The lichen flora of Germany – regional differences and biogeographical aspects

Volkmar Wirth, Ulf Schiefelbein and Birgit Litterski

Abstract: The lichen flora of Germany is characterized on the basis of "Die Flechten Deutschlands" (Wirth et al. 2013) which uses natural regions for biogeographical information. Almost exactly 2,000 lichen species have been recorded. The regions, with highest species diversity are the upland regions, especially the Alps, Black Forest, Odenwald-Spessart, Eifel, Weserbergland, Harz and Franconian Alb. In these regions, rocky outcrops are an important factor enhancing species diversity. The lowest diversity is found in intensely cultured landscapes of eastern Germany, between Elbe river and Erzgebirge. The most peculiar lichen flora exists in the Bavarian Alps due to terricolous and saxicolous species on calcareous substrates in the alpine belt. Within Germany, special distribution patterns show species which can be attributed to the arctic-alpine and boreal-high montane disjunctions, to the atlantic region, and species which can be characterized as members of xerothermic and oceanic elements in an ecological sense. During the last decades, the lichen biota were submitted to considerable changes. Ca. 50 species appeared as neobiota mainly from Western Europe, which is an increase of 24 % of the atlantic/subatlantic element among the epiphytes.

1. Introduction

When characterizing the lichen flora of a country, several questions arise. Some are easy to answer, such as "How many species occur?", "Are there remarkable differences in lichen diversity from region to region?", "Where is the lichen flora rich, and where poor, and what are the reasons?". Answers to other questions, such as "Are there typical distribution patterns and how can they be explained?", involve basic but complex investigations.

We know that climatic factors and substrate conditions are of decisive importance for the ecology and distribution of lichens. Climatic ecology of species is hard to define since the climate of a site/habitat is continually changing. Substrate features are more easily described.

Several relevant substrate groups are recognisable, such as carbonate rock, carbonate-free siliceous rock, tree bark, acidic or basic soil and detritus. Each of these substrate groups is represented by species which usually do not colonize other substrates. Therefore, if one of these substrate types is not present in the study area, then species diversity is negatively influenced to a considerable degree. The significance of different macroclimatic conditions on lichen biota can be studied exemplarily in the different altitudinal zones. In alpine regions other species occur as in mountainous regions or in lowlands. Climatic parameters override the substrate conditions, causing a floristic differentiation/variability within the substrate species groups.

In consequence, our questions can be more specific: "How far does the distribution of a lichen species in Germany reflect ecological conditions and differences, regionally as well as for the country as a whole? And "Are we able to specify climatic conditions or substrate restrictions influencing the regional distribution pattern?"

Germany is extensively subdivided in natural regions due to variations in geology, geomorphology and altitudinal extension, and consequently for vegetation and land use. The following discussion is based on the data for the German lichen flora (Wirth et al. 2013) which is based on this subdivision and uses 59 natural rather than political regions for biogeographical interpretation; here the number is reduced to 56 for practical reasons (see Schiefelbein et al. 2015 for further information on the data).

2. The lichen biota

2.1. Total species number and frequency

In Germany, actually 1,990 lichen species are known, and together with the lichen-related fungi which are traditionally considered in lichen floras, e.g. *Arthopyrenia, Naetrocymbe* and *Stenocybe*, the total is 2,040 species (Wirth et al. 2013, updated).

Based on the evaluation by Wirth et al. (2011) of the frequency of species recorded in Germany, Wirth et al. (2013) placed only 1.8 % and 4.8 % of the species into the categories "frequent" and "moderately frequent"; 7.8 % were classified as "quite rare", 17.2 % as "rare", 27.9 % as "very rare" and 28.0 % as "extremely rare". 9.4 % of the species had not been recorded since 1950 (further 3.1 % not evaluated). Consequently, only 6.6 % of the species were more or less frequent, whereas more than 80 % can be considered as rare or extinct. The rarity of many species is confirmed by the investigation of the exclusivity of records in Germany which shows that many species occur only in one or two natural regions (Schiefelbein et al. 2015).

2.2. Regional differences

The physical and ecological differences between the mentioned natural regions of Germany are the cause for very different species numbers on the one hand, and for a remarkable floristic peculiarity of many natural regions in relation to neighbouring regions on the other hand. Which are the factors which contribute significantly to the regional characteristics of the lichen flora?

2.2.1. Limitation of distribution by substrate restrictions

As outlined above, species diversity is strongly influenced by the presence or absence of any substrate group, particularly the occurrence of rocks. For this reason, there are remarkable differences between species numbers in natural regions in Germany due to the presence or absence of rock outcrops, in spite of the human importation of substrates such as stone walls and gravestones or the creation of artificial substrates such as concrete. Among the twelve natural regions with the highest species numbers only one does not have any autochthonous rock site (inclusive block fields), whereas almost all regions having less than 300 species are free of natural rock occurrences (Tab. 1, Fig. 1).

Tab.1: The 12 regions richest and poorest in species in respect to frequency of rock sites; (+) very few, + few, and +++ many rocks; ranking including extinct species; only actual records in brackets.

	species numbers total	rock	bark	calcareous rocks, frequency	siliceous
1 (2) Bavarian Alps (BayAlp)	1,050	403	383	+++	(+)
2 (1) Black Forest (Sch)	1,006	425	389	-	++
3 (3) Odenwald-Spessart (OSp)	854	327	347	-	++
4 (4) Eifel (Eif)	754	338	251	+	++
5 (16) Weserbergland (Wes)	742	303	247	+	+
6 (7) Harz (Hz)	730	314	228	+	++
7 (14) Franconian Alb (FrJu)	723	316	243	++	-
8 (6) Sauerland (Sau)	718	337	207	+	+
9 (5) Bohemian Forest (BayW)	714	303	254	((+))	++
10 (10) Schleswig Holst. Geest (SHG)	685	221	392	-	-
11 (9) Suabian Alb (SJu)	637	258	254	++	-
12 (8) Hessisches Bergland (He)	625	263	202	+	+
45 Rhein-Main-Lowland (MnT)	299	67	148	-	-
46 Oberpfälz.-Obermain.-Hügell. (Opf)	292	100	96	-	+
47 Westerwald (Wewa)	289	113	105	((+))	(+)
48 Oberlausitz (OLau)	266	101	99	-	+
49 Fläming (Flä)	250	91	101	-	-
50 Elbe-Mulde-Niederung (Elb-Mul)	249	74	98	-	-
51 Oberlausitzer Heideland (nöOLau)	247	61	103	-	-
52 Nördliches Harzvorland (nöHz)	220	92	62	-	(+)
53 Gutland (Gut)	212	70	96	(+)	(+)
54 Altmark-Wendland (Alt)	212	63	91	-	-
55 Pfälzer Muschelkalkgeb. (PfMk)	211	70	95	-	-
56 Northern Erzgebirge (nöErz)	191	69	70	-	-

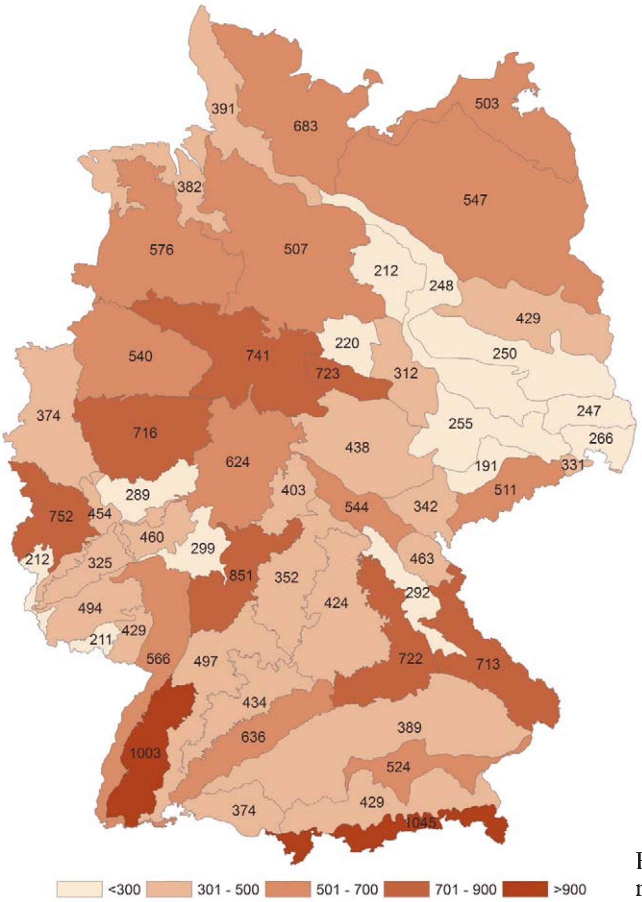

Fig. 1: Total species number in natural regions of Germany.

When comparing species numbers for the different regions it is necessary to consider the size of the region. It is probable that both ecological diversity and species number increase with area size. Therefore it is not surprising that most of the species-poor regions are small. By relating species numbers with size of the natural region and determining the species density this effect is corrected – a quite different ranking results. The highest density of species of German natural regions are found in the Elbsandsteingebirge (Elbsa) and the Palatinate Forest (PfW), followed by Harz (Hz), Bavarian Alps (BayAlp), Fichtelgebirge (Fi), Gutland (Gut), Taunus (Ts), Middle Rhine (MRh), Black Forest (Sch), Thuringian Forest (ThW), Rhön, Odenwald/Spessart (OSp) and Eifel (Eif) – altogether landscapes rich in relief (abbreviations according to Wirth et al. 2013). The lowest density values are found in the intensively agriculturally used and relief-poor regions of Mecklenburg (Me), Donau-Iller-Lech-plain (Do), eastern Lower Saxony (öNs), Elbe-Mulde-region (Elb-Mul), Fläming (Flä), Saxonian Hügelland (SäHü), western Lower Saxony (wNs), Thuringian basin (Th) and Lower Rhine (NRh) (for the location of these regions within Germany see Wirth et al. 2013 p. 54, a map of species density in the landscape units is presented by Schiefelbein et al. 2015). The common feature of both rankings, species number and density, is that the regions with lowest values are free of rocks. The species density is influenced by the size of the investigated area, but in a contrary sense: the larger the natural region, the smaller the gain of additional species.

If you combine both methods of ranking (e.g. adding up the rank numbers), the Bavarian Alps, the Harz and the Black Forest would appear on top as the regions of highest diversity, followed by the Odenwald/Spessart, Eifel, Thuringian Forest, Franconian (FrJu) and Suabian Alb (Ju) (total species number incl. extinct species). These positions approach the subjective impression of the species richness of German regions. The northeastern regions of Elbe-Mulde-lowland, Fläming and Altmark (Alt) take the last places in this ranking.

The occurrence of rock sites not only enhances species diversity but influences the character of the lichen biota of a region. This is especially obvious if the geological features of the region differ from the neighbouring regions; in such cases, lichenological criteria contribute to confirming the delimitation of natural regions. From an ecological and floristic point of view the Suabian Alb, Franconian Alb and the Bavarian Alps and less obviously, the limestone area of Thuringia and the adjoining Weserbergland and Sauerland, have a special position due to the rich occurrence of calciphilous species (Fig. 2). Moreover, in the Alps, the Suabian and Franconian Alb, and the Thuringian Basin widespread silicolous lichen species are lacking, such as *Chrysothrix chlorina*, *Lasallia pustulata, Micarea sylvicola* and *Montanelia disjuncta*. This double character “saxicolous lichen flora rich in species on calcareous rocks, but poor on siliceous rocks” caused by substrate restrictions reflects the peculiarity of these regions – in the case of the Bavarian Alps strengthened by the presence of an alpine belt (see later). In contrast to these limestone areas, the lichen floras of the natural regions of Erzgebirge (Erz), Thuringian Forest, Fichtelgebirge (Fi), Bohemian (BayW) and Black Forest differ since siliceous rock prevails and calcicolous lichen species have little possibilities to establish except on man-made habitats. However, the uplands Harz, Sauerland, Weserbergland (Wes) and Eifel, predominantly built up by siliceous rock, have a lichen flora including both, saxicolous species of calcareous and siliceous substrates due to some rare but floristically important occurrences of limestone.

On which scale is the number of saxicolous species present in the natural regions based only on the existence of man-made substrates? How significant is the number of species in natural regions where both calcareous and siliceous bedrock and outcrops are limited or absent? In most regions of eastern and northern Germany, for example, where nearly all calcicolous and most silicolous lichens occur exclusively on man-made substrates, each group contributes 10–15 % of the totally recorded species. In some landscapes of northern Germany many species were found only on allochthonous erratic boulders. The photophilous species among them owe their existence to human influence; by nature the boulders would be situated in forests and shadowed by trees which would allow only some shade-tolerant species to exist. So, when enlarging the definition of anthropogenic habitats, almost all saxicolous lichen species in areas without bedrock, such as Niedersachsen (wNs, öNs) and Mecklenburg (Me), owe their existence to human beings.

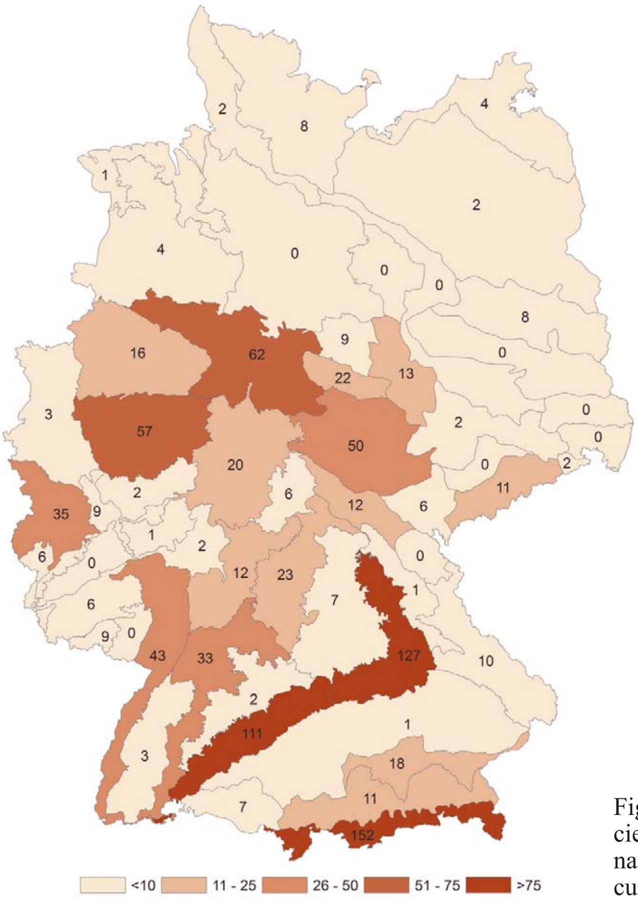

Fig. 2: Number of saxicolous species on calcareous substrate in the natural regions (excl. species occurring on man-made substrate)

The development of soil- and detritus-inhabiting lichens largely depends upon the geomorphological and geological conditions. As epigaeic lichens usually need habitats with little competition, areas with outcrops are favourable since they offer sites with shallow soils, as preferred by the acidophilous species of *Cetraria* and *Cladonia* and the basiphilous species of *Collema*, *Fulgensia*, *Psora* and *Toninia*. As a consequence, natural regions rich in saxicolous species are also rich in terricolous species. In northern and eastern

Germany sandy areas are also significant since they house extensive Cladonion communities.

By nature, the substrate type "tree bark" is found in all its different physico-chemical manifestations (e.g. acid, neutral, rough, smooth bark) in every natural region. Therefore differences in the epiphytic lichen flora between the regions are mainly due to climatic factors – with the exception of atmospheric pollution. The impact of acid air pollution several decades ago influenced the bark quality significantly. High pollutant concentrations combined with the lack of base-rich bark resulted in an extreme impoverishment of the epiphytic lichen flora especially in eastern Germany leaving only some few species – today some after-effects are still perceptible.

2.2.2. Influence of climatic factors

Epiphytes

Many epiphytic lichens show specific distribution patterns on the basis of the subdivision in natural regions. As outlined above, bark qualities cannot play a significant role for any explanation of regional distribution differences. Therefore distinct distribution patterns of epiphytes should be related to climatic factors – influence of emissions can be neglected since consideration is given to all lichen species ever recorded, including extinct ones. However, it is difficult to characterize the causal relations between climatic factors and distribution patterns since the meteorological data cover only a fraction of the climatic situation of the lichen habitats of the corresponding region. One is still forced to be content with paraphrases like "in oceanic regions" or "cool" or "cold" situations or "areas with high precipitation" or "high danger of late frost" or to use a rough parallelization with temperature averages or amplitudes or precipitation amounts. Temperature as an ecological factor is reflected by the preference of particular altitudinal belts.

Many epiphytes are restricted to the Bavarian Alps and the uplands, mainly the Black Forest, Bohemian Forest and Harz, and less distinctly, Fichtelgebirge, Erzgebirge and Thuringian Forest. These natural regions are distinguished from the other regions by a more or less distinct manifestation of the montane /high-montane element (Fig. 3). So, concerning the tree-inhabiting lichen biota, the Bavarian Alps do not have a unique characteristic as is the case with the saxicolous and epigaeic lichen flora, but can be compared to the Bohemian and Black Forests (Wirth et al. 2009). This group is represented by for example *Alectoria sarmentosa, Biatora helvola, B. fallax, Bryoria nadvornikiana, Chaenotheca subroscida, Chaenothecopsis consociata, Ch. viridialba, Elixia flexella, Frutidella pullata, Hypocenomyce friesii, Hypogymnia austerodes, H. bitteri, H. vittata, Lecidea nylanderi, Mycoblastus affinis, M. sanguinarius, Ochrolechia alboflavescens, Stenocybe maior, Usnea barbata, Xylographa vi-*

tiligo and *X. parallela*. Some lowland occurrences of single species of that group in Northern Germany have a relict character and do not question the evaluation of this species group as high-montane. As most of these species are rare, at least today, the mentioned upland regions are more accurately characterized by a rather high abundance of more frequent species, such as *Parmeliopsis hyperopta, Bryoria capillaris*, *Usnea dasopoga*, *Biatora efflorescens, Cladonia cenotea, Ochrolechia androgyna, O. microstictoides, Loxospora elatina, Hypogymnia farinacea* and *Vulpicida pinastri*, which are rare in most other natural regions.

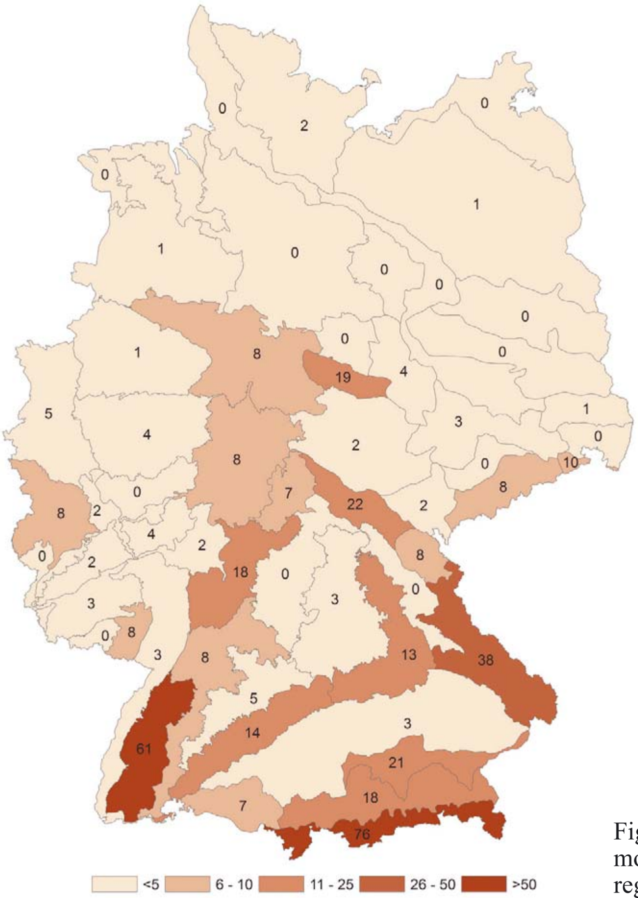

Fig. 3: Number of montane/high-montane epiphytes in the natural regions

There is a further group of species which can be treated in connection with the montane element, since their occurrences are also concentrated in mountain regions. However, they also occur in lowlands of the western part of Germany (Fig. 4) extending to the lowlands of France as far as the maritime areas. Such a distribution pattern can be seen in connection with the oceanic climate in these regions – with moderate annual temperature amplitudes and lack of severe late frosts, as well as high air humidity and high precipitation. Representative species are *Normandina pulchella, Nephroma laevigatum, Parmotrema perlatum, P. reticulatum, Hypotrachyna laevigata* and *Fuscidea lightfootii*, which are typical of a mild oceanic climate, together with *Hypotrachyna sinuosa, Lobaria pulmonaria, Lobarina scrobiculata, Arthonia leucopellaea* and *Lecanactis abietina*, which are typical of a cooler oceanic climate. Oceanic climatic conditions prevail in the montane belt of upland areas, as well as in the humid lowlands of western parts of Germany. Nowadays some of these species have disappeared from several lowland regions – more because of anthropogenic than climatic causes. In the mountainous areas oceanic species prefer the rainy windward side and protected valleys, whereas the leeward regions with a more continental climate are avoided. Biogeographically this phenomenon can be demonstrated by comparing the distribution of a typical oceanic lichen species with a more continental species (e.g. *Normandina pulchella* versus *Cetraria sepincola*).

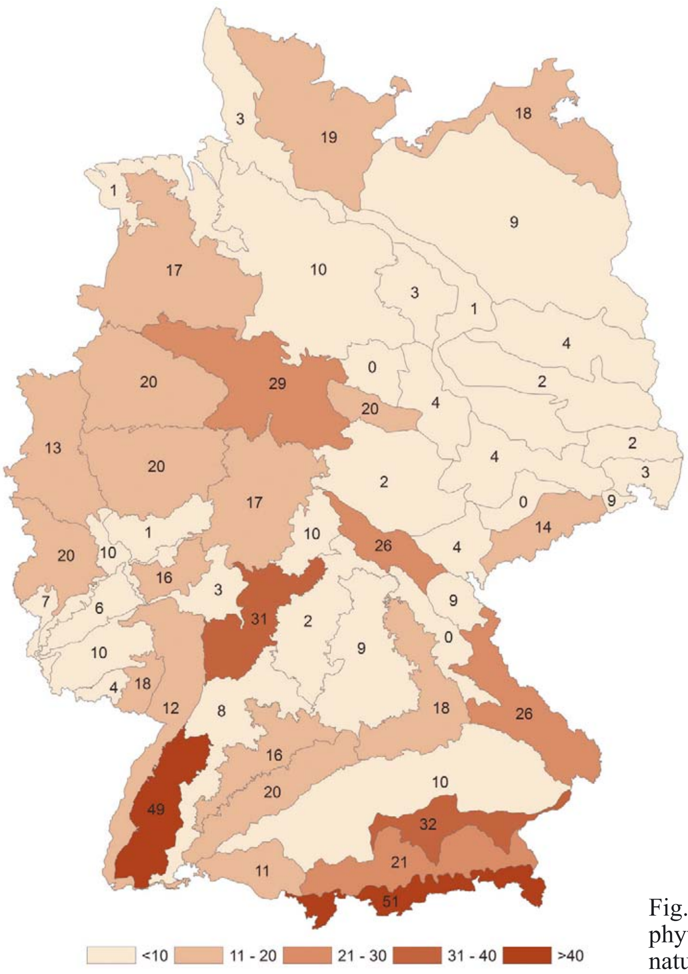

Fig. 4: Number of oceanic epiphytes in ecological sense in the natural regions

Another group of species, restricted to lowlands, avoids winter-cold areas; examples are listed in table 2. Many species of table 4 are also members of this group.

Tab. 2: Examples of epiphytes with a planar-colline(-submontane) distribution.

Bactrospora corticola
Bactrospora dryina
Flavoparmelia soredians
Graphis elegans
Graphis inustuloides
Hyperphyscia adglutinata
Maronea constans
Opegrapha vermicellifera
Opegrapha viridileprosa
Parmotrema stuppeum
Pertusaria heterochroa
Pertusaria trachythallina
Phaeographis spec.
Physcia leptalea
Physciella chloantha
Physconia grisea
Porina leptalea
Pyrenula nitidella
Teloschistes chrysophthalmus
Usnea rubicunda
Varicellaria velata

The distribution types treated above show relatively distinct patterns. There are further ones, of course, but the distribution – demonstrated on basis of natural regions – often appears diffuse, because the special ecological conditions are realized at least locally in too many of the natural regions and are not reflected in clear distribution patterns within the area of Germany.

Saxicolous and terricolous species

Naturally, climatic factors also influence the distribution of saxicolous and terricolous lichen species. Many saxicolous or soil-inhabiting species are restricted to distinct altitudinal zones. This is especially true for the alpine belt which, in Germany, is only present in the region of the Bavarian Alps. More than 50 species living on soil, detritus or terricolous mosses are restricted to this region; examples are *Allocetraria madreporiformis, Anaptychia bryorum, Buellia elegans, Caloplaca ammiospila, C. bryochrysion, C. jungermanniae. C. saxifragarum, C. schoeferi, Cladonia acuminata, C. cyanipes. Dactylina ramulosa, Ochrolechia upsaliensis, Pertusaria bryontha, P. geminipara, So-*

lorina bispora, S. crocea, S. monospora and *S. octospora.* Only the Alps offer the ecological conditions (a sufficient surface area) for these species. Nevertheless a few alpine terricolous lichens have survived in the higher upland areas outside the Alps (Black Forest, Bohemian Forest, Harz, Fichtelgebirge), but mostly in one or two regions and very few localities; examples are *Flavocetraria cucullata, F. nivalis, Cladonia amaurocraea, C. bellidiflora, C. stellaris, Caloplaca tiroliensis, C. schistidii, Catolechia wahlenbergii, Rinodina olivaceobrunnea, Lecidoma demissum, Thamnolia vermicularis, Gyalecta incarnata, Ainoa geochroa, Alectoria ochroleuca, Protothelenella sphinctrinoides, Lichenomphalia hudsoniana, Protomicarea limosa* and *Frutidella caesioatra*. Their occurrences have the characterictics of relics, being highly endangered, and some may be already extinct.

The special character of the Bavarian Alps is also pronounced for species on calcareous rock – around 65 species are confined to this region within Germany – since other natural regions with limestone habitats do not reach even as high as the alpine belt, the Suabian Alb reaching 1,000 m and the Franconian Alb only 656 m; both regions house therefore – in spite of the neighbourhood to the Alps – only few representatives of the alpine element, e.g. *Atla alpina*, *Caloplaca erodens, Eiglera homalomorpha, Farnoldia jurana, Hymenelia epulotica, H. heteromorpha, Sporodictyon schaererianum, Thelidium decipiens* and *Zahlbrucknerella calcarea.*

The situation concerning the species on siliceous rock is very different. As this type of rock is quite rare in the Alps, the number of such species is generally low on natural habitats. This is one reason why the silicolous lichen flora of the Bavarian Alps does not show that degree of peculiarity as in the case of the calcicolous and terricolous lichen biota. Another reason is that – unlike the limestone-regions – some regions with acid rocks, such as the Black Forest and Bohemian Forest, almost reach up to the subalpine belt where a more or less high diversity of subalpine or alpine species also occurs. Furthermore, in some other upland areas, namely Harz (Hz,), Rhön, Fichtelgebirge (Fi) and Erzgebirge (Erz), alpine glacial relics are found (Fig. 6). As table 3 illustrates, the diversity is highest in the Black Forest (Sch) and Bohemian Forest (BayW) and drops considerably in areas with altitudes 200–300 m lower. In mountainous areas below 900 m, such as Taunus (880 m), Sauerland (Sau, 843 m), Hunsrück (816 m) and Eifel (747 m), only a few alpine species survive.

A species-poor but very remarkable element is the xerothermic species group which are adapted to a dry, summer-warm climate – climatologically the counterpart to the oceanic element. The xerothermic element was considered by Suza (1925, 1935); in Middle Europe it is well represented in Bohemia, Moravia and Wachau. In Germany, the localities concentrate in the neighbourhood of the Harz, partly in the natural region of the Thuringian basin and partly in the Middle German Chernozem region (MSE). The most characteristic representatives are *Acarospora placodiiformis, Psora saviczii, Gyalidea asteriscus, Caloplaca raesenenii, Rinodina terrestris, Diploschistes diacapsis, Fulgensia bracteata* and *Xanthoparmelia pokornyi*. Associated vascular plants include *Stipa capillata, S. pulcherrima, Fumana procumbens, Seseli hippomarathrum, Astragalus danicus, A. exscapus, Adonis vernalis* and *Achillea pontica*. Further species, which prefer dry and warm habitats, occur in the Middle Rhine region, Nahe valley, Franconian Alb and Hegau, such as *Caloplaca areolata* s.l., *C. demissa, C. rubelliana, C. subsoluta, C. viridirufa, C. xerica, Lichinella stipatula, Lecanora garovaglioi, Lobothallia praeradiosa, Peltula euploca, Phaeophyscia constipata* and *Rhizocarpon disporum* (Fig. 5).

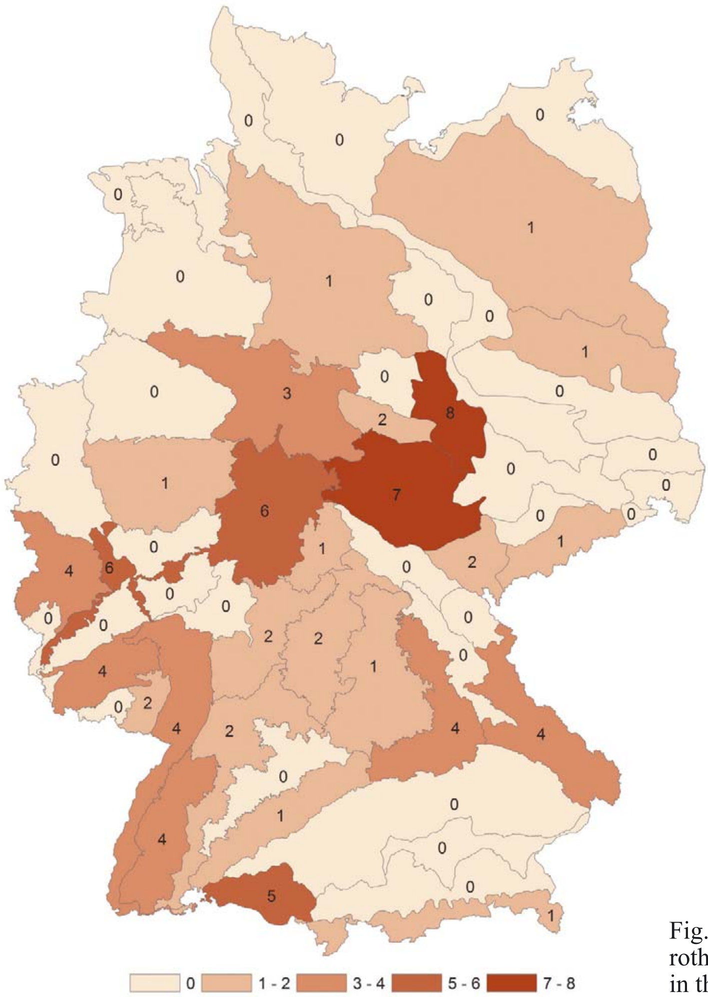

Fig. 5: Distribution of 20 xerothermic species mentioned in the text

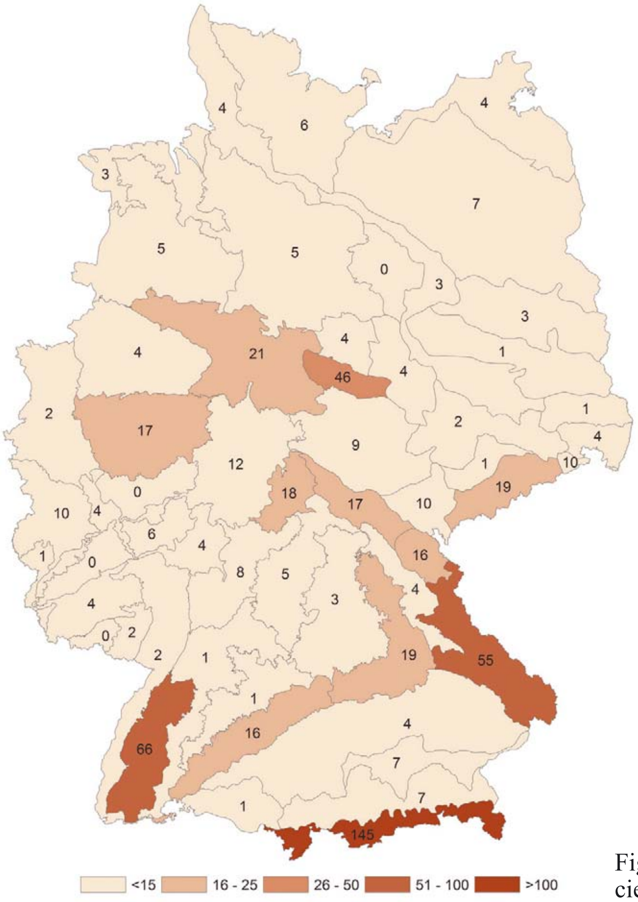

Fig. 6: Number of artic-alpine species in the natural regions

2.3. Integration of the German lichen flora in pan-European areals

For vascular plants, distribution can be described by areal formulas with three parameters; zonality (the extension of the area in north-south direction), oceanity or continentality (the extension of the area in west-east-direction) and the altitudinal belt. The different centres and extensions of the areas have an ecophysiological basis and are related to the macroclimate which changes zonally from north to south as well from maritime regions of the continents towards "continental" regions far from oceans.

The macroclimatic conditions and differences are also relevant to the microclimatic relations of the individual habitats. The lichen habitats, however, show a greater variability concerning the climatic manifestation than the corresponding macroclimate, therefore the survival of species is possible at localities far from the distribution centre – as defined by the "Gesetz der relativen

Standortskonstanz" – law of the relative constancy of environmental conditions (Poelt 1987).

Tab. 3: Alpine lichens on siliceous rock recorded in upland areas outside the Alps (*not recorded from Bavarian Alps, brackets: not recorded since 1950).

	Sch	**BayW**	**Hz**	**Rhön**	**Fi**	**Erz**	**Sau**
	1,493	**1,456**	**1,142**	**950**	**1,053**	**1,214**	**843 m**
*Adelolecia pilati**	+	+	+	-	-	-	-
*Amygdalaria panaeola**	+	+	+	+	-	-	-
*Amygdalaria pelobotryon**	-	-	-	+	-	-	-
*Arctoparmelia centrifuga**	-	+	+	-	-	-	-
Aspilidea myrinii	-	-	+	-	-	-	-
Bellemerea cinereorufescens	+	(+)	-	-	-	-	-
*Brodoa intestiniformis**	+	+	+	-	+	+	+
*Caloplaca magni-filii**	-	+	-	-	-	-	-
*Calvitimela aglaea**	+	+	+	+	(+)	-	-
*Calvitimela armeniaca**	-	+	-	-	-	-	-
*Cetrariella commixta**	+	(+)	+	-	+	(+)	(+)
*Clauzadeana macula**	+	+	-	-	-	-	-
*Collema glebulentum**	+	-	-	-	-	-	-
Cornicularia normoerica	+	+	+	-	+	-	-
*Dimelaena oreina**	+	-	-	-	-	-	-
*Euopsis pulvinata**	(+)	-	-	-	-	-	-
*Fuscidea mollis**	-	+	-	-	-	-	-
Gyalecta russula	+	-	-	-	-	-	-
*Ionaspis odora**	+	+	-	-	-	-	-
Ionaspis suaveolens	+	-	-	-	-	-	-
Koerberiella wimmeriana	+	-	-	-	-	-	-
*Lecanora caesiosora**	+	+	-	-	-	-	-
Lecanora cenisia	+	+	+	+	+	+	-
*Lecanora latro**	-	+	-	-	-	-	-
Lecanora dispersoareolata	+	-	-	-	-	-	-
*Lecanora frustulosa**	+	-	-	-	-	-	-
*Lecanora reagens**	+	-	-	-	-	-	-
*Lecanora viridiatra**	+	-	-	-	-	-	-
Lecidea confluens	+	+	+	+	+	-	+
*Lecidea silacea**	+	+	+	-	-	+	-
Melanelia hepatizon	+	+	+	+	+	+	+
*Metamelanea umbonata**	+	-	-	-	-	-	-
*Miriquidica complanata**	+	CZ	-	-	-	-	-
Miriquidica garovaglioi	+	+	-	+	-	+	-
*Miriquidica intrudens**	+	-	-	+	-	-	-
*Miriquidica nigroleprosa**	+	+	+	+	+	+	+
Ophioparma ventosa	+	+	+	+	+	+	-
*Physcia magnussonii**	+	+	-	-	-	-	-

	Sch 1,493	BayW 1,456	Hz 1,142	Rhön 950	Fi 1,053	Erz 1,214	Sau 843 m
Placynthium asperellum	+	-	-	-	-	-	-
*Placynthium flabellosum**	+	+	-	-	-	-	-
Protoparmelia nephaea	+	+	-	-	-	-	-
Pseudephebe pubescens	+	+	+	-	+	+	-
Pseudephebe minuscula	+?	+	-	-	-	+	-
*Pseudosagedia guentheri**	+	-	+	-	-	-	-
*Pseudosagedia grandis**	+	-	-	-	-	-	-
*Psorinia conglomerata**	-	+	-	-	-	-	-
Rhizocarpon alpicola	+	+	+	(+)	+	+	-
Rhizocarpon atroflavescens	+	-	-	-	-	-	-
Rhizocarpon carpaticum	+	+	-	-	-	-	-
*Rhizocarpon leptolepis**	+	+	-	-	-	+	-
*Rimularia gibbosa**	+	+		+	+	+	+
*Schaereria cinereorufa**	+	-	-	+	-	-	+
Schaereria tenebrosa	+	+	+	+	+	-	+
*Sphaerophorus fragilis**	+	+	+	+	+	(+)	(+)
Sporastatia polyspora	-	+	-	-	-	-	-
*Sporodictyon cruentum**	+	(+)	-	-	-	-	-
*Thelidium methorium**	+	-	-	-	-	-	-
*Thelignya lignyota**	+	-	-	-	-	-	-
*Umbilicaria crustulosa**	+	+	-	-	-	-	-
*Umbilicaria hyperborea**	-	+	+	-	+	+	-
*Umbilicaria proboscidea**	(+)	+	+	-	(+)	-	-
*Umbilicaria torrefacta**	+	+	+	+	+	(+)	-
Total	49	39	21	16	16	16	9

The descriptions of areas with areal formulas are also applicable to lichens (see e.g. Litterski & Ahti 2004). In a similar way, the areas of lichens are influenced from temperature decline from south to north and from the decrease in oceanity from west to east in spite of the fact that ecophysiologically the poikilohydric lichens are involved in different water uptake mechanisms. Considering all three variables for describing the extension of areas to get meaningful characteristics of areas one gets a great number of different areal formulas (Wirth et al. 2013) – too many for a general overall view. Even when strongly simplifying and uniting the submediterranean and mediterranean zones, about 30 different area diagnoses remain. Therefore zonality and oceanity here is brought into the focus in a unidimensional and simplifying manner.

Germany is situated in the centre of Europe, consequently centrally in the temperature range between arctic and mediterranean climate of Europe, and between the euoceanic climate in Western Europe (France, Great Britain) and the steppe climate of Eastern Europe. Consequently it is not surprising that the temperate zone is part of nearly all areal formulas of species occurring in Germany:

6.3 % of the 1980 species considered in Wirth et al. (2013) are distributed from arctic regions unto the Mediterranean (arctic–mediterranean), 12.3 % from the boreal zone to the Mediterranean (boreal–mediterranean) and 5.6 % from southern boreal zone to the Mediterranean (south boreal–med), in total 24.2 %, are very widespread in respect to zonal distribution. Furthermore, 23.7 % have a temperate–mediterranean distribution, 16 % are temperate (2.2 % of which are temperate-alpine), 2.0 % of the species are classified as arctic–temperate, 5.4 % as boreal–temperate, 2.6 % as southern boreal–temperate, 10 % as arctic-alpine, 1.3 % as arctic–boreal-alpine, 2.4 % as arctic–boreal-montane, 1.6 % as boreal-alpine and 6.9 % as boreal-montane.

Only 82 species (4.1 %) are so rare in the temperate zone (usually restricted to the southern or northern floristic zones) that in the lichen flora the designation "temperate" is omitted in the areal formulas, or put into brackets, or is restricted to "south temperate"; 22 of these have their centre in the Arctic or in the boreal zone and strongly decline towards Middle Europe, such as *Arctoparmelia centrifuga, Nephroma expallidum* and *Amygdalaria pelobotryon*, and c. 60 species are concentrated in the mediterranean and submediterranean zone, such as *Toninia toniniana, Porpidinia tumidula, Clauzadea chondrodes, Caloplaca haematites, Caloplaca lactea* s.str. and *Pyxine sorediata*. Such species are in the focus of attention because (1) they are very rare and the outposts of their areas and (2) the question is implicated how the occurrences of species can be explained when their main distribution regions are situated far from Central Europe. Therefore Suza was interested in the boreal *Melanohalea olivacea* (Suza 1937) and the arctic-boreal *Arctoparmelia centrifuga* and *Nephroma expallidum* (Suza 1936), both represented in the Alps by only a few occurrences, whereas the other boreal and arctic species represented in Central Europe usually show an arctic-alpine or boreal-montane distribution with considerable populations in the Central European mountains.

A significant proportion on the German lichen flora is composed of arctic-alpine and boreal-montane species. These areal types are well known and historically of interest since they play a considerable role in the German mountain areas (mainly in the Black Forest, Bohemian Forest and Harz, Figs. 3, 6), as well as the Alps. More or less 200 species can be assigned to the arctic-alpine areal type in Germany. Early biogeographically oriented publications have already attended to these species (Suza 1925). Almost all of the species listed in Table 3 belong to this distribution type.

370 species have atlantic and subatlantic distributions – thus this group is very large and reflects the position of Germany in the oceanity gradient, the atlantic species group being particularly well represented, especially in the

northwest, with, for example, *Varicellaria velata, Enterographa crassa, Phaeographis dendritica, Ph. inusta, Ph. smithii, Graphis inustuloides, G. elegans, Arthonia insulata, Cyphelium notarisii, Strigula taylorii* and *Parmotrema reticulatum* (Fig. 7).

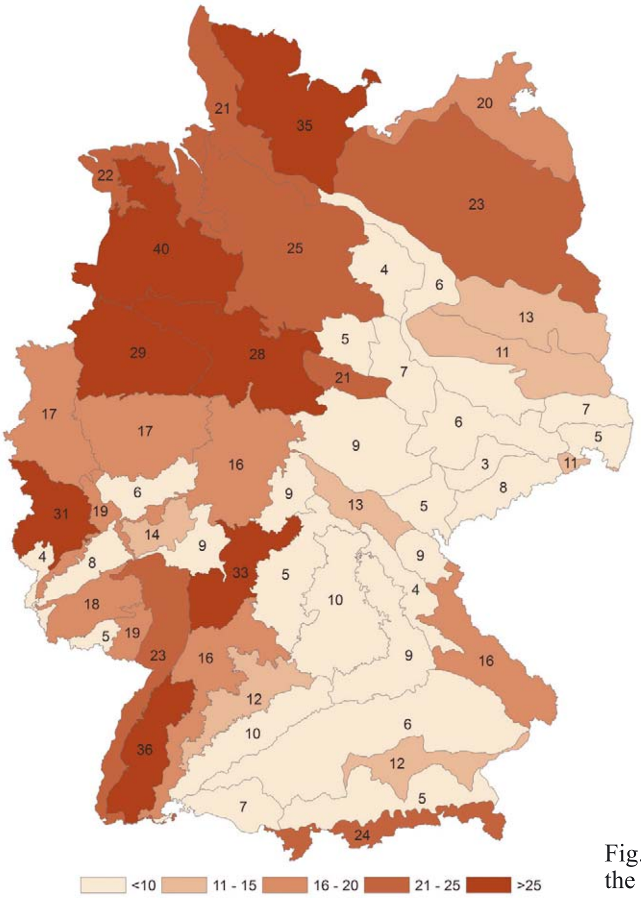

Fig. 7: Number of atlantic species in the natural regions

Compared with the atlantic distribution type, there are considerably fewer species characteristic of continental or subcontinental climate (57 species), most examples already treated as representatives of the xerothermic element, such as *Psora saviczii, Gyalidea asteriscus, Caloplaca raesenenii, Rinodina terrestris, Diploschistes diacapsis* and *Fulgensia bracteata* subsp. *deformis*, or, as members of the boreal-montane or montane element *Usnea glabrata, U. glabrescens, U. lapponica, U. longissima, U. substerilis, Tuckermannopsis chlorophylla, Nephromopsis laureri, Evernia divaricata, E. mesomorpha, Bryoria kuemmerleana, B. simplicior, B. furcellata* and *Melanohalea olivacea*.

A very remarkable chorological group represent lichens which are widespread in the Mediterranean and occur northwards as far as the Alps, but seldom beyond. In the Alps, these lichens occur in the alpine or subalpine belt, often in the dryer regions or on xeric sites, e.g. on vertical rock faces. In the Mediterranean, they are partly confined to the high mountains too, partly they are widespread also in lower altitudes. Thus their distribution is temperate/alpine-mediterranean/alpine or temperate/alpine-mediterranean. Among the lichens there are many *Caloplaca* species. To the first distribution type belong *Caloplaca aurea, C. biatorina, C. coccinea, C. isidiigera, C. nubigena, C. proteus, C. pruinosa, C. schistidii, Squamarina lamarckii, Staurothele rufa, Stenhammarella turgida, Umbilicaria laevis* and *Verrucaria fischeri,* to the second *Caloplaca schoeferi, C. erodens, Lecanora pruinosa, L. reuteri, Squamarina gypsacea, Tetramelas thiopolizus* and *Thelidium auruntii*. Some species appear to be restricted to the alpine and praealpine region of the Alps and Carpathian Mountains (*Caloplaca arnoldiiconfusa* and *C. australis*).

2.4. Dynamics

In a survey of changes of the lichen flora and lichen vegetation in Germany published 40 years ago (Wirth 1976), negative aspects clearly prevailed, especially the decline of lichens caused by acid air pollution and intense forestry and agricultural management. Positive aspects, such as an extended range and colonization of new habitats, referred largely to the continuing spread of mainly saxicolous lichens onto man-made substrates. The spread and increase of epiphytes were confined to a few acidophile species such as *Lecanora conizaeoides, Scoliciosporum chlorococcum* and *Lepraria incana*, a phenomenon accompanying the collapse of the natural epiphytic lichen vegetation.

During the past 25 years, the conditions have changed fundamentally: lichen vegetation has altered considerably, particularly an increase in diversity, within a very short time. The changes concern the epiphytes (Wirth et al. 1999). The natural epilithic lichen vegetation has remained stable – as already in times of influence of acid pollution – corresponding to the less dynamic saxicolous communities which often conserve their thallus pattern for decades (Frey 1959). Surprisingly, this is also observed with established epiphytic crustose communities, (Wirth et al. 1999). Changes are most obvious in connection with colonization of young tree stems and branches.

Changes to the epiphytic vegetation not only involve a return of lichen biota and a re-expansion of areas (Kandler & Poelt 1984) of disappeared or diminished species, but a change in the composition of the lichen flora composed of nitrophytes and neutrophytes to the disadvantage of acidophytes, beginning with the disappearance of populations of *Lecanora conizaeoides* (Wirth 1993, Massara et al. 2009). Reasons for the change are the strong reduction of acid pollution combined with incessant or increasing emissions of gaseous nitrogen compounds and fertilizing dust. On the other hand, one can observe a really concerted increase and expansion of populations of many species from regions with a mild climate which can be interpreted as a result of climate warming during the last decades (van Herk et al. 2002, Aptroot & Herk 2007, Kirschbaum et al. 2012), such as *Physciella chloantha, Hyperphyscia adglutinata, Parmotrema perlatum, Hypotrachyna revoluta*-complex, *Physcia clementei, Fellhanera bouteillei* and *Punctelia borreri* (Kirschbaum et al. 2012). During the expansion of the area of such indigenous species, an immigration of species not recorded before in Germany also took place, originating apparently from western Europe. Figure 8 illustrates their distribution in Germany and underlines their origin from the west and southwest. Today, these new species (neobiota) represent 24 % of the subatlantic and atlantic epiphytic species of the actual lichen flora of Germany. An impressive example is *Flavoparmelia soredians*. To this group belong the lichens listed in table 4, bearing in mind that one or more species were already present but overlooked in Germany – as discussed by Wirth (1997) and indeed confirmed, such as *Protoparmelia hypotremella.*

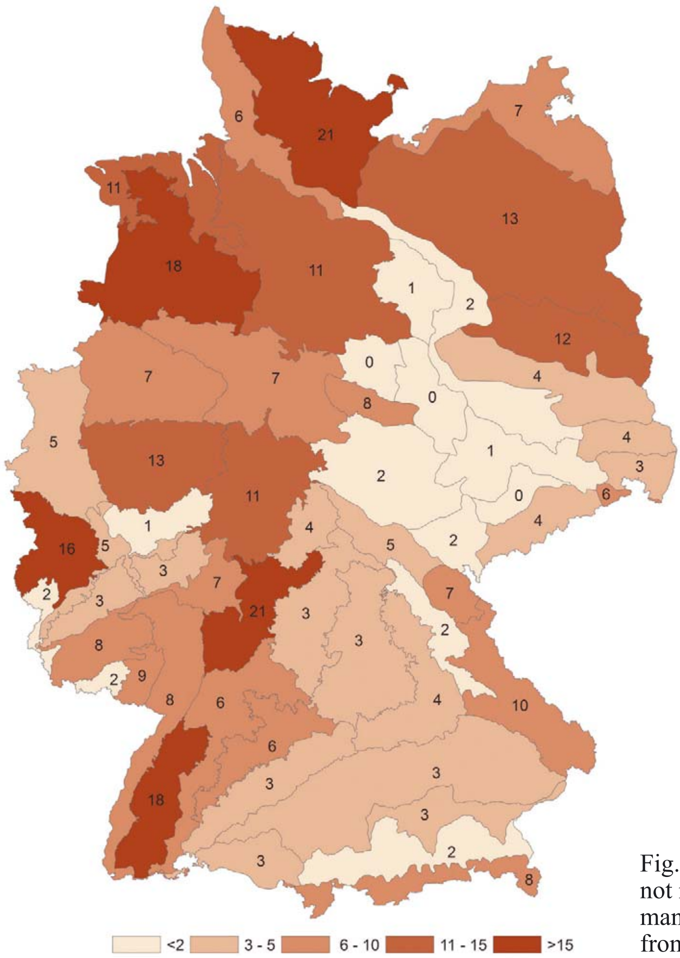

Fig. 8: Immigration of species not recorded before 1975 in Germany, originating apparently from western Europe

Tab. 4: Epiphytes with atlantic distribution tendencies newly recorded in Germany during the last 40 years – *recorded after the publication of Wirth et al. (2013).

Agonimia allobata	*Lecanora barkmaniana*
Agonimia flabelliformis	*Lecanora compallens*
Agonimia repleta	*Lecanora hybocarpa*
Agonimia vouauxii	*Lecanora quercicola*
Anisomeridium ranunculospora	*Lecanora sinuosa*
Arthonia lignaria	*Lecanora sublivescens*
Arthopyrenia carneobrunnea	*Lithothelium hyalosporum*
Bacidina adastra	*Lithothelium septemseptatum*
Bacidina brandii	*Micarea myriocarpa*
Bacidina neosquamulosa	*Micarea nigella*
Caloplaca ulcerosa	*Micarea pycnidiophora*
Celothelium lutescens	*Micarea viridileprosa*
Cladonia norvegica	*Opegrapha viridileprosa**
Collemopsidium subarenisedum	*Parmotrema pseudoreticulatum*
Dictyocatenulata alba	*Psoroglaena abscondita*
Fellaneropsis vezdae	*Psoroglaena stigonemoides*
Fellhanera gyrophorica	*Pycnora leucococca*
Fellhanera ochracea	*Ramonia chrysophana*
Fellhanera subtilis	*Ramonia interjecta*
Fellhanera viridisorediata	*Ropalospora viridis*
Flavoparmelia soredians	*Scoliciosporum curvatum*
Fuscidea pusilla	*Scoliciosporum pruinosum*
Gyalectidium setiferum	*Strigula jamesii*
Halecania viridescens	*Strigula taylorii*
Jamesiella anastomosans	*Usnea flavocardia*

In addition to the expansion of species from mild regions, it has also been noted the immigration or expansion of some species preferring a cool or cold, or at least continental, climate – namely species which are at home mainly in boreal and temperate-continental zones, exemplified by *Evernia divaricata*, which in the last decades has been found in many localities far from montane forests, and *Nephromopsis laureri, Bryoria furcellata, B. simplicior, Usnea lapponica* and *Evernia mesomorpha*. It is remarkable that these species appear in the lowland of the formerly impoverished northeast of Germany (Mecklenburg-Western Pomerania, Brandenburg). Furthermore, *Physcia biziana*, a thermophilous species with continental tendencies, was only recorded in eastern Germany for the first time a few years ago. However, to date, there are no indications for an immigration of obligate saxicolous species.

3. Discussion

Theoretically, a region shows the maximal species diversity if all significant lichen substrates are represented in each climate region, i.e. all substrate types in all altitudinal belts from lowland unto nival zone. In Germany *as a whole* all lichen-relevant substrates and all altitudinal belts from planar to alpine are found.

Is the species number of 2,000 recorded for Germany a relatively high or low figure? For example, in Great Britain SMITH et al. (2009) indicate 1,873 species inclusive of fungi traditionally recorded by lichenologists; this number has now increased to 1,908 lichen species + 63 fungi (SEAWARD *in litt.*), which are 4 % less – a comparable figure. However, in Austria, covering less than a quarter of the area of Germany, 2,237 species are recorded (HAFELLNER & TÜRK 2001) – now increased to 2,400 species – a considerably more diverse lichen flora. Switzerland, with an area less than one eighth that of Germany, has only 10 % less species (1,795 or c. 1,845 species inclusive lichen-related fungi, CLERC & TRUONG 2012), and France, with an 80 % larger area than Germany, has 2,577 (2,648 resp.) species (ROUX 2014), which is 28 % more. The differences in species-numbers are not alone justified by ecological reasons; they may also be due to different degrees of investigation. Austria‘s high species number, especially in relation to Switzerland with similar ecological conditions, is also a result of extremely thorough floristic research by ARNOLD in Tirol and POELT and his disciples (this book, HERTEL 2018).

The discrepancy between Austria and Germany appears noteworthy. What is the reason? Which ecological parameters are missing in Germany? Checking the list of species present in Austria but lacking in Germany, such well known and widespread species names are striking: *Acarospora intricata, Alectoria nigricans, Bellermerea alpina, B. diamartha, B. subsorediza, Brodoa atrofusca, Bryodina rhypariza, Lecanora orbicularis, Lecidea atrobrunnea, L. promiscens, L. rapax, Lobothallia melanaspis, Rhizocarpon effiguratum, Rh. pusillum, Rh. renneri, Rhizoplaca melanophthalma, Rh. chrysoleuca, Rinodina milvina, Stereocaulon botryosum, St. glareosum* and *Umbilicaria decussata.* These are alpine species growing on siliceous rock and acid soils. In the German alpine belt, siliceous rock is almost completely absent and acid soils are rare; furthermore, if local occurrences of schistose rocks and hornstone, especially in Allgäu, which support, for example, *Carbonea distans, Gyalecta erythrozona, Lecanora marginata, Orphniospora moriopsis, O. mosigii*, *Sporastatia testudinea* and *Umbilicaria laevis*, did not exist, then the balance would be even more less favourable.

To Germany's credit, littoral species can be listed which are naturally missing in Austria, but there are only c. 40 species since Germany's coastline, although extensive, is unfavourable for lichen colonization; there are very few natural rock sites, which helps to explain why widespread species such as *Anaptychia runcinata* are absent.

Clerc and Truong (2012) relate species number to the logarithm of the area of some countries. In this comparison of species density, Germany holds an average position whereas Austria, Switzerland, Slovakia and Italy are above average, and Poland, Netherlands and Great Britain are below average. Unlike Germany, in Austria, Switzerland, Slovakia and Italy a considerable diversity in the geology from lowland up to the alpine belt favours lichen diversity. In Italy and other countries (e.g. France) a further diversity-enhancing fact is their extension over more than one chorological zone.

A very high proportion of c. 80 % of the German lichen species are classified as more or less rare or exinct, and only less than 7 % as frequent. Even if no agreement exists regarding “rare” or “frequent”, the numbers reveal a strong imbalance of the frequency categories and reflect the problematic ecological conditions for many lichen species in Germany with a densely populated and intensively exploited landscape. Nevertheless, the ecological diversity is still considerable – hence the presence of 2,000 species – but many lichen habitat types which are important for lichen diversity only exist in small isolated patches, such as gypsum outcrops, basic and ultrabasic siliceous rocks, old forest trees, open nutrient-poor grassland, ephemeral, but permanently available sites on sand and loam, and siliceous coastal rocks. Rareness and endangerment of many of the habitat types by intensive management, mining and quarrying etc. explains the rareness of the corresponding lichens. Many species, such as *Porpidia nadvornikiana, Rinodina trachytica, R. furfurea, Lichinella stipatula, Buellia epigaea, Stereocaulon leucophaeopsis* and *Collema glebulentum*, must be rare. Where rocks or erratic boulders or rock outcrops of unusual mineralogical composition (serpentinite, gypsum) are rare, they should be the focus of attention by nature conservation authorities. Apart from climatical factors, the unequal distribution of rock outcrops and boulders in general, and of the mentioned special substrate types in particular, are the main reasons for the regional imbalance of lichen diversity in Germany.

One of the most surprising insights in recent decades of lichen studies is the fact that epiphytic lichen vegetation over large areas can considerably change through enrichment and the appearance of neobiota within a few years. Hitherto, only detrimental effects on lichen vegetation were thought to occur over short periods of time. The existence of neobiota among lichens was still questioned 40 years ago (Wirth 1976). Nevertheless, the very high degree (23 %) of extremely rare, specialized species in Germany shows how vulnerable the lichen flora is. Endangerment may occur for many reasons, particularly by intense land use and eutrophication of lichen sites, but one should not forget over-collection by lichenologists.

4. Acknowledgements

We are very much indebted to Mark SEAWARD for his valuable help in translating the German text.

5. Literature

APTROOT, A. & VAN HERK, C.M. 2007: Further evidence of the effects of global warming on lichens, particularly those with *Trentepohlia* phycobionts. — Environ. Pollut. **146**: 293–298.

CLERC, P. & TRUONG, C. 2012: Catalogue des lichens de Suisse. (http://www.ville-ge.ch/musinfo/bd/cjb/cataloguelichen – Version 2.0, 11.06.2012).

HAFELLNER, J. & TÜRK, R. 2001: Die lichenisierten Pilze Österreichs: eine Checkliste der bisher nachgewiesenen Arten mit Verbreitungsangaben. — Stapfia **76**: 1–167.

HERTEL, H. 2018: Josef POELT – on his personality and his foodprints in the history of lichenology. — Biosyst. Ecol. Ser. **34**: 1 –100. — Wien: Verlag der ÖAW.

KANDLER, O. & POELT, J. 1984: Wiederbesiedlung der Innenstadt von München durch Flechten. — Naturwiss. Rundsch. **1984**: 90–95.

KIRSCHBAUM, U., CEZANNE, R., EICHLER, M., HANEWALD, K. & WINDISCH, U. 2012: Long-term monitoring of environmental change in German towns through the use of lichens as biological indicators: comparisons of 1970, 1980, 1985, 1995, 2005 und 2010 in Wetzlar and Giessen. — Environ. Sci. Europa **24**: 1–19.

LITTERSKI, B. & AHTI, T. 2004: World distribution of selected European *Cladonia* species. — Symb. Bot. Ups. **34**: 205–236.

MASSARA, A.C., BATES, J.W. & BELL, J.N.B. 2009: Exploring causes of the decline of the lichen *Lecanora conizaeoides* in Britain: effects of experimental N and S application. — Lichenologist **41**: 673–681.

POELT, J. 1987: Das Gesetz der relativen Standortskonstanz bei den Flechten. — Bot. Jahrb. Syst. **108**: 363–371.

ROUX, C. 2014: Catalogue des lichens et champignons lichénicoles de France métropolitaine. — Association française de lichénologie (AFL). — Fougères: Henry des Abbayes.

SCHIEFELBEIN, U., JANSEN, F., LITTERSKI, B. & WIRTH, V. 2015: Naturräumlich-ökologische Analyse der Flechtenflora von Deutschland. — Herzogia **28**: 624–643.

SMITH, C.W., APTROOT, A., COPPINS, B.J., FLETCHER, A., GILBERT, O.W., JAMES, P.W. & WOLSELEY, P. 2009: The Lichens of Great Britain and Ireland. — London: The British Lichen Society.

SUZA, J. 1925: A sketch of the distribution of lichens in Moravia with regard to the conditions in Europe (in czech). — Publ. Fac. Sci. Univ. Masaryk **55**: 1–152.

SUZA, J. 1935: Das xerotherme Florengebiet Südwestmährens (ČSR). — Beih. Bot. Centralbl. **53** (B): 440–484.

SUZA, J. 1936: Das arktische Element als Glazialrelikt in der Flechtenflora der alpinen Vegetationsstufe der Westkarpathen (ČSR), bzw. Mitteleuropas. — Vestník Kral. Čes. Spol. Nauk. **1935**: 1–30 (Sep.pag.).

SUZA, J. 1937: Einige wichtige Flechtenarten der Hochmoore im Böhmischen Massiv und in den Westkarpathen. — Vestník Kral. Čes. Spol. Nauk. **1937**: 1–33 (Sep.pag.).

VAN HERK, C. M., APTROOT, A. & VAN DOBBEN, H.F. 2002: Long-term monitoring in the Netherlands suggests that lichens respond to global warming. — Lichenologist **34**: 141–154.

WIRTH, V. 1976: Veränderungen der Flechtenflora und Flechtenvegetation in der Bundesrepublik Deutschland. — Schr.reihe Veg.kd. **10**: 177–202.

WIRTH, V. 1993: Trendwende bei der Ausbreitung der anthropogen geförderten Flechte *Lecanora conizaeoides*. — Phytocoenologia **23**: 625–636.

WIRTH, V. 1997: Einheimisch oder eingewandert? Über die Einschätzung von Neufunden von Flechten. — Biblioth. Lichenol. **67**: 277–287.

WIRTH, V., CEZANNE, R. & EICHLER, M. 1999: Beitrag zur Kenntnis der Dynamik epiphytischer Flechtenbestände. — Stuttg. Beitr. Nat.kd. A, **595**: 1–17.

WIRTH, V., HAUCK, M., DEBRUYN, U., SCHIEFELBEIN, U., JOHN, V. & OTTE, V. 2009: Flechten aus Deutschland mit Verbreitungsschwerpunkt im Wald. — Herzogia **22**: 79–107.

WIRTH, V., HAUCK, M., VON BRACKEL, W., CEZANNE, R., DE BRUYN, U., DÜRHAMMER, O., EICHLER, M., GNÜCHTEL, A., JOHN, V., LITTERSKI, B., OTTE, V., SCHIEFELBEIN, U., SCHOLZ, P., SCHULTZ, M., STORDEUR, R., FEUERER, T. & HEINRICH, D. 2011: Rote Liste und Artenverzeichnis der Flechten und flechtenbewohnenden Pilze Deutschlands. — Nat.schutz Biol. Vielfalt **70**: 7–122.

WIRTH, V., HAUCK, M. & SCHULTZ, M. 2013: Die Flechten Deutschlands. 2 vol. — Stuttgart: Eugen Ulmer.

Address of the authors:

Prof. Dr. Volkmar WIRTH
Fr.-Ebert-Str. 68, D-71711 Murr
Email: volkmar.wirth@online.de

Dr. Ulf SCHIEFELBEIN
Blücherstr. 71, D-18055 Rostock
Email: ulf.schiefelbein@gmx.de

Dr. Birgit LITTERSKI
DUENE e. V.
Soldmannstr. 15, D-17489 Greifswald
Email: littersk@uni-greifswald.de