pojark. ex Grossh.) are not uncommon (Figs. 2, 3). Lianas are absent from most of the trees. The dominant herbs include *Brachypodium sylvaticum* (Huds.) P.Beauv., *Buglossoides purpurocaerulea* (L.) I.M.Johnst., *Carex sylvatica* Huds., *Euphorbia amygdaloides* L. and *Sanicula europaea* L. This core forest is the forest type richest in epiphytic lichen species and most of the species in our list were recorded here.

Woodlands with sparse tree cover are formed by the warm temperate Liana-tugai forest (Fig. 1). This is the only place in Russia where some Hyrcanian elements occur (e.g. *Hedera pastuchowii* Woronow, *Pyracantha coccinea* M.Roem., etc.; see YAROVENKO et al. 2004). Although this forest type is rich in plant species (70 woody plants and about 300 species of herbs; NOVIKOVA & POLYANSKAYA 1994), its epiphytic lichen flora is poor, partly due to the scarcity of substrata – tree trunks are usually strongly shaded by lianas (e.g. *Clematis orientalis* L., *C. vitalba* L., *Hedera pastuchowii, Humulus lupulus* L., *Lonicera caprifolium* L., *Periploca graeca* L., *Rubus* spp., *Smilax excelsa* L. and *Vitis silvestris* C.C.Gmel.; LITVINSKAYA & MURTAZALIEV 2015). This liana forest is dominated by *Alnus barbata* C.A.Mey., *Juglans regia* L., *Populus nigra* L., *Pyrus caucasica* Fed. and *Salix alba* L.

Open areas along the sea shore and along large delta channels are dominated by wormwood-grassy semi-desert complexes and psammophilous/halophilous vegetation with the shrubs *Elaeagnus angustifolia* L. and *Tamarix ramosissima* Ledeb., and with herbaceous dominants *Artemisia tschernieviana* Besser, *Cakile euxina* Pobed., *Convolvulus persicus* L., *Elymus giganteus* Vahl., *Plantago arenaria* Waldst. & Kit. and *Tournefortia sibirica* L. (YAROVENKO et al. 2004).

Material and methods

The specimens of lichens, lichenicolous fungi and non-lichenized saprophytic fungi were collected from 11 localities (see the list below) in Samurski forest in July 2015 (Fig. 4). The work occupied six hours in each of three days and was performed by three lichenologists (first three authors); the total field time is thus about 54 person-hours. One of the three days was selected for a survey of lichen diversity in a 1 ha square plot of well preserved old-growth forest dominated by *Acer campestre*, *Carpinus betulus* and *Quercus robur* (locality 9 in the list below). Lichens recorded in the plot are included in the list of recorded species below. Diversity results from the plot are discussed separately in the context of existing fixed-area/fixed-effort surveys of forest lichens.

Fig. 1: Lianas in the warm temperate Liana-tugai forest (photo from loc. 11)

Fig. 2: Forest dominated by *Carpinus betulus* (photo from loc. 2)

Morphological and microscopic investigations were done by light microscopy and with the use of routine spot tests (KOH, hypochlorite, paraphenylenediamine and UV light). The main sources for the identification of lichens and allied fungi were: Clauzade & Roux (1985), Egea & Torrente (1994), Nimis & Martellos (2004), Smith et al. (2009), Dymytrova et al. (2011), Guzow-Krezmińska et al. (2012), Arup et al. (2013), Wirth et al. (2013), Frisch

Fig. 3: Forest dominated by *Quercus robur* (photo from loc. 9)

et al. (2014), Otálora et al. (2014) and Frisch et al. (2015). Nomenclature follows the most recent concepts (see the references above). The specimens are deposited in the herbaria of Mountain Botanical Garden Dagestan Science Centre (DAG), Institute of Botany, Academy of Sciences of the Czech Republic (PRA) and in the private herbarium of G. Urbanavichus.

Presence/absence data for epiphytic lichens from Central European old-growth forest inventories mainly from the Czech and Slovak Republic abstracted by Vondrák et al. (2015, 2016) were supplemented by some recent data and resulted in a dataset from 41 localities (Table 2). We applied the same taxonomic concepts when extracting data as we used in our own dataset. Similarity in species composition (only epiphytic/epixylic lichens) of Samurski forest with Central European old-growth woodlands was assessed by the number of shared lichen species (Table 2), by Sørensen's similarity index (Sørensen 1948), and by the Detrended Correspondence Analysis (DCA). DCA ordination in Canoco 5 (Ter Braak & Šmilauer 2012), based solely on species presences/absences in all 42 localities (including Samurski), was employed to display (1) similarities of localities according to lichen species assemblages, and (2) similarities among lichen species based on their occurrence at the localities.

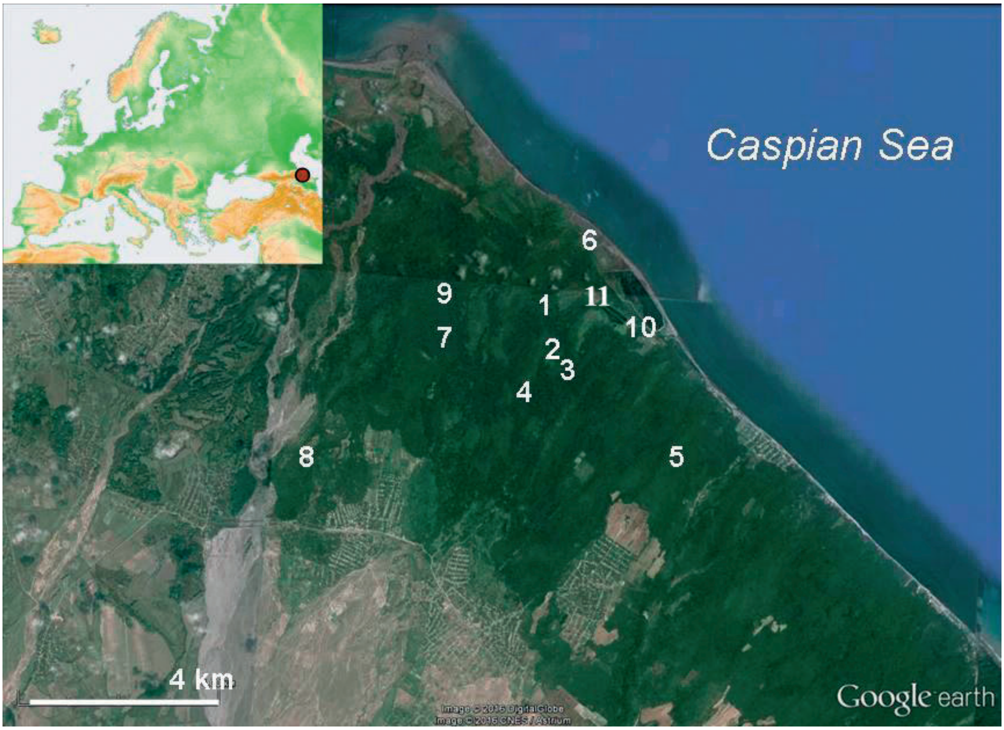

Fig. 4: The study area with investigated sites numbered according to the list in the text.

The significance of selected characteristics of the localities (dominant tree species in localities, forest type, altitude and geographical coordinates) was tested in Canonical Correspondence Analysis (CCA, in Canoco 5) using Monte-Carlo permutation tests with 999 permutations, as marginal effects (Table 3). Marginal effect is the effect of a single predictor, independent of the others. In the datasets for all analyses (also for Sørensen's similarity indices), we have excluded all saxicolous species from Samurski and species only recorded in sites 6 and 10 (coastal communities with shrubs and poplar trees). For the CCA and DCA dataset, we excluded species that occurred at a single locality (the whole Samurski is considered here as locality); modified dataset contains 472 lichen species.

List of the investigated sites

For all sites: Russia, North Caucasus, Republic of Dagestan, Magaramkentsky district, State Nature Sanctuary "Samurski".

1 41°51'50.60"N/48°31'35.00"E, alt. 0 m, forest dominated by *Carpinus betulus*

2 41°51'22.00"N/48°31'48.80"E, alt. 5 m, forest dominated by *Carpinus betulus*

3 41°51'13.50"N/48°31'59.90"E, alt. 10 m, mixed forest dominated by *Carpinus betulus* and *Quercus robur*

4 41°50'58.80"N/48°31'40.00"E, alt. 17 m, mixed forest dominated by *Carpinus betulus* and *Quercus robur*

5 41°50'13.80"N/48°33'59.50"E, alt. 3 m, edge of open forest along forest road with low trees of *Crataegus* sp., *Quercus robur*, *Ulmus campestris*

6 41°52'56.30"N/48°32'10.50"E, alt. -25 m, coastal vegetation on the dunes (*Artemisia* sp., *Tamarix ramosissima*)

7 41°51'38.40"N/48°30'13.10"E, alt. 11 m, forest dominated by *Quercus robur*

8 41°49'42.70"N/48°27'59.70"E, alt. 35 m, mixed forest with *Acer campestre*, *Alnus* sp., *Carpinus betulus*, *Crataegus* sp., *Populus nigra*, *Quercus robur* and *Ulmus campestris*

9 41°51'54.80"N/48°30'11.40"E, alt. 7 m, 1 ha plot in the old growth forest dominated by of *Quercus robur*, *Acer campestre* and *Carpinus betulus*

10 41°51'59.40"N/48°33'19.80"E, alt. -23 m, coastal site, sparse vegetation, single trees of *Populus nigra* and *Elaeagnus angustifolia*

11 41°52'12.60"N/ 48°32'20.99"E, alt. -13 m, forest glade after cutting, single trees of *Populus nigra* and *Quercus robur*

List of substrata and their abbreviations (for the species list below)

Acer campestre (Ace), *Alnus* sp. (Aln), *Artemisia tschernieviana* (Art), calcareous stone (cal), *Carpinus betulus* (Car), corticolous (cor), epixylic (epix), *Juglans regia* (Jug), *Mespilus germanica* (Mes), *Populus nigra* (Pop), *Quercus robur* (Que), siliceous pebbles (sil), slate (sla), soil (soil), *Tamarix ramosissima* (Tam), twigs (twi), *Ulmus campestris* (Ulm).

Results

List of species

The 138 recorded lichen species are listed in alphabetical order followed by locality numbers and substrata (see above), and voucher specimen data (acronyms of collectors with number of specimens). New species to Russia are marked with “*”, new to Asia with “!!!”, new to the Greater Caucasus with “!!”, and new to Dagestan with “!”. The list includes 125 epiphytic/epixylic and few saxicolous lichen species. 82 epiphytic/epixylic lichen species recorded on the 1 ha plot of old-growth forest dominated by *Acer campestre*, *Carpinus betulus* and *Quercus robur* are also included (loc. 9). Five lichenicolous and non-lichenized taxa are listed below the lichen species list.

!***Acrocordia cavata*** (Ach.) R.C.Harris: 1 (cor Que) AI, GU

Acrocordia gemmata (Ach.) A.Massal.: 1, 9 (cor Ace, Car, Que) AI2, GU4, JV

*!!***Agonimia borysthenica*** L.V.Dymytrova, O.Breuss & S.Ya.Kondr.: 1, 7 (cor Que) AI, GU

!!***Agonimia flabelliformis*** Halda, Czarnota & Guzow-Krzemińska: 4, 7, 9 (cor Car, Que) AI, GU2, JV2

Alyxoria varia (Pers.) Ertz & Tehler: 1, 2, 4, 8, 9 (cor Car, Que) AI, GU5, JV2

Amandinea punctata (Hoffm.) Coppins & Scheid.: 6, 9 (cor Tam, Que) GU

Anaptychia ciliaris (L.) Flot.: 1 (cor Que) GU

Anaptychia setifera (Mereschk.) Räsänen: 5, 9 (cor Que, Ulm) GU

Anisomeridium biforme (Schaer.) R.C.Harris: 1, 2, 5, 9 (cor Car, Que) AI, GU, JV (anamorph)

Anisomeridium polypori (Ellis & Everh.) M.E.Barr: 1, 9 (cor Que) AI, JV

Arthonia atra (Pers.) A.Schneid.: 1, 2, 5, 6, 8, 9 (cor Ace, Aln, Car, Que, Tam, Ulm) GU9, JV2

!!***Arthonia exilis*** (Flörke) Anzi: 4 (cor Pop) AI2

Arthonia punctiformis Ach.: 9 (cor Que) GU

Arthonia radiata (Pers.) Ach.: 1 (cor Que) GU

!***Arthonia spadicea*** Leight.: 7 (cor Que) AI

!***Arthothelium spectabile*** A.Massal.: 1, 2, 3, 4, 9 (cor Ace, Car, Jug). Differs from *A. spectabile* s.str. by brown epihymenium turning olive in KOH; ascospores darken in early stage. AI, GU5, JV2

!***Athallia cerinelloides*** (Erichsen) Arup, Frödén & Søchting: 1 (cor Que) AI, GU

Athallia pyracea (Ach.) Arup, Frödén & Søchting: 1, 5, 9 (cor Ace, Que, Ulm) AI, GU2, JV

!***Athallia skii*** (Khodos., Vondrák & Šoun) Arup, Frödén & Søchting: 6 (twi Art) AI, GU, JV

!***Athallia vitellinula*** (Nyl.) Arup, Frödén & Søchting: 5 (sil) GU

!!***Bacidia auerswaldii*** (Hepp ex Stizenb.) Mig.: 9 (cor Car, Que). Ascospores often only 3-septate, but well-developed spores with more septa rarely observed. Characterized by tiny granules, distinctly smaller than in *B. rubella*. JV2

!***Bacidia fraxinea*** Lönnr.: 9 (cor Que) GU, JV

!***Bacidia incompta*** (Borrer) Anzi: 9 (cor Ulm) JV

Bacidia rubella (Hoffm.) A.Massal.: 1, 4, 5, 8, 9 (cor Car, Que, Ulm) AI4, GU5

*!!***Bacidina adastra*** (Sparrius & Aptroot) M.Hauck & V.Wirth: 9 (cor Ace). Apothecia without pigmentation in section; thallus forming entirely sorediate crust; i.e. without delimited soralia. JV

Bacidina delicata (Larbal. ex Leight.) V.Wirth & Vězda: 3, 9 (cor Car, Jug, Que) JV2

!***Bacidina phacodes*** (Körb.) Vězda: 9 (cor Ace) JV2

!***Bactrospora dryina*** (Ach.) A.Massal.: 4, 9 (cor Car, Que). Ascospores rarely dividing into 2-cell segments; some samples not clearly distinct from *B. homalotropa*. AI2, GU, JV2

!***Bryostigma*** aff. ***muscigenum*** (Th.Fr.) Frisch & G.Thor: 9 (cor Car). All characters similar to *B. muscigenum*, but the minute ascospores (10–12 µm long) 3-septate. JV2

Calicium glaucellum Ach.: 5, 9 (epix Que) AI2

Calicium salicinum Pers.: 5 (epix Que)

Caloplaca cerina (Hedw.) Th.Fr: 1, 9 (cor Ace, Que) GU

!***Caloplaca lucifuga*** G.Thor: 4 (cor Car) AI

Caloplaca obscurella (J.Lahm ex Körb.) Th.Fr.: 1 (cor Que) GU

!!***Caloplaca raesaenenii*** Bredkina: 5 (cor Que) AI

Caloplaca teicholyta (Ach.) J.Steiner: 11 (sla) AI

!!***Caloplaca tominii*** (Savicz) Ahlner: 11 (sla) AI

!***Caloplaca ulcerosa*** Coppins & P.James: 10 (cor Pop) AI, GU

Candelariella antennaria Räsänen: 1 (cor Que) GU

Candelariella aurella (Hoffm.) Zahlb: 5, 11 (sil, sla) AI, GU

!!!***Candelariella superdistans*** (Nyl.) Malme: 4 (cor Pop) AI, GU

Candelariella xanthostigma (Ach.) Lettau: 1, 5, 9 (cor Que, Ulm) AI2, GU3

Catillaria nigroclavata (Nyl.) J.Steiner: 1, 9 (cor, twi Que) GU, JV

!***Catinaria atropurpurea*** (Schaer.) Vězda & Poelt: 3 (cor Jug) GU

Chaenotheca brunneola (Ach.) Müll.Arg.: 7, 9 (epix Que) AI, GU

!***Chaenotheca hispidula*** (Ach.) Zahlbr.: 9 (cor Car) AI, GU, JV

Chaenotheca trichialis (Ach.) Th.Fr.: 9 (epix Que)

Circinaria calcarea (L.) A. Nordin, S.Savić & Tibell: 5 (cal)

Cladonia chlorophaea (Flörke ex Sommerf.) Spreng.: 5 (epix Que) AI

Cladonia coniocraea (Flörke) Spreng.: 9 (epix Que)

Cladonia fimbriata (L.) Fr.: 5 (base of trunk Car)

Cladonia foliacea (Huds.) Willd.: 5 (soil)

Cladonia rangiformis Hoffm.: 5 (soil)

Coenogonium pineti (Ach.) Lücking & Lumbsch: 9 (cor Que)

Collema furfuraceum (Arnold) Du Rietz: 5 (cor Que)

Collema subflaccidum Degel.: 4, 5 (cor Que) AI

!***Coniocarpon cinnabarinum*** DC: 1 (cor Car) AI

!***Dendrographa decolorans*** (Turner & Borrer) Ertz & Tehler: 4, 8, 9 (cor Car, Que) AI2, GU2, JV2

!***Diplotomma chlorophaeum*** (Hepp ex Leight.) K.P. Singh & S.R.Singh: 5 (sil) GU

!***Enchylium conglomeratum*** (Hoffm.) Otálora, P.M.Jørg. & Wedin: 5 (cor Que) AI

!***Enterographa crassa*** (DC.) Fée: 1, 2, 4, 7, 9 (cor Aln, Car, Que) AI3, GU4, JV

!***Enterographa hutchinsiae*** (Leight.) A.Massal: 9 (cor Car) AI, GU, JV

Evernia prunastri (L.) Ach.: 5, 6 (cor Tam, Ulm) GU2

Flavoparmelia caperata (L.) Hale: 9 (twi, cor Que)

Flavoplaca flavocitrina (Nyl.) Arup, Frödén & Søchting: 5 (cal) GU

!***Graphis betulina*** (Pers.) Ach.: 1, 9 (cor Car, Que) AI2, GU2

Graphis scripta (L.) Ach.: 1, 5, 9 (cor Aln, Car, Mes, Que) AI, GU2, JV2

!***Gyalecta truncigena*** (Ach.) Hepp: 5 (cor Que) AI

Gyalolechia flavorubescens (Huds.) Søchting, Frödén & Arup: 9 (cor Que)

Hyperphyscia adglutinata (Flörke) H.Mayrhofer & Poelt: 1, 5, 9 (cor Que, Ulm) GU3, JV

!***Inoderma byssaceum*** (Weigel) Gray: 9 (cor Que) JV (anamorph)

!***Lecania croatica*** (Zahlbr.) Kotlov: 9 (cor Car, Que) GU2

Lecania cyrtella (Ach.) Th.Fr.: 6 (twi Art, Tam) GU

Lecania cyrtellina (Nyl.) Sandst.: 6 (twi Art) GU

!***Lecania fuscella*** (Schaer.) A.Massal.: 4 (cor Pop) AI

Lecania naegelii (Hepp) Diederich & van den Boom: 1, 5, 9 (cor Ace, Car, Que) AI, GU3, JV

*!!***Lecanographa lyncea*** (Sm.) Egea & Torrente: 4, 9 (cor Car, Que). Although most characters fit *L. lyncea*, numerous soft brownish spots on thallus better fit *L. amylacea*. AI2, JV

!***Lecanora argentata*** (Ach.) Malme: 4 (cor Car) AI

Lecanora carpinea (L.) Vain.: 1, 2, 5, 9 (cor Ace, Car, Que) AI2, GU2

Lecanora dispersa (Pers.) Flörke: 5 (sil) GU

!***Lecanora expallens*** Ach.: 9 (cor Car)

Lecanora glabrata (Ach.) Nyl.: 4 (cor Car) AI

Lecanora hagenii (Ach.) Ach.: 6 (cor Tam) GU

!***Lecanora leptyrodes*** G.B.F.Nilsson: 9 (cor Ace, Car, Que) JV

!***Lecanora populicola*** (DC.) Duby: 4 (cor Pop) AI2, GU

Lecanora saligna (Schrad.) Zahlbr.: 5, 9 (epix Que) AI, GU

!***Lecanora sambuci*** (Pers.) Nyl.: 6 (twi Art, Tam) GU

Lecanora saxicola (Pollich) Ach.: 5 (sil) GU

!***Lecidea erythrophaea*** Flörke ex Sommerf.: 1, 9 (cor Ace, Car, Que) AI, GU2, JV4

Lecidella elaeochroma (Ach.) M. Choisy: 9 (cor Que) f. ***soralifera*** (Erichsen) D.Hawksw.: 9 (cor Ace, Car) GU, JV3

Lecidella euphorea (Flörke) Kremp.: 5 (cor Que) AI, JV

Lecidella laureri (Hepp) Körb.: 1, 5, 8, 9 (cor Ace, Car, Que, Ulm) GU7

!***Lepraria finkii*** (Hue) R.C.Harris: 9 (cor Ace, Car, Que) AI, GU2, JV

Melanelixia subaurifera (Nyl.) O.Blanco et al.: 1, 5, 9 (cor Que) AI, GU2

Micarea inconspicua ined.: 9 (epix). Belongs to the *M. prasina* group, but has inconspicuous film-like thallus without goniocysts, and small (<<0.2 mm diam) apothecia without pigmentation; description being prepared by Czarnota et al. JV

!***Micarea micrococca*** (Körb.) Gams ex Coppins: 9 (epix). JV

!***Micarea prasina*** Fr.: 7, 9 (epix Que) AI, JV

Micarea substipitata ined.: 9 (epix Car). Peculiar ecology: growing in dry hollows in bark or hard wood in ancient woodlands; apothecia without pigmentation; ascospores 0–1-septate, 8–10 × 2.5–3 µm; pycnidia doliiform, without pigmentation; conidia 5 × 1.5 µm; all tissues C-; description being prepared by Palice. JV2

!***Opegrapha niveoatra*** (Borrer) J.R.Laundon: 9 (cor Ace, Car) JV

!***Opegrapha vermicellifera*** (Kunze) J.R.Laundon: 1, 7, 9 (cor Ace, Car, Que) AI4, GU4, JV2

!***Opegrapha vulgata*** auct. (the name is used in the usual sense, on the assumption that a recent conservation proposal will succeed): 8 (cor Que) GU

!***Pachnolepia pruinata*** (Pers.) Frisch & G.Thor: 4 (cor Car) AI

Parmelia sulcata Taylor: 9 (cor Car, Que) GU

Parmelina tiliacea (Hoffm.) Hale: 1, 5, 9 (cor Que) AI, GU2

Parmotrema perlatum (Huds.) M.Choisy: 5 (cor Que) AI

Pertusaria albescens (Huds.) M.Choisy & Werner: 5 (cor Que) AI

Phaeophyscia nigricans (Flörke) Moberg: 5 (cor Que) AI

Phaeophyscia orbicularis (Neck.) Moberg: 5, 9 (twi, cor Ace, Que, Ulm) AI2, GU3

Phlyctis agelaea (Ach.) Flot.: 1, 5, 9 (cor Ace, Car, Que, Ulm) AI, GU2

Phlyctis argena (Spreng.) Flot.: 1 (cor Car) AI

Physcia adscendens H.Olivier: 1, 5, 9 (twi, cor Ace, Car, Que, Ulm) AI2, GU6

Physcia aipolia (Ehrh. ex Humb.) Fürnr.: 1, 9 (cor Que) GU

Physconia distorta (With.) J.R.Laundon: 9 (twi, cor Que)

Physconia enteroxantha (Nyl.) Poelt: 4, 5, 9 (cor Que) AI2, GU

Physconia perisidiosa (Erichsen) Moberg: 4, 5, 9 (cor Que) AI, GU

Placynthiella dasaea (Stirt.) Tønsberg: 5, 7 (epix Que) AI2

Placynthiella icmalea (Ach.) Coppins & P.James: 1, 9 (epix Que) AI, GU

Porina aenea (Wallr.) Zahlbr.: 1, 2, 3, 5, 9 (cor Ace, Car, Jug, Que, Ulm) Some specimens have longer spores (25–28 µm). GU7, JV2

!***Pyrenula chlorospila*** Arnold: 1, 2, 5, 9 (cor Ace, Car, Que, Ulm) AI2, GU6, JV

!***Pyrenula macrospora*** (Degel.) Coppins & P.James: 9 (cor Car). Similar to *P. nitida*, but distinguished by the larger perithecia lacking K + purple-red substances, presence of pseudocyphellae and longer spores (33–36 µm long). GU

Pyrenula nitida (Weigel) Ach.: 9 (cor Que) GU

Pyrenula nitidella (Flörke ex Schaer.) Müll.Arg.: 1, 2, 9 (cor Ace, Car) AI, GU2, JV2

Ramalina farinacea (L.) Ach.: 5, 9 (twi, cor Car, Ulm) GU2

Ramalina pollinaria (Westr.) Ach.: 5 (cor Que)

!***Sclerophora farinacea*** (Chevall.) Chevall.: 9 (cor Car, Ulm). Spores 5–8 µm diam., samples with smaller spores may be identified as *S. amabilis*, but strong white pruina on exciples is distinct. JV2

!***Strigula affinis*** (A.Massal.) R.C.Harris: 9 (twi Que). Similar to *Porina aenea*, but with apically thickened asci, larger and obtuse spores and inconspicuous pale thallus. JV

!***Strigula glabra*** (A.Massal.) V.Wirth: 1, 3 (cor Car, Jug) AI, GU2

Thelenella modesta (Nyl.) Nyl.: 1, 9 (cor Que) GU2

Tornabea scutellifera (With.) J.R.Laundon: 5, 9 (twi, cor Que, Ulm) AI, GU

!!***Verrucaria umbrinula*** Nyl.: 5 (sil) GU

Xanthoria parietina (L.) Th. Fr.: 1, 5, 6, 9 (cor Ace, Car, Que, Tam, Ulm) AI, GU7

!***Zwackhia viridis*** (Ach.) Poetsch & Schied.: 1 (cor Car) AI

Lichenicolous and non-lichenized taxa (excluded from all analyses below)

Chaenothecopsis pusilla (Ach.) Alb.Schmidt: 5 (epix Que) AI

!!***Cresporhaphis wienkampii*** (J.Lahm ex Hazsl.) M.B.Aguirre: 9 (cor Que) JV

Milospium graphideorum (Nyl.) D.Hawksw: 4, 8, 9 (on sterile lichen with *Trentepohlia* sp. Car) AI, GU3

Mycocalicium subtile (Pers.) Szatala: 5, 9 (epix Que) AI, JV

!***Peridiothelia fuliguncta*** (Norman) D.Hawksw.: 1, 8, 9 (cor Que) AI2, GU3

!***Xanthoriicola physciae*** (Kalchbr.) D.Hawksw.: 6 (on apothecia of *Xanthoria parietina* Que) GU

Table 1: Selected characteristics of lichen diversity in Samurski forest. Substrate abbreviations follow the “List of substrata” in the text. Numbers in brackets are percentages from all 138 species. “No. of specialists” is the number of species recorded on a single substrate type.

Substrate													
	Ace	Aln	Art	Car	Jug	Mes	Pop	Que	Tam	Ulm	wood (log. snag)	soil	cal. sil. sla
No. of species	25 (18.1%)	3 (2.1%)	4 (2.9%)	52 (37.7%)	5 (3.6%)	1 (0.7%)	5 (3.6%)	79 (57.2%)	7 (5%)	18 (13.1%)	15 (10.8%)	2 (1.4%)	11 (7.7%)
No. of specialists	2 (1.4%)	0	2 (1.4%)	11 (7.7%)	1 (0.7%)	0	5 (3.6%)	37 (26.8%)	1 (0.7%)	1 (0.7%)	13 (9.4%)	2 (1.4%)	11 (7.7%)
Growth forms													
	Fruticose				Foliose				Microlichens (incl. lichenicolous and non-lichenized species)				
No. of species	10 (7.2%)				18 (13.1%)				110 (79.7%)				
Reproductive strategies													
	reproduction by spores prevail						vegetative diaspores prevail						
No. of species	103 (74.6%)						35 (25.4%)						
Photobionts													
	green globose cells				trentepohlioid			cyanobacteria			Others		
No. of species	93 (67.4%)				36 (26.1%)			3 (2.1%)			1 (0.7%)		
Prevailing systematic units													
	Arthoniomycetes		Coniocybomycetes		Dothideomycetes		Eurotiomycetes		Lecanoromycetes		Sordariomycetes		Incertae sedis
No. of species	20 (14.5%)		4 (2.9%)		7 (5.1%)		9 (6.5%)		95 (68.8%)		1 (0.7%)		2 (1.4%)

Table 2: Basic data for Central European old-growth forest lichen inventories and their similarity in species composition with the Samurski forest. Localities are sorted according to forest types. Four groups of forest types are separated by horizontal lines; from above: lowland forests, maple-lime scree forests, beech-dominated forests and coniferous forests. Tree species abbreviations: AA – *Abies alba*, AC – *Acer campestre*, APL – *Acer platanoides*, APS – *Acer pseudoplatanus*, CB – *Carpinus betulus*, FE – *Fraxinus*, FS – *Fagus sylvatica*, PA – *Picea abies*, PIN – *Pinus*, QU – *Quercus*, TIL – *Tilia*.

no. on Figure 5	locality (country abbreviation)	forest type	no. of lichen species	no. of lichen species shared with Samur forest	Sørensen's Similarity Index to Samur forest	area (ha)	altitude (m)	latitude	longitude	dominant tree species	references
1	Soutok Moravy a Dyje (CZ)	lowland deciduous	216	69	0,44	3000	150	48.660421	16.944199	AC, CB, FE, QU	Vondrák et al. 2016
2	Horný les (SK)	lowland deciduous	103	45	0,45	85	140	48.3534039	16.8638483	AC, CB, FE, QU	Vondrák et al. (unpublished)
3	Otok, Mukachevo (UA)	lowland deciduous	159	64	0,5	350	190	48.219974	22.791930	AC, CB, FE, QU	Vondrák et al. (unpublished)
4	Libický luh (CZ)	lowland deciduous	71	33	0,39	446	200	50.1106431	15.1670331	AC, CB, FE, QU	Malíček et al. (unpublished)
5	Oslava a Chvojnice (CZ)	lowland deciduous	130	47	0,41	261	350	49.1391869	16.2446314	AC, CB,QU	Šoun et al. (unpublished)
6	Hluboká (CZ)	lowland deciduous	81	36	0,4	10	400	49.0759569	14.4519764	CB, FS, QU, TIL	Vondrák et al. (unpublished)
7	Pleš (CZ)	mapple-lime, on scree	132	33	0,29	28	790	49.5501125	12.6387808	APL, APS, FS, TIL	Peksa et al. (unpublished)
8	Nad Hutí (CZ)	mapple-lime, on scree	112	30	0,28	14	680	49.5384839	12.6547111	APS, FS, TIL	Peksa et al. (unpublished)
9	Cigánka (SK)	mapple-lime, on scree	149	42	0,34	40	1275	48.7561500	20.0570072	APS, FE, FS, QU, TIL	Guttová & Palice 2005

no. on Figure 5	locality (country abbreviation)	forest type	no. of lichen species	no. of lichen species shared with Samur forest	Sørensen's Similarity Index to Samur forest	area (ha)	altitude (m)	latitude	longitude	dominant tree species	references
10	Dlouhý vrch (CZ)	mapple-lime, on scree	87	27	0,29	21	600	49.5734947	12.6466086	APS, FS, TIL	Peksa et al. (unpublished)
11	Javorníková dolina (SK)	mapple-lime, on scree	95	35	0,36	170	790	48.7360469	20.0062469	APL, APS, FS, TIL	Guttová & Palice 2002
12	Hrdzavá dolina (SK)	mapple-lime, on scree	104	33	0,33	104	860	48.7489067	20.0097661	APS, FE, FS, QU, TIL	Guttová & Palice 1999
13	Starý Herštejn (CZ)	mapple-lime, on scree	72	21	0,25	72		49.4699306	12.7144886	APL, APS, FE, FS, PA, TIL	Peksa et al. (unpublished)
14	Ve Studeném (CZ)	mapple-lime, on scree	64	24	0,3	64	375	49.4961458	18.3119836	FS, PA, TIL	Vondrák & Malíček (unpublished)
15	Velká Javořina (CZ)	mapple-lime, on scree	78	27	0,31	160	1070	48.8612431	17.6769053	APS, FE, FS, QU, TIL	Malíček & Vondrák (unpublished)
16	Čertův mlýn (CZ)	mapple-lime, on scree	76	20	0,23	50	750	49.4893369	18.3013794	APS, FS	Vondrák & Malíček (unpublished)
17	Malý Zvon (CZ)	dominated by beech	86	28	0,3	8	770	49.5351419	12.6444800	FS	Peksa et al. (unpublished)
18	Chejlava (CZ)	dominated by beech	90	33	0,35	26	580	49.5366553	13.5567981	FS	Peksa (unpublished)
19	Jizerskohorské bučiny (CZ)	dominated by beech	39	10	0,14	952	740	50.8583389	15.1484250	FS	Malíček (unpublished)

no. on Figure 5	locality (country abbreviation)	forest type	no. of lichen species	no. of lichen species shared with Samur forest	Sørensen's Similarity Index to Samur forest	area (ha)	altitude (m)	latitude	longitude	dominant tree species	references
20	Čerchov (CZ)	dominated by beech	106	28	0,27	170	900	49.3753494	12.8030950	APS, FS	Peksa (unpublished)
21	Karlovské bučiny (CZ)	dominated by beech	30	9	0,14	42	440	50.7753486	14.9682492	FS	Malíček et al. (unpublished)
22	Stužica (SK)	dominated by beech	228	50	0,3	630	970	49.088382	22.544935	AA, APS, FS	Vondrák et al. 2015
23	Ugolka-Shyrokyi Luh (UA)	dominated by beech	196	43	0,29	10400	880	48.298785	23.688140	FS	Dymytrova et al. 2013
24	Žofínský prales (CZ)	dominated by beech	222	34	0,21	98	780	48.664866	14.706696	AA, FS, PA	Malíček & Palice 2013
25	Stuzhitsa (UA)	dominated by beech	218	52	0,33	2492	850	49.083840	22.574118	AA, APS, FS, PA	Kondratyuk et al. 1998, Kondratyuk & Coppins 2000, Motiejūnaitė et al. 1999
26	Boubínský prales (CZ)	dominated by beech	139	25	0,21	47	1040	48.9751644	13.8138372	AA, FS, PA	Budějcká (unpublished)
27	Neuwald (A)	dominated by beech	127	27	0,24	1	950	47.7713292	15.5222253	AA, FS, PA	Hafellner & Komposch 2013
28	Razula (CZ)	dominated by beech	89	23	0,24	23	785	49.3595764	18.3820217	AA, FS, PA	Malíček et al. (unpublished)
29	Luxensteinwand (A)	dominated by beech	84	32	0,34	30	850	48.6418469	14.7288997	APS, FS, PA	Malíček et al. 2013
30	Hojná Voda (CZ)	dominated by beech	67	22	0,27	9	840	48.7060061	14.7533444	AA, FS, PA	Malíček et al. 2012
31	Salajka (CZ)	dominated by beech	56	16	0,21	18	765	49.4015075	18.4182764	AA, FS, PA	Malíček et al. 2013

no. on Figure 5	locality (country abbreviation)	forest type	no. of lichen species	no. of lichen species shared with Samur forest	Sørensen's Similarity Index to Samur forest	area (ha)	altitude (m)	latitude	longitude	dominant tree species	references
32	Rajhenavski Rog (SLO)	dominated by beech	86	19	0,21	50	885	45.6607664	15.0091175	AA, FS	Bilovitz et al. 2011
33	Hraničník (CZ)	dominated by beech	188	34	0,24	c.100	1150	48.763408	13.893805	AA, FS, PA	Palice et al. (unpublished)
34	Rotwald (A)	dominated by beech	175	38	0,28	500	1180	47.7829317	15.0923206	AA, FS, PA	Türk & Breuss 1994, Bilovitz 2007
35	Červené blato (CZ)	montane coniferous	62	9	0,11	330	470	48.8648722	14.8071094	PA, PIN	Malíček & Vondrák (unpublished)
36	Rašeliniště Jizery (CZ)	montane coniferous	51	8	0,11	153	850	50.8566053	15.3244808	PA, PIN	Malíček & Vondrák 2014
37	Trojmezná (CZ)	montane coniferous	148	18	0,14	588	1275	48.772881	13.833413	PA	Palice et al. (unpublished)
38	Fábova hola (SK)	montane coniferous	114	21	0,2	260	1380	48.7715275	19.8862558	PA	Guttová et al. 2012
39	Boubín - top (CZ)	montane coniferous	58	9	0,11	100	1280	48.9917478	13.8210469	PA	Vondrák (unpublished)
40	Kněhyně (CZ)	montane coniferous	63	7	0,08	100	1130	49.4962056	18.3118853	PA	Malíček & Vondrák (unpublished)
41	Reschbach Klause (DE)	montane coniferous	57	7	0,09	50	1140	48.9652239	13.5628747	PA	Vondrák & Pouska (unpublished)

Characteristics of recorded species

Functional and taxonomic classifications of lichen diversity in Samurski are summarized in Table 1. Lichen crusts predominate, with 80 % of species; macrolichens are less significant. The high proportion of lichens with *Trentepohlia* photobiont and the high number of Arthoniomycetes are notable. Most species were recorded on at least one of the three dominant trees, but *Quercus robur* harbors the highest diversity of epiphytic lichens: 79 species, 37 of which were only recorded on oak. Few species were recorded on *Populus nigra*, none of those few were recorded elsewhere (*Arthonia exilis*, *Caloplaca ulcerosa*, *Candelariella superdistans*, *Lecania fuscella*, *Lecanora populicola*). Lichens on wood are few, but they are fairly faithful to that substrate; 13 of 15 these species were only found on wood. Coastal shrub vegetation with *Artemisia* sp. and *Tamarix ramossisima* has a specific lichen assemblage including *Athallia skii*, *Lecania cyrtella*, *Lecanora hagenii* and *Lecanora sambuci*.

Samurski versus Central European forests

When compared with the main Central European forest types, the epiphytic (and epixylic) lichen flora of Samurski is most closely related to that of the lowland deciduous forests (Table 2, Figs 5, 6); the average number of species shared with Samurski is 49, which is distinctly more

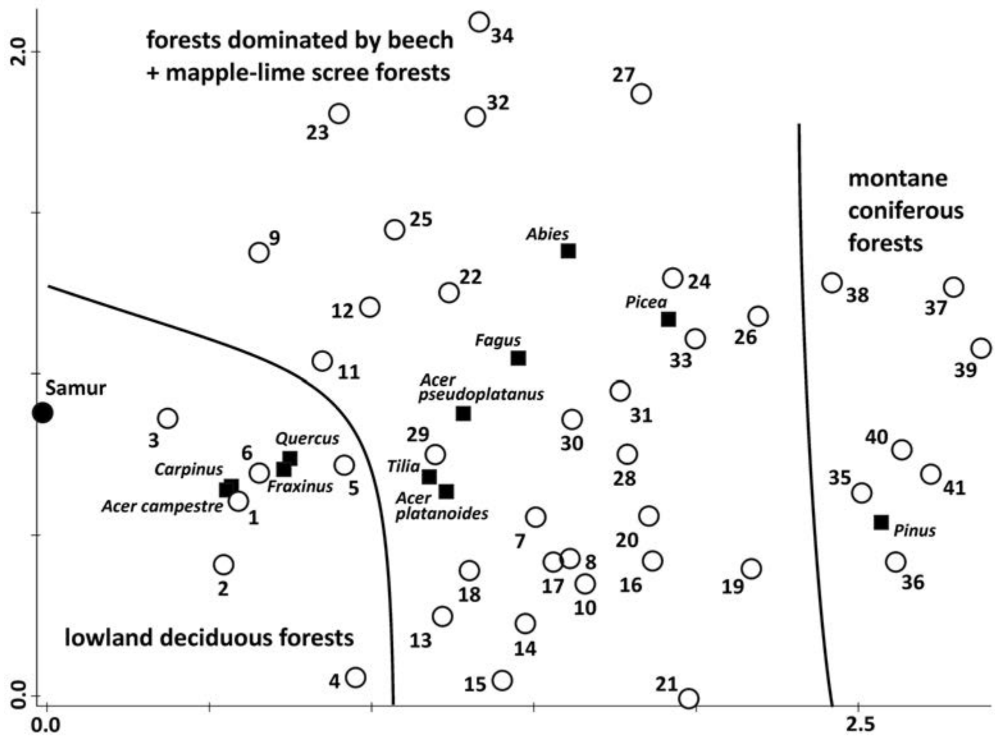

Fig. 5: DCA ordination diagram showing similarities in lichen species composition among Central European old-growth forest localities (white circles) and their relationship to the Samurski forest (black circle), localities numbered according to the Table 2. Black squares represent passively inserted dominant tree species. The first (horizontal) and second (vertical) axes are shown, together explaining 17.1 % of the variability in species data.

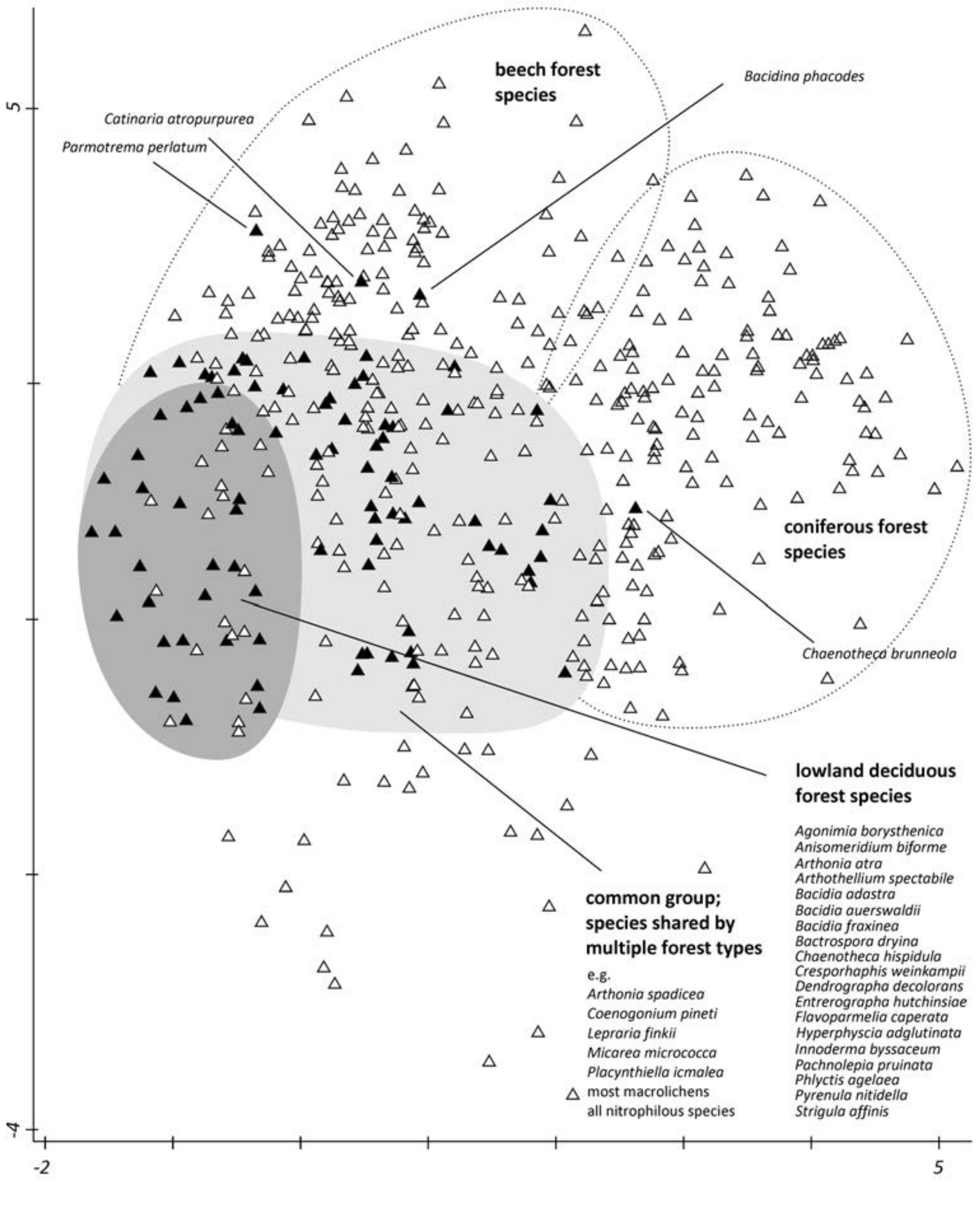

Fig. 6: DCA ordination diagram of lichen species reported from 41 Central European forest inventories (Table 2) and Samurski. Species distributed into rough groups according to forest types. Dark grey – lowland forest species group; pale grey – "common group" of species occurring in multiple forest types. Black triangles – species recorded in Samurski. Species listed in the bottom right belong to particular groups that occur in Samurski.

than 29 for beech and maple-lime forests, and 11 for montane coniferous forests (Fig. 7). Close relationships in species compositions between Samurski and Central European oak-hornbeam lowland forests is also presented by the DCA ordination diagram based on presences/absences of species in localities (Fig. 5). The extreme left position of Samurski in the plot (Fig. 5) is explained by the few species present in Samurski but absent in all Central European localities (discussed below). In general, the lichen flora of Samurski is formed of "lowland deciduous forest species" and a "common group", i.e. species shared by multiple forest types (see clusters and lists in Fig. 6). According to data in Table 2, only a few beech-dominated forests (Stužica, Stuzhitsa, Ugolka) and one mixed scree forest (Cigánka) share more than 40 species with Samurski, but these four localities include deep valleys at low altitudes containing species characteristic of lowland forests (e.g. *Arthothelium spectabile*, *Inoderma byssaceum*, *Lecania croatica*, *Opegrapha vermicellifera* and *Zwackhia viridis*) that also occur in Samurski.

The high ratio of species with trentepohlioid photobiont (15–30 %) and the high number of Arthoniomycetes (10–15 %) in Samurski is in common with lowland deciduous forests (VONDRÁK et al. 2016, Vondrák, unpublished, this study). The ratio of species with *Trentepohlia* tends to decrease with altitude; it is highest in lowland deciduous forests, slightly lower in

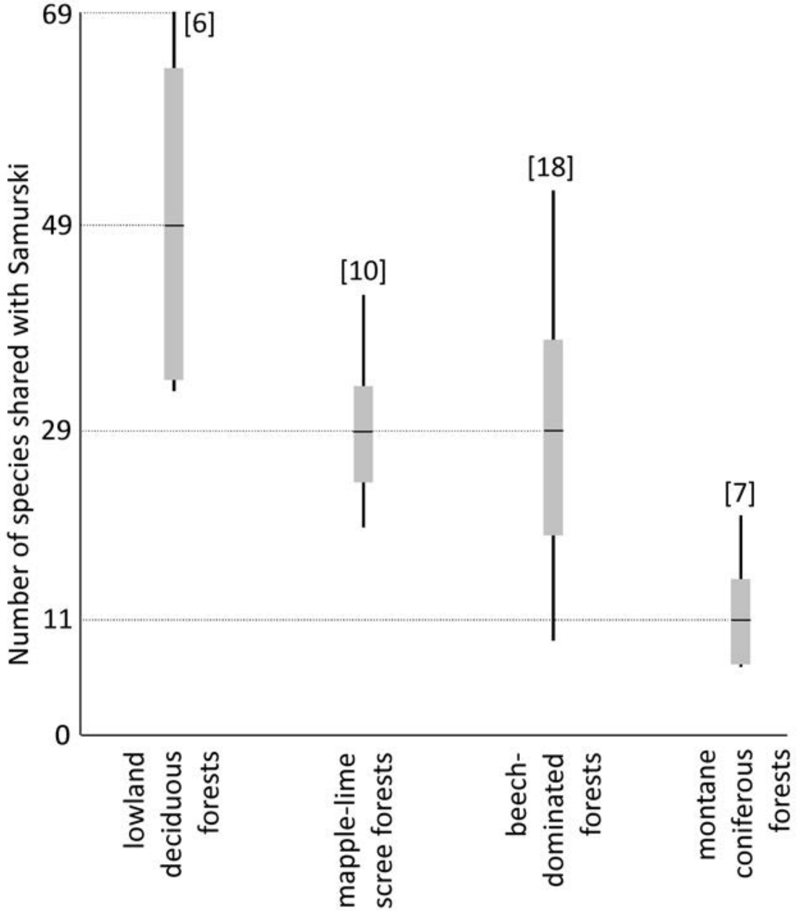

Fig. 7: Similarity between lichen species composition in Samurski forest and four groups including most Central European forest types. Y axis shows the number of species shared with Samurski. Data are visualized as mean (black bar), SD (grey box) and extremes (ends of whiskers). Numbers in square brackets are numbers of analyzed localities in each group.

beech-dominated forests and in scree forests and distinctly lower in montane coniferous forests (see references in Table 2). Although the ratio of macrolichens (foliose and fruticose lichens) is probably lowest in lowland forests among studied forest types (20–25 %; only 20 % in Samurski), but this ratio is only slightly higher in well-surveyed localities of other forest types in Central Europe (e.g. Vondrák et al. 2015).

Discussion

Links between Samurski and West European oceanic forests

Several lichen species occurring in Samurski have oceanic (Atlantic) distribution in Europe, namely *Enterographa crassa*, *Lecanographa lyncea* and *Pyrenula macrospora*. They are absent from the surveyed Central European forest localities, but the former two species were sporadically recorded in more oceanic regions of Germany (Wirth et al. 2013). All three species are very rare in Russia, the first and last species are known only from Caucasus (Urbanavichus 2010) and the second is new to Russia. The presence of these three species in Samurski is presumably linked geographically to the humid Hyrcanian forests and/or to extremely oceanic forests on western slopes of Caucasus that share many other lichen species with Western Europe (Urbanavichus & Urbanavichene 2002, 2003).

One-hectar plot α-diversity

Only a few published lichen inventories provide diversity data for 1 ha plots, but we can compare our 82 species with 112 species in an old-growth lowland forest in the Czech Republic (Vondrák et al. 2016) and with 127 species in a mixed montane forest dominated by beech in Austria (Hafellner & Komposch 2007). Possible reasons for the lower number of species in Samurski in comparison with a similar forest in the Czech Republic might include: (1) lower research effort, such as 3 specialists per 6 hours vs. 8 specialists per 3 hours; (2) the relict character of the Samurski forest - it is an isolated and rather small lowland forest remnant; (3) Samurski forest area is considerably drier (400 mm annual) and warmer (implies higher evaporation) than lowland deciduous forests in Central Europe. The second and third explanations seem more plausible to us, because some unpublished lowland deciduous forest inventories on 1 ha plots in Central Europe resulted in >100 listed species although research efforts were comparable with Samurski (Vondrák, unpublished).

The effect of dominant tree species on lichen flora

The similarity of Samurski and Central European lowland forests is probably caused by their similar climate; although average annual temperature is slightly lower and annual precipitation is slightly higher in the Central European forests, some of them, like Samurski, receive high air humidity owing to the proximity of brooks/rivers and a high groundwater level. Climatic (and other abiotic) factors directly influence formation of tree species in forests and also epiphytic lichen composition, but the lichen species composition is supposed to be influenced by available substrata derived from the tree species composition. Our tests of locality characteristics (Table 3) showed significant effects of the dominant tree species from all 42 localities (locs. in Table 2 & Samurski) on lichen species composition, except for *Acer platanoides*, *Pinus* (rare in datasets) and *Tilia*. Tree dominants in Samurski, *Acer campestre*, *Carpinus betulus* and *Quercus robur* had the strongest effects in the test. On the other hand, occurrences of particular tree species are logically linked with particular forest types (see the tree species distribution on Fig. 5). We report a high number of “specialists” (lichen species recorded on a single tree species) in our inventory (Table 1) that suggests linkage between lichen and phorophyte species, but our results are definitely distorted by incomplete sampling. In fact, the same bias may occur in other published inventories. Most lichen species may at first appear to be substrate-specific, but detailed survey usually reveals most of them on more than one tree species. Compilations based on much field experience (e.g. Smith et al. 2009, Wirth et al. 2013) report substrate preference of numerous epiphytic lichen species, but it is generally known that most epiphytes are not confined to a single tree species. In this respect, data on tree species abundances and lichen species abundances on each tree species (both absent in our dataset) are necessary for evaluation of tree species effect. Although we do not provide data that demonstrate conclusively an effect of tree species, we do assume that there is a strong linkage between tree and lichen species. In other words, the presence of the same tree dominants in Samurski and Central European lowland deciduous forests contributes to their similar lichen species compositions.

Table 3: Marginal effects of locality characteristics on lichen species composition; tested in CCA. Significant p-values are in bold. “0" after effect name means the absence of the tree species.

Simple Term Effects:				
Name	**Explains %**	**pseudo-F**	**P**	**P(adj)**
Carpinus betulus	7,7	3,3	**0,001**	**0,00158**
Carpinus betulus 0	7,7	3,3	**0,001**	**0,00158**
forest type: lowland	7,7	3,3	**0,001**	**0,00158**
Acer campestre	7,2	3,1	**0,001**	**0,00158**
Acer campestre 0	7,2	3,1	**0,001**	**0,00158**
forest type: coniferous	7,2	3,1	**0,001**	**0,00158**
Quercus robur / *Q. petraea*	7,2	3,1	**0,001**	**0,00158**
Quercus robur / *Q. petraea* 0	7,2	3,1	**0,001**	**0,00158**
altitude	6,9	3	**0,001**	**0,00158**
Picea abies 0	5,8	2,5	**0,001**	**0,00158**
Picea abies	5,8	2,5	**0,001**	**0,00158**
Fagus sylvatica	5,7	2,4	**0,001**	**0,00158**
Fagus sylvatica 0	5,7	2,4	**0,001**	**0,00158**
longitude	5,7	2,4	**0,001**	**0,00158**
Fraxinus angustifolia / *F. excelsior*	5,7	2,4	**0,001**	**0,00158**
Fraxinus angustifolia / *F. excelsior* 0	5,7	2,4	**0,001**	**0,00158**
latitude	5,1	2,2	**0,001**	**0,00158**
Abies alba	5,1	2,1	**0,002**	**0,003**
Abies alba 0	5,1	2,1	**0,001**	**0,00158**
forest type: dominated by beech	5	2,1	**0,001**	**0,00153**
Acer pseudoplatanus	3,6	1,5	**0,013**	**0,01857**
Acer pseudoplatanus 0	3,6	1,5	**0,014**	**0,01909**
forest type: mixed on scree	3,3	1,4	**0,034**	**0,04435**
Pinus mugo s.lat. / *P. sylvestris*	3,1	1,3	0,161	0,18577
Pinus mugo s.lat. / *P. sylvestris* 0	3,1	1,3	0,177	0,19667
Tilia cordata / *T. platyphyllos*	3	1,2	0,092	0,115
Tilia cordata / *T. platyphyllos* 0	3	1,2	0,101	0,1212
Acer platanoides	2,4	1	0,449	0,46448
Acer platanoides 0	2,4	1	0,425	0,45536

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