DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS
106

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106

LICHENS AND LICHENICOLOUS FUNGI IN ESTONIA: DIVERSITY, DISTRIBUTION PATTERNS, TAXONOMY

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CONTENTS

LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following publications, which are referred in the further text by their Roman numerals:

I. Suija, A. 2005a: Lichenicolous fungi and lichens in Estonia I. Ascomycota. *Nova Hedwigia* 80(1–2): 247–267.
II. Suija, A. 2005b: Lichenicolous fungi in Estonia II. Basidiomycota and conidial fungi. *Nova Hedwigia* 80(3): 349–366.
III. Suija, A. & Alstrup, V. 2004: *Buelliella lecanorae*, a new lichenicolous fungus. *Lichenologist* 36(3–4): 203–206.
IV. Randlane, T., Saag, A. & Suija, A. 2002: Biodiversity of lichenized taxa in Estonia: distribution of rare species. *Biblioth. Lichenol.* 82: 99–109.
V. Jüriado, I., Suija, A. & Liira, J. Biogeographical determinants of lichen species diversity on islets in West-Estonian Archipelago. Manuscript submitted to *J. Veg. Sci*.
VI. Suija, A. Character study of some two-celled species of the lichenicolous genus *Abrothallus.* Manuscript submitted to *Ann. Bot. Fenn*.

OTHER RELEVANT PUBLICATIONS

I. Suija, A. & Jüriado, I. 2002: Lichens and lichenicolous fungi of the Hiiumaa Islets Landscape Reserve (Estonia). *Folia Cryptog. Estonica* 39: 37–50.
II. Jüriado, I., Lõhmus, P., Nilson, E., Randlane, T., Saag, A., Saag, L. & Suija, A. 2004: *Eesti Pisisamblikud* [*Estonian Microlichens*]. Tartu University Press, 583 pp.

The contribution of A. Suija to the relevant publications is the following:
Paper III: anatomical-morphological examination, description of species and writing (80%); paper IV: data provision and writing (20%); and paper V: lichen collection, determination, database development and writing (30%).

INTRODUCTION

Lichens represent a model system of symbiosis consisting of at least two symbiotic partners: a heterotrophic fungus (mycobiont) and an autotrophic green alga or cyanobacterium (photobiont). Besides the lichen fungus itself, lichens host a variety of microfungi including incidental cohabitants and lichenicolous fungi. Lichenicolous fungi are relatively small and inconspicuous and therefore they remain frequently unnoticed. Moreover, because of such an unusual substrate, they are mostly collected and studied by lichenologists and not by mycologists.

The tradition of the lichenological investigations in Estonia dates back to the second half of the 18th century (Randlane & Saag 2000) and the first list, which includes also Estonian lichens, was published already at the end of the 19th century (Bruttan 1870). Owing to more than 200 years of floristic exploration, the diversity of the Estonian lichen flora is rather well characterized (Randlane & Saag 2000) and up to now 1007 species of lichens, lichenicolous and allied fungi have been recorded (Randlane et al. 2005). Because of the suitable geographic location, specific features of climate, habitats and substrate variety, the highest richness and diversity of lichen species has been observed on the West- and North-Estonian islands (e.g. Randlane 1986; Nilson & Piin 1998; Suija & Jüriado 2002). In spite of these intensive investigations, studies of the determinants underlying species richness are yet in the beginning phase (e.g. Lõhmus & Lõhmus 2001; Jüriado et al. 2003). Moreover, not all ecological groups are equally well studied (Randlane & Saag 2000).

One of these groups, which was almost totally neglected until recently, is the group of the lichen-inhabiting (lichenicolous) fungi. Lichenicolous fungi constitute a highly specialized an ecological group of fungi which are adapted to growing on the surface or inside lichens (Lawrey & Diederich 2003; Gams et al. 2004) and have the ability to obtain fixed carbon from their lichen host (Hawksworth 1988). Phylogenetically, these fungi represent a diverse assemblage of taxa, indicating that the lichenicolous habit has arisen several times during fungal evolution (Hawksworth 1988; Lutzoni et al. 2001; Lawrey & Diederich 2003). Moreover, an hypothesis has been proposed about the origin of non-lichenized ascomycetes from the lichenized ancestors through the transition phase of lichenicolous habit (Lutzoni et al. 2001).

The first comprehensive treatise on lichenicolous species was published by the British lichenologist W. L. Lindsay (1869). As far as it is known, he was also the man who first used the term *lichenicolous* (Hawksworth 2003). A new starting point and a rise in interest appeared owing to the studies of D. L. Hawksworth (e.g. 1979; 1981; 1982; 1983). His papers on the diversity of these fascinating fungi stimulated further research of many lichenologists. By now, the process is on the rise, indicated by the constantly increasing number of publications dealing with various aspects (systematics, biology, distribution, ecology, biomonitoring) of lichenicolous species (Lawrey & Diederich 2003). A

recent estimate of the species richness of lichenicolous fungi in the world is c. 1500 species. However, based on the latest judgements, the actual number might even exceed 3000 species (Gams et al. 2004). Although ascomycetes form an overwhelming majority of the lichenicolous taxa, basidiomycetes and conidial fungi are known as well (Lawrey & Diederich 2003).

Host specificity appears to be exceptionally high among the lichenicolous species. About 95% of the described species are specialized to grow on a single species, on a closely related species or on a monophyletic group (Lawrey & Diederich 2003). Even if the degree of host specificity is to some extent overestimated – many of the described species are known only from a few collections or the species delimitation of some genera (e.g. *Abrothallus*) are controversial – the percentage still remains very high.

There is increasing interest in the ecology of parasite populations and communities focusing on the processes underlying parasite-host-environment interactions (Guegan et al. 2005). For example, studies of plant communities have revealed that plant diseases play an important role in plant community succession, influencing changes in species composition (see review in Gilbert 2002). Parasitic microfungi too are important components of the lichen communities. However, there are only a few studies which deal with their role in alteration of the structure of the lichen community (Arvidsson 1979; Glenn et al. 1997; Lücking & Bernecker-Lücking 2000; Hedenås et al. 2002) and therefore their functioning in natural systems is largely unknown. It has been hypothesized that the number of lichenicolous fungi rises during natural community succession due to the increasing host diversity; and moreover, species in communities of more recent succession stage tend to be more specialized and less aggressive (Lawrey & Diederich 2003).

This study is based on the various topics concerning the lichens and lichenicolous fungi in Estonia, and focuses on the diversity of lichenicolous fungi. It covers three main topics:

(1) Papers I, II and III deal with the diversity of lichenicolous fungi in Estonia. Papers I and II are compilations which include data of the author's original determinations as well as data from earlier publications. Several taxa are pointed out for either biogeographical, ecological or taxonomical reasons. Paper III represents a description of a new species, *Buelliella lecanorae*. The data from the recent publications (Jüriado et al. 2004; Aptroot et al. 2005; Suija et al. 2005) are also included in the analysis of species composition and host diversity.

(2) Papers IV and V are more general accounts, dedicated to the distribution patterns of Estonian lichens and lichenicolous fungi. The reasons for the high share of rare taxa in the Estonian lichen flora are discussed in paper IV. Paper V focuses on the biogeographical determinants (islet size, biotope diversity and isolation) of species richness on the islets of the West-Estonian Archipelago.

(3) Paper VI discusses the problems of species delimitation in the morphologically well characterized, exclusively lichenicolous genus *Abrothallus,* concentrating on two-celled species. Because of the controversial interpretation of characters by different authors, the circumscription of species is confounding and unclear. This study is the first attempt to assess statistically the value of the characters which have been used in earlier papers to delimit the two-celled species of *Abrothallus*.

MATERIALS AND METHODS

Materials

This study is based on the collections of dried lichen specimens preserved in various lichenological herbaria (C, H, S, TAA, TAM, TALL, TU, UGDA-L, UPS) as well as on the fresh material collected by the author herself and by co-workers (I. Jüriado, P. Lõhmus) from different localities in Estonia between 1998 and 2004. The material for paper V was collected from 32 islets around the island of Hiiumaa; for a precise description of the sampling methods see in "Materials and methods" of paper V. All collected material is deposited in the lichenological herbarium of the University of Tartu (TU).

Microscopy

The examinations of specimens were carried out with the stereomicroscopes TECHNIVAL 2 (Carl Zeiss Jena) and Olympus SZ51 (magnifications x5–x50); and with the microscopes PZO and Olympus CX41 (magnifications x100–x1200). Routine methods of light microscopy were used: cross-sections were made using a freezing microtome or by the hand using a razor blade. The squash preparations were examined in water and mounted later with c. 50% HNO_3 (N), c. 10% KOH (K) or Lugol's solution (I). For paper II, the Scanning Electron Microscopy (Philips SEM 515, Geocenter, University of Copenhagen) was performed for a detailed investigation of the surface structure of some conidial fungi.

Data provision

For papers I, II, and IV, the frequency classes were formed to appraise the share of rare and frequent species. The *rare species* is defined here as a species known from up to ten localities across the country, although a more detailed division has been proposed by Randlane & Saag (1999). The following studies have been used for categorizing *frequent* and *rare* species: Jüriado et al. 1999; Jüriado et al. 2004; Aptroot et al. 2005; Suija et al. 2005.

For papers IV and V, the lichens and lichen habiting fungi were divided into the following groups based on substrate preference: (1) epiphytic lichens on deciduous trees; (2) epiphytic species on coniferous trees; (3) epilithic lichens on granite; (4) epilithic species on calcareous rocks and pebbles (incl. mortar and brick); (5) epilithic lichens on sandstone; (6) lichens on mosses and plant debris; (7) lichens on soil; (8) lichens on wood (incl. decaying wood); (9) lichenicolous fungi/lichens. In paper V, the groups of lichens on soil and lichens

on mosses were combined into a group of ground layer lichens because of the low representation of the species occurring on epigeic mosses.

The following books were used to find out the distribution borders of certain lichen species: Nimis 1993; Trass & Randlane 1994; Jüriado et al. 2004. The distribution maps were compiled with the program package DMAP (Morton 1999).

Data analysis: determinants of species richness on islets (V)

A generalized linear model (GLIM) analysis with Poisson error distribution, implemented in the program package Statistica 6.5, was applied to study the effect of islet traits (islet area, number of biotopes and distance from the mainland) on the number of lichen species (incl. lichenized, lichenicolous and allied fungi). The number of lichen species on an islet was estimated at two levels: (1) total number of lichen species, and (2) number of lichen species on a particular substrate. In the models, all continuous environmental variables were log-transformed. The factor effect profile method, using the semi-residuals of the model, was used for the graphic presentation of the factor effect on species richness.

Frequently registered species, observed at least on six islets (104 taxa), were used to explain species-specific trends of dispersal and colonization. The occurrence predictability of each lichen species on an islet according to islet parameters was tested with logistic regression analyses in GLIM analysis (binomial error distribution, logit link-function) (proc GENMOD, SAS Institute Inc. 1989). The existence of a species-specific behaviour was tested as the significance of the interaction term between the discrete factor 'Species' and a continuous trait of the islet. The MIXED model analysis (Littell et al. 1996) was built with the fixed factor 'Species' and a random factor 'Islet' to assess the relationship of abundance of lichen species to islet area, number of biotopes and distance from the mainland.

Data analysis: character study of *Abrothallus* (VI)

Searching for implications for species delimitation in the exclusively lichenicolous genus *Abrothallus*, 68 specimens of earlier identified species from eight different host genera (*Hypogymnia, Melanelia*, *Parmelia*, *Platismatia*, *Sticta*, *Usnea*, *Vulpicida, Xanthoparmelia*) were exploited. Host specificity was the main criterion for species determination. Altogether eleven characters were selected using available data from the literature; of them four characters were quantitative, six were qualitative and one was a calculated ratio.

List of the characters used and their abbreviations:

1. ASCD – diameter of the ascoma (mm)
2. ASLEN – length of the ascospore (μm)
3. ASWI1 – width of the upper cell of the ascospore (μm)
4. ASWI2 – width of the lower cell of the ascospore (μm)
5. ASRA – the ratio of the ascospore length to upper cell width
6. HYMCO – colour of the crystalline layer above the hymenium (0 – red; 1 – brown)
7. LUG – reaction with Lugol's solution (0 – reaction negative; 1 – reaction positive)
8. CONID – absence or presence of conidiomata (0 – absence; 1 – presence)
9. ASCP – pruinosity of the ascomata (0 – without green pruina; 1 – with green pruina)
10. HYPCOL – colour of the hypothecium (0 – dark brown; 1 – brown; 2 – light brown)
11. ASCS – shape of the ascomata (0 – globose; 1 – flattened).

In order to test the concordance of the conventional classification and the predicted classification of individuals, classificatory discriminant analysis (CDA) with a direct method was implemented using Statistica 6.5. In CDA, the host species was chosen as a grouping variable. The descriptive statistics (mean, standard deviation, minimum and maximum value) were calculated for all quantitative characters (length and width of ascospores, diameter of ascomata). As conidiomata appeared on specimens on *Vulpicida* and *Xanthoparmelia* rather constantly, they were measured and basic statistics were calculated for these characters as well. The mean values of the measurements were compared with the Student's t-test.

RESULTS

Diversity of lichenicolous fungi (I, II, III)

As a result of the present study, 137 of species of lichenicolous fungi and lichens were found on the territory of Estonia. Most of them belong to the ascomycetes (91 species; 66%), followed by the groups of conidial fungi (36; 26%) and basidiomycetes (10; c. 7%).

The majority of the determined species are widely distributed worldwide. However, the occurrence of some species (*Clypeococcum cetrariae* Hafellner, *Endococcus nanellus* Ohlert, *Karsteniomyces tuberculous* Alstrup & D. Hawksw., *Lichenopeltella ramalinae* Etayo & Hafellner*, Taeniolella cladinicola* Alstrup*, Tremella ramalinae* Diederich and *Zwackhiomyces physciicola* Alstrup) should be pointed out as they have been recorded from a few scattered localities around the world. In addition, a new host species has been determined for two lichenicolous fungi: *Dactylospora homoclinella* (Nyl.) Hafellner, known from the species of *Lecanora* so far, has been found on *Buellia griseovirens* (Turner & Borrer) Almb.; *Arthonia intexta* Almq. reported previously only from apothecia of saxicolous *Lecidella* species, was detected on corticolous species of the same genus.

In the course of my research, an unknown lichenicolous fungus growing on *Lecanora pulicaris* (Pers.) Ach. was collected. Additional specimens were found in the lichenological collections of TU. Based on this material, the new species *Buelliella lecanorae* Suija & Alstrup was described. The species is most similar to *B. trypethelii* (Tuck.) Fink and to *B. inops* (Triebel & Rambold) Hafellner, yet differing by in some anatomical details and in host preferences (Table 1). Moreover, *B. lecanorae* is the second species of the genus known from Europe.

The host spectrum of the lichenicolous fungi found in Estonia is relatively large – the species have been determined from 103 lichen host species from 50 genera. The prevalence of foliose and fruticose hosts is notable: dominating are records from the representatives of *Parmeliaceae* (36 records), *Peltigeraceae* [mainly on *Peltigera* (24)] and *Cladoniaceae* [mainly on *Cladonia* (28)] (Table 2). The family of crustose lichens *Lecanoraceae* and especially the genus *Lecanora* host also numerous lichenicolous species, 35. The lichen species whose distribution area embraces several phytogeographic regions (multiregional and cosmopolitan species) prevail among the species for which three or more lichenicolous species have been determined (Table 3).

Among the Estonian material, 112 out of the 137 species should be regarded as *specialists* hosting on a single species or on phylogenetically related species or genera. Only 23 should be considered as *generalists* known from various unrelated lichens.

Table 1. Comparison of *Buelliella inops*, *B. trypethelii* and *B. lecanorae*.

	B. inops	*B. trypethelii*	*B. lecanorae*
Size of ascomata (µm)	150–200	300–450	–200
Size of spores (µm)	16–17 x 6–8	16–19 x 8–11.5	17–19 x 7.5–9.5
Hymenium height (µm)	45–55	55–65	60–65
Epihymenium (colour)	Dark brown	Reddish black	Reddish brown
Epihymenium reaction with K	Negative	Negative	Negative
Epihymenium reaction with N	Negative	Red	Slightly red
Size of asci (µm)	34–50 x 14–17	35–45 x 17–23	50–57 x 18–20
Distribution	Australia, Mexico, USA	USA, Guyana	Estonia
Host species	*Caloplaca* spp.	*Trypethelium* spp.	*Lecanora* spp.

Table 2. Summary of the host spectrum of Estonian lichenicolous species.

Host family	Host genus	No. of records
Acarosporaceae	*Acarospora*	1
Bacidiaceae	*Bacidia*	4
	Lecania	1
	Tephromela	1
Candelariaceae	*Candelariella*	4
Chrysothricaeceae	*Chrysothrix*	1
Cladoniaceae	*Cladina*	1
	Cladonia	28
Collemataceae	*Collema*	1
Coniocybaceae	*Chaenotheca*	3
Graphidaceae	*Graphis*	2
Hymeneliaceae	*Aspicilia*	1
Lecanoraceae	*Lecanora*	31
	Lecidella	5
Lecideaceae	*Hypocenomyce*	1
	Lecidea	5
Lobariaceae	*Lobaria*	3
Mycoblastaceae	*Mycoblastus*	1
Parmeliaceae	*Cetraria*	3
	Evernia	3
	Hypogymnia	5
	Melanelia	2

Table 2. (Continuation)

Host family	Host genus	No. of records
	Parmelia	7
	Parmeliopsis	1
	Platismatia	2
	Tuckermannopsis	1
	Usnea	7
	Vulpicida	2
	Xanthoparmelia	3
Peltigeraceae	*Peltigera*	24
	Solorina	1
Pertusariaceae	*Ochrolechia*	1
	Pertusaria	8
Phlyctidaceae	*Phlyctis*	1
Physciaceae	*Amandinea*	2
	Anaptychia	1
	Buellia	2
	Phaeophycia	4
	Physcia	14
	Physconia	1
Psoraceae	*Protoblastenia*	2
Ramalinaceae	*Ramalina*	5
Rhizocarpaceae	*Rhizocarpon*	3
Stereocaulaceae	*Lepraria*	1
	Stereocaulon	1
Teloschistaceae	*Caloplaca*	4
	Xanthoria	6
Theleotremataceae	*Diploschistes*	2
	Thelotrema	1
Verrucariaceae	*Verrucaria*	3
Unknown	Unknown	1

Table 3. Lichens on which three and more lichenicolous species have been recorded, and their general world-scale distribution.

Host family	Host species	No. of fungi	Host distribution
Cladoniaceae	*Cladonia digitata*	5	multiregional
	C. ochrochlora	3	multiregional
Lecanoraceae	*Lecanora argentata*	4	multiregional
	L. carpinea	3	multiregional
	L. chlarotera	4	multiregional
	L. dispersa	3	multiregional
	L. pulicaris	3	circumpolar
	Lecidella elaeochroma	4	cosmopolitan
Lecideaceae	*Lecidea lapicida*	3	cosmopolitan
Lobariaceae	*Lobaria pulmonaria*	3	nemoral
Parmeliaceae	*Evernia prunastri*	3	nemoral
	Hypogymnia physodes	4	multiregional
	Parmelia saxatilis	3	multiregional
	P. sulcata	4	multiregional
Peltigeraceae	*Peltigera canina*	6	multiregional
	P. didactyla	6	boreal
	P. praetextata	3	boreal
	P. rufescens	3	multiregional
Pertusariaceae	*Pertusaria pertusa*	3	multiregional
Physciaceae	*Phaeophycia orbicularis*	4	multiregional
	Physcia caesia	4	multiregional
	P. stellaris	3	multregional
	P. tenella	3	nemoral
Ramalinaceae	*Ramalina fraxinea*	3	nemoral
Teloschistaceae	*Xanthoria parietina*	5	multiregional

The distribution maps were compiled for two host species and their parasites to detect their overlapping pattern: (1) *Lobaria pulmonaria* (L.) Hoffm. with *Dactylospora lobariella* (Nyl.) Hafellner and *Plectocarpon lichenum* (Sommerf.) D. Hawksw. (Fig. 1a) and (2) *Lecanora rupicola* (L.) Zahlbr. with *Rimularia insularis* (Nyl) Hertel & Rambold (Fig. 1b). Both coincidence maps revealed only a limited overlapping of the distribution areas of the host species and their lichenicolous fungi.

Twelve lichenicolous species out of the recorded 137 are known from more than ten localities in Estonia; three of these frequent species (*Athelia arachnoidea* (Berk.) Jülich, *Diploschistes muscorum* (Scop.) R. Sant., *Lichenoconium erodens* M. S. Christ. & D. Hawksw.) are *generalists* with a destructive mode of life.

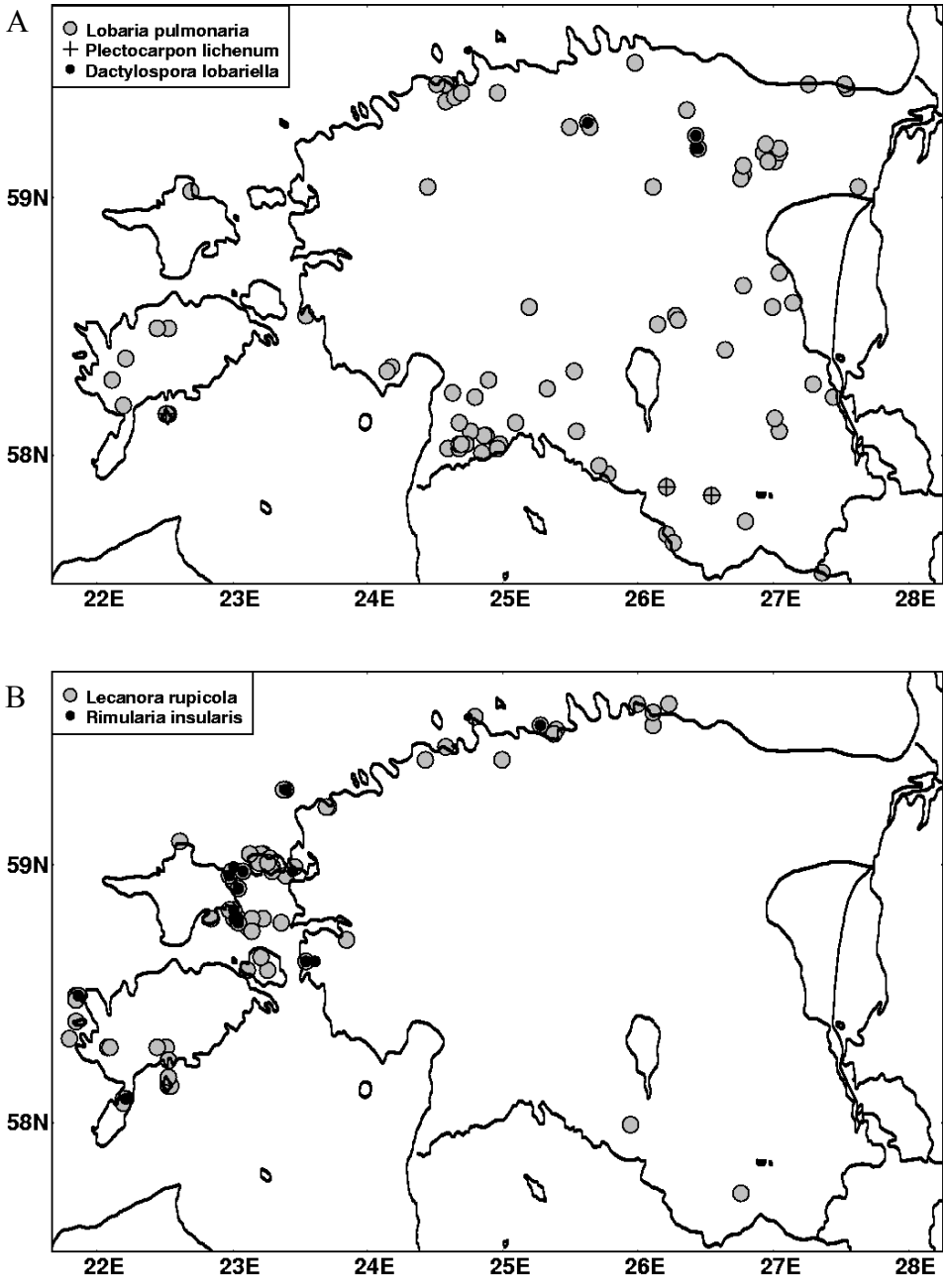

Fig 1. Distribution maps of lichens and their lichenicolous fungi: a) (above) localities of *Lobaria pulmonaria*, *Dactylospora lobariella* and *Plectocarpon lichenum;* b) (below) *Lecanora rupicola* and *Rimularia insularis*.

Rare species in the Estonian lichen flora (I, II, IV, V)

Of the 863 infrageneric taxa of lichens, lichenicolous and allied fungi recorded by Jüriado et al. (1999), more than half (64%) have been considered *rare species* in the Estonian lichen flora. Taking into account the latest number of Estonian lichens (1007 species), the proportion of rare taxa (65%) has remained almost the same. The share of *rare species* is not equal in all regions of Estonia. Species richness is the highest in the islands of the West-Estonian Archipelago. At the same time, more than half of the taxa (51%) recorded from this region are rare (IV). However, regarding the area within the archipelago, i.e. the islets in the Väinameri Sea, the share of rare species is rather low (13%) in comparison with the lichen flora of whole Estonia (V).

The distribution of rare taxa is not even considering different substrate types. The highest percentage of rare taxa has been recorded for the groups of epilithic lichens on granite (70%) and for lichenicolous fungi (90%) (IV). A similar trend was observed for the lichen flora of the islets of the Väinameri Sea (V).

Summarizing all available the data, 125 lichenicolous species (91%) out of the total 137 should be regarded as rare, while only 12 taxa are frequent (Table 4). Almost the same proportion of rare taxa (25 of the recorded 28 species; 90%) was estimated for the lichenicolous fungi occurring on the islets of the Väinameri Sea (V).

Table 4. Frequent lichenicolous species and their host spectrum. The "Records" indicates the number of known localities.

Taxon name	Records	Host spectrum
Athelia arachnoidea	>30	various epiphytic lichens (and algae)
Biatoropsis usnearum	12	*Usnea* spp.
Chaenothecopsis consociata	>10	*Chaenotheca chrysocephala*
Chaenothecopsis pusiola	>10	mainly *Chaenotheca xyloxena*
Chaenothecopsis savonica	>20	*Chaenotheca* spp., epiphytic algae
Diploschistes muscorum	15	various epigeic lichens
Lichenoconium erodens	10	various epiphytic lichens
Microcalicium disseminatum	>10	*Chaenotheca* spp.
Muellerella hospitans	11	*Bacidia fraxinea*, *B. rubella*
Rimularia insularis	20	*Lecanora rupicola*
Vouauxiella lichenicola	>20	*Lecanora argentata*, *L. chlarotera*
Vouauxiomyces ramalinae	>10	*Ramalina fraxinea*, *R. fastigiata*

Species diversity and islet traits as determinants of species richness (V)

Altogether, 326 species of lichenized, lichenicolous and allied fungi have been recorded from the 32 islets of the West-Estonian Archipelago. This makes up approximately one-third of the species number known in Estonia. The lichens on deciduous trees (114 species) and on granite (93) were dominating; the least represented groups were lichenicolous fungi (28) and ground layer lichens (35). From the regional species pool of forest lichens (Lõhmus 2003), only 11 calicioid, 11 cyanobacterial and five pendulous lichens were recorded.

A general trend in the impacts of the islet traits was observed: total number of species increased with islet area (Fig. 2) and with number of biotopes (Fig. 3), while it decreased with increasing distance from the mainland (Fig. 4). However, group specific variations were detected as well (Table 6). The positive effect of islet area was found to be important for species on coniferous trees, on dead wood and on soil (Fig. 5). Except for species on dead wood, a positive relationship with biotope diversity was observed for the rest of the groups (Fig. 6). The negative impact of distance was detected for five substrate groups out of seven (Fig. 7). Two substrate groups have only one significant environmental predictor of species richness – number of species on deciduous trees and on limestone was determined only by number of biotopes on an islet.

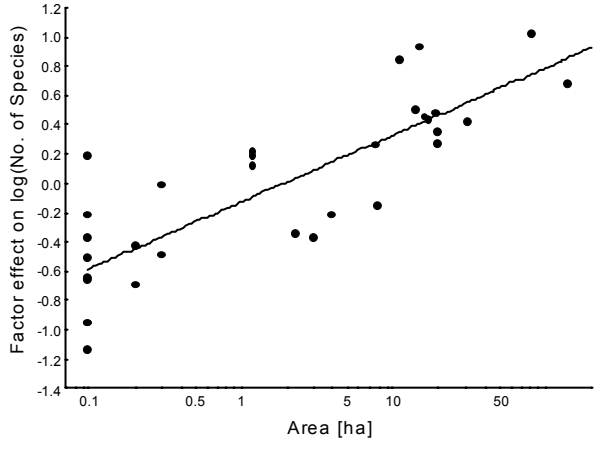

Fig. 2. The effect of islet area on log-number of species on islet, presented as a model semi-residuals of species richness conditioning on the two factors in the model (see Table 5).

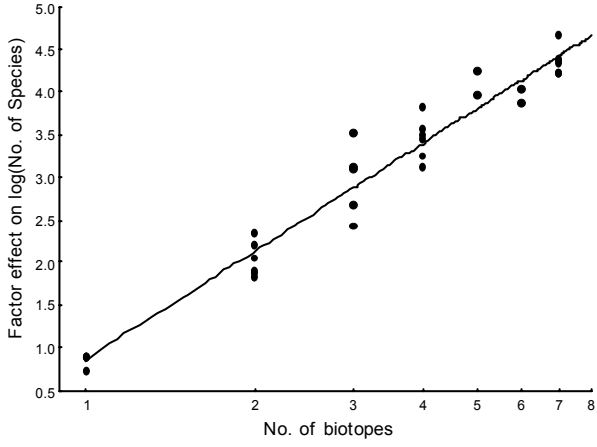

Fig. 3. The effect of number of biotopes on log-number of species on islet, presented as a model semi-residuals of species richness conditioning on the two factors in the model (see Table 5).

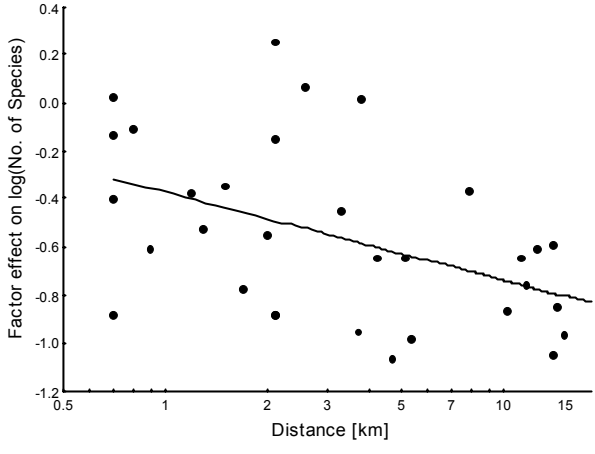

Fig. 4. The effect of distance on log-number of species on islet, presented as a model semi-residuals of species richness conditioning on the two factors in the model (see Table 5).

Table 5. Results of GLIM analysis about the effect of the islet area, number of biotopes and distance on the number of lichen species on islet. GLIM model specifications are: Poisson error distribution, log-link function and Pearson correction-coefficient for overdispersion. 'Area', 'No. of biotopes' and 'Distance' are log-transformed. Estimated slope parameter with standard error is presented.

Variable	df	Wald statistic	*p*	Slope (±SE)
Intercept	1	1.52	0.2170	0.510 (±0.413)
Area	1	18.99	0.0001	0.393 (±0.090)
No. of biotopes	1	64.20	0.0001	2.112 (±0.264)
Distance	1	15.95	0.0001	–0.671 (±0.168)

Table 6. Results of the GLIM analysis on the effect on the islet area, number of biotopes on the number of lichens species on an islet. GLIM model specifications are: Poisson error distribution, log-link function and Pearson correction-coefficient for overdispersion. 'Area', 'No. of biotopes' and 'Distance' are log-transformed.

Variable	df	Wald statistic	*p*
Intercept	1	14.19	0.0001
Area	1	40.15	0.0001
No. of biotopes	1	56.07	0.0001
Distance	1	37.74	0.0001
Substrate type	6	34.71	0.0001
Substrate type*Area	6	29.53	0.0001
Substrate type*No. of biotopes	6	26.03	0.0002
Substrate type*Distance	6	41.68	0.0001

All three biogeographic islet traits affected the occurrence and abundance of lichen species on the islets, but this effect was species dependent. Seventy-eight out of 104 common species revealed a significant relationship to one or two (in a few cases three) studied islet traits. Among the species whose presence was predicted by the islet traits, the species growing on trees, dead wood and granite dominated. The results based on the presence/absence data demonstrated that the most significant predictor was number of biotopes affecting the occurrence of 32 species.

Both islet area and number of biotopes had an strong positive effect on abundance of all analysed species. The effect of area was significant for 41 taxa and the effect of biotopes, for 31 taxa. Species abundance on an islet increased with distance from the mainland for eight species, and decreased for ten taxa.

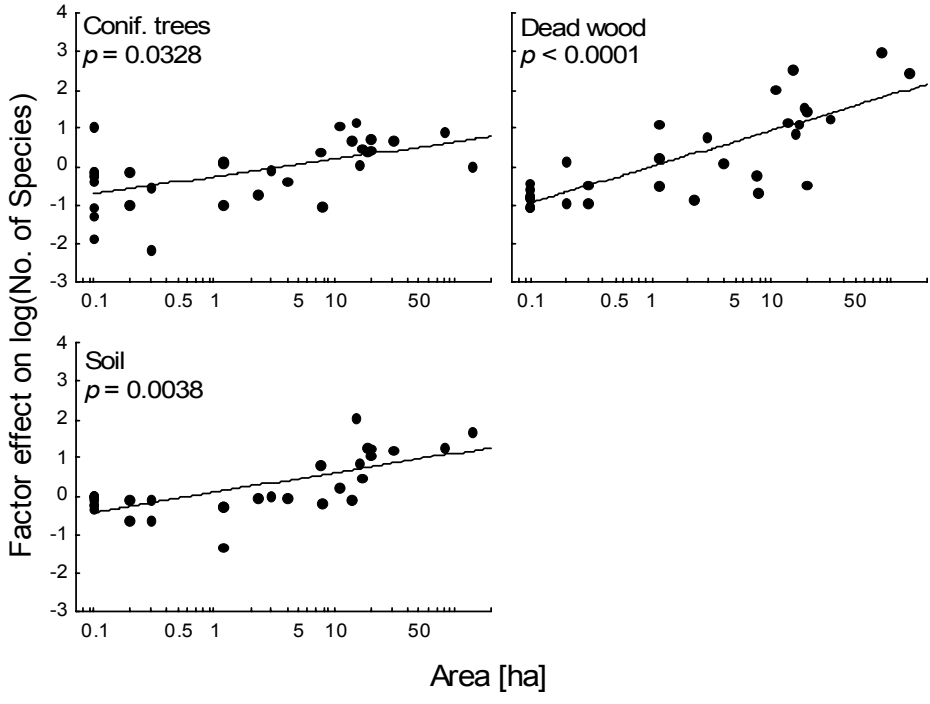

Fig. 5. The effect of islet area on log-number of species on different substrates, presented as a model semi-residuals of species richness conditioning on the two factors in the model GLIM analysis.

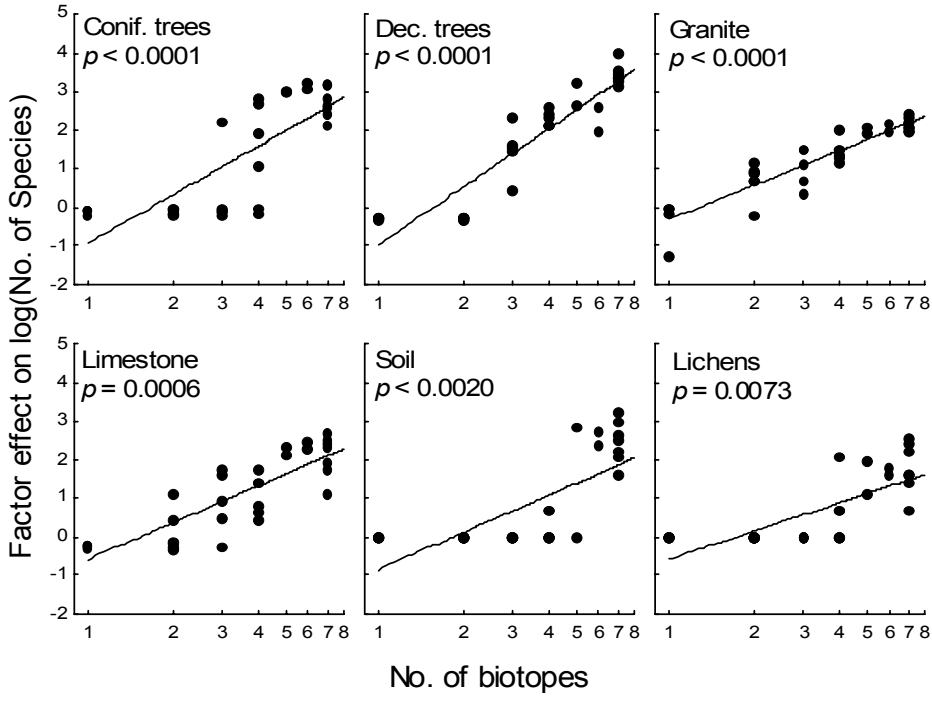

Fig. 6. The effect of islet number of biotopes on log-number of species on different substrates, presented as a model semi-residuals of species richness conditioning on the two factors in the model GLIM analysis.

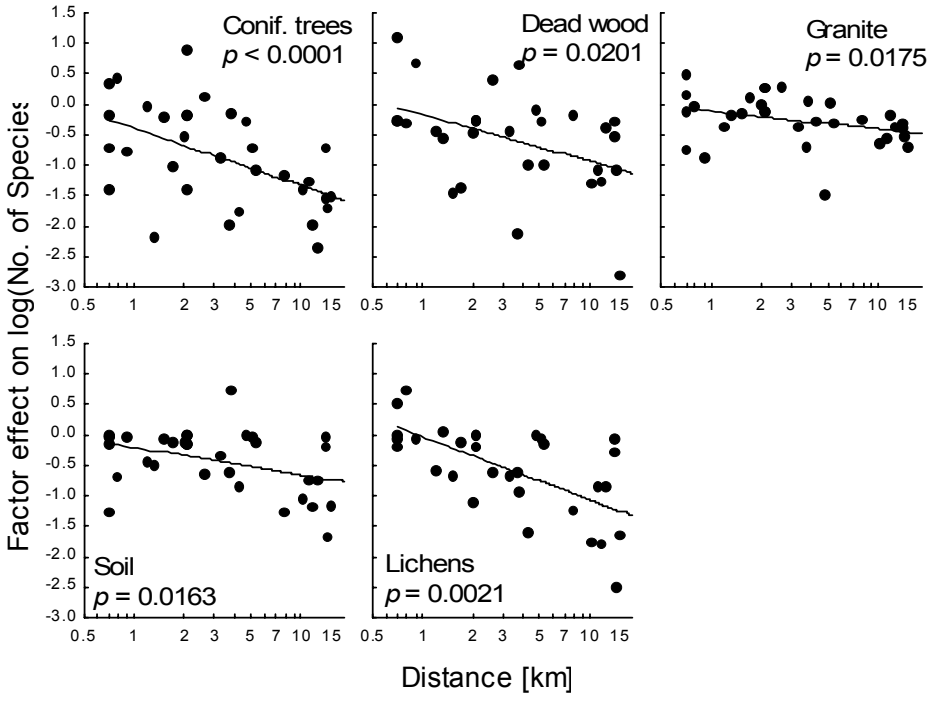

Fig. 7. The effect of distance on log-number of species on different substrates, presented as a model semi-residuals of species richness conditioning on the two factors in the model GLIM analysis.

Characters of the lichenicolous genus *Abrothallus* (VI)

The exclusively lichenicolous genus *Abrothallus* comprises species with (1) globose to almost globose immarginate ascomata, sometimes with green pruina; (2) bitunicate asci with eight brown, 2- to 4-celled, warted asymmetric ascospores; (3) ramified-anastomosed paraphyses and (4) coloured, crystalline layer above the hymenium, which dissolves in potassium hydroxide (KOH).

The results of the classificatory discriminant analysis (CDA) with the "Host species" as a grouping variable showed a classification accuracy of 79.4%; 12 of the total of 68 specimens were re-classified into the other groups (Table 7).

Five characters out of eleven appeared to be the most reliable in distinguishing between the taxa of *Abrothallus* (Table 8). The most important features (listed in descending order) were: (1) colour of the crystalline layer above the hymenium, (2) Lugol reaction, (3) pruinosity of ascomata, (4) colour of the hypothecium and (5) shape of the ascomata.

According to CDA, the mean values of the quantitative characters (size of ascomata, length and width of ascospores, ascospore length-width ratio) were

not significant for the separation of taxa. However, for some taxa, the comparison of the mean values by Student's t-test showed statistical significance ($p < 0.05$) distinction. The specimens on *Sticta* spp. differed from the others in all quantitative characters: the mean values of the dimensions of ascomata and ascospores were higher than the respective values for the rest of taxa. On the contrary, the mean values of ascospore dimensions of specimens growing on *Usnea* spp. and *Vulpicida* spp. were lower in comparison with those on other species, but there was revealed no significant distinction between specimens growing on *Vulpicida* spp. and on *Usnea* spp.

The comparison of conidia between the specimens on *Vulpicida* spp. and on *Xanthoparmelia* spp. revealed that the conidia of specimens on *Xanthoparmelia* spp. were longer and slender in contrast to those on *Vulpicida* spp. on which the conidia were shorter and thicker.

Table 7. Classification matrix. Rows: Observed classifications. Columns: Predicted classifications. The number in brackets after the group name corresponds to the number of specimens. Abbreviations: *Hyp* – specimens on *Hypogymnia*, *Mel* – on *Melanelia*, *Par* – on *Parmelia*, *Pla* – on *Platismatia*, *Sti* – on *Sticta*, *Usn* – on *Usnea*, *Vul* – on *Vulpicida* and *Xan* – on *Xanthoparmelia*.

Group	% correct	*Hyp*	*Mel*	*Par*	*Pla*	*Sti*	*Usn*	*Vul*	*Xan*
Hyp (4)	100	4	0	0	0	0	0	0	0
Mel (10)	90	0	9	1	0	0	0	0	0
Par (18)	77.8	0	2	14	2	0	0	0	0
Pla (10)	60	1	0	2	6	0	0	1	0
Sti (4)	100	0	0	0	0	4	0	0	0
Usn (6)	100	0	0	0	0	0	6	0	0
Vul (9)	66.7	0	0	1	0	0	0	6	2
Xan (7)	71.4	0	0	0	0	0	0	2	5
Total	79.4	5	11	18	8	4	6	9	7

Table 8. Summary of classificatory discriminant Analysis (CDA): importance of characters in the identification of specimens. ns – non-significant. Wilks' Lambda: 0.00419; approx. F (79.41)=5.9548; p<0.0000. Abbreviations of the characters see "Data analysis: character study of *Abrothallus*".

Character	Wilks'	F	*p*
ASCD	0.0048	0.86	ns
ASLEN	0.0052	1.43	ns
ASWI1	0.0051	1.26	ns
ASWI2	0.0051	1.28	ns
ASRA	0.0053	1.65	ns
HYMCO	0.0358	51.96	< 0.005
LUG	0.0075	5.23	< 0.005
CONID	0.0045	0.34	ns
ASCP	0.0076	5.38	< 0.005
HYPCOL	0.0069	4.29	< 0.005
ASCS	0.0072	4.81	< 0.005

DISCUSSION

Diversity of lichenicolous fungi

Many studies have attempted to explain the processes underlying the diversity and distribution of parasitic organisms (e.g. Price 1980; Boulinier et al. 2001; Guegan et al. 2005), but only a few of them deal with lichen-habiting fungi (Lawrey 2000; Glenn et al. 1997; Hedenås et al. 2002). However, it is clear as in the case of lichens, there are other factors, besides substrate availability, which determine the distribution of such fungi. For example, changes in a local climate (Parmasto 1998; Gilbert 1988), air pollution (Arvidsson 1979; Glenn et al. 1997), damages to lichen thallus (Glenn et al. 1997), presence of other parasitic fungi (Lawrey 2000) have been shown to influence spread of lichenicolous species. Patchiness of the host population is an additional factor limiting the distribution of lichenicolous fungi. *Lobaria pulmonaria* is an abundant but sparsely distributed forest lichen in Estonia (Jüriado & Liira, unpubl.), on which the the co-occurrence of lichenicolous fungi *Dactylospora lobariella* and *Plectocarpon lichenum* has been observed only in a few cases (Fig. 1a). Another lichenicolous species, *Rimularia insularis* whose host species *Lecanora rupicola* grows more or less evenly in coastal areas (Fig. 1b), the disjunct distribution has been probably caused by other dispersal limitations. Analysing the number of lichenicolous species in the context of islet traits (Fig. 6), clear association was found between biotope diversity and number of lichenicolous taxa. This effect might be explained by the higher diversity of lichens in areas with different biotopes, which indirectly increases the probability of parasite presence.

One of the basic questions regarding parasite communities is why some host groups harbour more parasitic organisms than others (Guegan et al. 2005). Lichens are not exceptions: it has been observed that *Peltigeraceae*, *Cladoniaceae* and *Pertusariaceae* have more associated fungi than other groups (Hawksworth 1982; Lawrey & Diederich 2003). This is explained by long-term co-evolution assuming that these lichen groups are primal (Hawksworth 1982; Hawksworth & Miadlikowska 1997). A considerable portion of Estonian lichenicolous species have been detected namely from among the representatives of *Peltigeraceae* and *Cladoniaceae* (Table 2). Based on studies of various organisms, it has been demonstrated that widespread hosts tend to have more parasites than those with a restricted geographical range (e.g. Gregory 1990). Considering world scale, preliminary observations of Estonian lichens, on which more than three lichenicolous species have been found, indicate a dominance of multiregional and cosmopolitan species (Table 3). The richness of the parasites has been explained also by the body size of host species, analogously to species-area relationship. This hypothesis is based on the argument that large body size ensures presence of a variety of micro-niches for associated organisms (e.g. Guegan & Hugueny 1994). This statement can

explain the multitude of parasitic species on lichens with big thalli: *Peltigera* (Hawksworth & Miadlikowska 1997), but also *Lobaria* (Etayo & Diederich 1996) and *Pseudocyphellaria* (Kondratyuk & Galloway 1995).

Another hypothesis has been proposed to elucidate the species richness of lichenicolous fungi on *Peltigera*. The species of this lichen genus grow preferably in moist and sheltered habitats (Vitikainen 1994). Such environmental conditions have been presumed to favour development of lichenicolous fungi in general (Hawksworth & Miadlikowska 1997). At least for one lichenicolous species, *Athelia arachnoidea*, the conditions of high air humidity have been demonstrated to induce its development (Gilbert 1988).

Finally, it is evident that there are more parasite species in huge families in comparison with small families (Price 1980). The lichen family *Parmeliaceae* is one of the biggest lichen families consisting of 2,319 species (Kirk et al. 2001). When one estimates the numbers of lichenicolous fungi on *Parmeliaceae,* as reported in different papers (Hawksworth 1983; Clauzade et al. 1989, etc.) as well as in this study, this regularity becomes obvious for lichenicolous fungi as well.

Determinants of species richness, diversity and rarity

Environmental traits (size of an investigated area and environmental variability) as well as the variety of organism-organism interactions (parasitism, competition) are generally regarded as the main determinants of species richness and diversity. Islands and island-like communities in particular, have been in the focus of interest already for decades because of their limited area and the isolation from the species pool affecting the formation of the biota (e.g. MacArthur & Wilson 1963, 1967; Gilbert 1980; Ås et al. 1997; Kryus & Jonsson 1997).

Lichens are essential components of natural systems, growing in almost all terrestrial habitats. Simple comparison of the species lists compiled in different countries (IV) indicated that, besides the area under investigation, the number of vegetation zones (both horizontal and vertical) are important factors determining the number of lichen species in this area. In a more specific study carried out in a fragmented landscape of the islets (V), both islet size as well as biotope diversity had a positive impact on total species number, while an additional factor, islet isolation, had an obvious negative impact. However, these impacts are not similar on the level of specific lichen groups, established according to substrate preference, as well as on the level of individual species. Besides availability of a certain substrate, local factors (habitat and climate peculiarities, disturbance rate) and species-specific factors (dispersal ability, colonization rate) are proposed to explain these phenomena. In some cases human influence has also a positive effect on the distribution of some species groups (lignicolous, ground layer lichens) through the creation of new habitats for their growth.

Rarity of species or species groups is of some importance in the context of conservation biology (e.g. Hartley & Kunin 2003; Edwards et al. 2004). It has been proposed that there are a variety of biological traits (morphology, life-history characteristics, habitat preference, etc.) which characterize rare taxa (e.g. Rabinowitz 1981; Thomson et al. 1999; Hilmo 2002). Yet simple estimation of rarity is clearly dependent on the (1) definition of rarity and (2) size of the geographic range (Dietrich & Scheidegger 1997; Hartley & Kunin 2003). In some cases rarity reflects only the insufficient knowledge of the species group under investigation. In fact, larger organisms with a broader geographic range are usually better studied than smaller organisms with a narrow geographic range (Poulin 1997). Parasitic organisms form a special case as they are already by their nature rarer than their hosts (Nuismer et al. 2003).

The estimated proportion of rare taxa (incl. lichenicolous fungi) in the Estonian lichen flora is relatively high. For this three main reasons have been pointed out in paper IV. Firstly, many of the rare lichens belong to the floristic elements (arctic-alpine, xerocontinental, submediterranean) which are atypical for this region. It has been suggested that most of these lichens are relicts from the post-glacial period, which have persisted in a few refugia (Trass 1970). Secondly, several species occur in their southern or northern limits of their geographical range because of the special position of the country in the transitional area of the hemiboreal zone (Ahti et al. 1968; Randlane & Saag 2000). And, thirdly, in some ecological groups (epilithic lichens, lichenicolous fungi), the high percentage of rare taxa simply reflects the poor knowledge of their actual distribution in the territory, caused by insufficient sampling. It is notable that the first two mentioned trends have been observed also for rare vascular plants in Estonia (Kull et al. 2002).

The proportion of rare species is not equal in all regions of Estonia. The relatively low share of rare taxa compared to the whole lichen flora has been noted for the fragmented area of the Väinameri islets (V). Environmental conditions on the islets are rather harsh mainly due to the direct influence of the sea (salinity, action of waves, ice and wind). Therefore, the islets are first of all colonized by marine species, common in coastal areas, and by habitat generalists (Suija & Jüriado 2002). The low share of rare taxa is partly explained by lack or patchiness of habitats essential for species with highly specific requirements. For example, natural forests with a long ecological continuity have persisted only as fragments on larger islets (Rebassoo 1972).

Characters of the genus *Abrothallus* and implications for taxonomy

The exclusively lichenicolous genus *Abrothallus* is a rather well known and widespread genus which shows almost no phylogenetic affinities to the other taxonomic entities (Kirk et al. 2001). Despite the clear distinction of the genus, subgeneric division has remained controversial because different authors

attribute significance to different characters (Kotte 1909; Keissler 1930; Clauzade et al. 1989). For example, Kotte (1909) emphasized the importance of iodine reaction of the hyphae, the dimensions of the ascospores and conidia as well as preference to a certain host as diagnostic features. In contrast, Keissler (1930) denied the relevance of iodine reaction and host preference, and used, instead, characters like presence of greenish pruina on the ascomata, colour of the epithecium and reaction of the hymenium with KOH.

According to the contemporary point of view, the host specificity of lichenicolous species is exceptionally high in comparison with other organisms (Lawrey & Diederich 2003), and the genus *Abrothallus* does not to be an exception. This analysis based on 68 samples from eight host genera showed a clear tendency towards specialization of *Abrothallus* species. However, the general trend was not so obvious for specimens occurring on *Parmelia* spp. and *Platismatia* spp.

Two of the characters, presence of the green pruina and amyloid reaction of hyphae, which are considered in most studies (Kotte 1909; Keissler 1930; Hawksworth 1983; Clauzade et al. 1989), showed more variation than expected prior to analysis. The presence of greenish pruina has been mainly observed on younger ascomata and, hence, even if a character itself is advantageous, one has to be careful when using it. Considering the studied material, the presence or absence of the amyloid reaction of the vegetative hyphae seems to be an applicable feature for species delimitation, with one exception. The specimens occurring on *Parmelia* spp. included ones with positive and negative reaction to a more or less equal degree, which may indicate that probably more than one *Abrothallus* species can grow on the host genus *Parmelia.*

The data of the dimensions of the diaspores (ascospores and conidia) vary in the literature because of the different concepts of species used (Kotte 1909; Keissler 1930; Hawksworth 1983) or because of over generalized data (Clauzade et al. 1989). This makes the comparison of ascospores dimensions with literature data difficult or even impossible. Although according to the CDA, the mean values of ascospores and ascomata were insignificant for grouping of specimens, comparison of the mean values still revealed some significant trends.

It has been presumed, basing on the evidence of frequent co-occurrence of the *Vouauxiomyces*-type conidiomata and *Abrothallus* ascomata, that the anamorph genus *Vouauxiomyces* represents an asexual stage of *Abrothallus* (e.g. Tulasne 1852; Kotte 1909; Hawksworth 1981; Wedin 1994). In some cases, as revealed in the analysis of the specimens on *Vulpicida* spp. and *Xanthoparmelia* spp., the dimensions of conidia appear to be better delimiters than the characters derived from the sexual stage of the genus.

CONCLUSIONS

(1) Up to now 137 lichen-habiting (lichenicolous) species have been recorded in Estonia, of these species occurring on *Cladoniaceae, Lecanoraceae, Parmeliaceae* and *Peltigeraceae* dominate. Most of the species found are ascomycetes (66%), while conidial fungi (26%) and basidiomycetes (10%) are less represented.

(2) A new species, *Buelliella lecanorae* Suija & Alstrup, was described on the basis of material collected in Estonia. The species grows on epiphytic species of the lichen genus *Lecanora*.

(3) More than half of the recorded species of lichenized and lichenicolous fungi are categorized as rare in Estonia. The high share of rare species is caused by the geographic location and historical background of the country as well as by the insufficient knowledge of certain species groups (eplithic lichens, lichenicolous fungi).

(4) Isolation of host lichen populations has been proposed to be among the reasons which hampers the distribution of lichenicolous fungi, besides the substrate availability.

(5) The area, number of biotopes and distance from the mainland have evident impacts on lichen species richness in the fragmented landscape of the islets. The total number of species increased with the increasing area and biotope diversity and decreased with islet isolation. On the level of individual species and certain species groups, these responds of area and number of biotopes were not uniform but a species-specific and group-specific trends have been observed. For lichenicolous fungi, the impact of biotope diversity was the most obvious.

(6) The host-specificity of the genus consisting exclusively of lichenicolous fungi, *Abrothallus,* was ascertained. However, such specificity is not universal nor applicable to all "species". Qualitative characters (colour of the layer above the hymenium, pruinosity of ascomata, Lugol reaction, etc.) delimited the taxa of *Abrothallus* better compared with quantitative characters, even when the variation of some of them (e.g. pruinosity) was higher than expected prior to the study. In some cases, the morphological characters of anamorph defined taxa of *Abrothallus* better than the characters of teleomorph.

KOKKUVÕTE

Omapäraseks, heterotroofse seene (mükobiont) ja autotroofse rohevetika või tsüanobakteri (fotobiont) kooseluvormiks on samblikud. Samblikud võivad asustada väga erinevaid kasvupindu olles samal ajal ka ise kasvupindadeks mitmetele teistele organismidele, sealhulgas samblikele kohastunud ehk lihhenikoolsetele seentele.

Käesoleval tööl oli kolm eesmärki. Esiteks, anda ülevaade samblikel kasvavate seente mitmekesisusest ja levikust Eestis; teiseks, analüüsida haruldaste samblike ja neile lähedaste seente liikide suure osakaalu põhjuseid Eesti lihhenoflooras ning kirjeldada samblike üldist liigirikkust määravaid tegureid Lääne-Eesti saartestiku (Hiiumaa ümbruse) laidudel, ning kolmandaks hinnata liigispetsiifilisi diagnostilisi tunnuseid lihhenikoolsete seente perekonnas *Abrothallus*.

Eestist on tänaseks teada 870 sambliku ja 137 samblikel kasvava seene liiki. Lihhenikoolsete seente hulgas domineerivad kottseened (66%), vähem on leitud teis- ja kandseente rühmadesse (vastavalt 26% ja 10%) kuuluvaid taksoneid. Valdav enamik lihhenikoolseid seeni on määratud sugukondadesse *Cladoniaceae*, *Lecanoraceae*, *Parmeliaceae* ja *Peltigeraceae* kuuluvatelt samblikelt. Kirjeldati ka uus lihhenikoolse seene liik, *Buelliella lecanorae* Suija & Alstrup, mis kasvab epifüütsetel liudsamblikel (*Lecanora*).

Hoolimata taksonite suurest arvust Eestis, on üle poole neist (65%) haruldased s.t. teada kuni kümnest leiukohast. Näidati, et haruldaste liikide suur hulk on ühelt poolt tingitud Eesti geograafilisest asendist ja arenguloost, mistõttu mitmed liigid on oma leviku lõuna- või põhjapiiril või kuuluvad antud piirkonnale ebatüüpilistesse floristilistesse elementidesse (arktoalpiinne, kserokontinentaalne, submediteraanne). Teine põhjus on mõnede samblike rühmade (näiteks epiliitsed liigid) vähene uuritus.

Uurimuse andmetel on ka enamus lihhenikoolsetest taksonitest haruldased kuigi nende peremeesliigid on laiema levikuga. Hariliku kopsusambliku (*Lobaria pulmonaria*) ning temale spetsialiseerunud seente (*Dactylospora lobariella*, *Plectocarpon lichenum*) näitel võib üheks levikut piiravaks teguriks olla peremees-liigi populatsioonide hajutatus territooriumil.

Analüüsides samblike (ja neil kasvavate seente) liigirikkust Hiiumaa ümbruse laidudel arvestades laiu pindala, biotoopide arvu ja kaugust lähimast punktist maismaal, ilmnesid mõned üldistatavad seaduspärad. Liikide arv laiul tõusis nii pindala kui ka biotoopide arvu suurenedes ning vähenes kaugusega maismaast. Siiski eri substraatidel kasvavatel samblikel ei ole seosed laiu suuruse ja biotoopide arvu ning liigirikkuse vahel ühesugused. Samblike esinemist laidudel määravad nii substraadi olemasolu, kui ka välised mõjutegurid (elukeskkonna häiritus, inimmõju) ja samblike individuaalsed omadused (levimisvõime, ellujäämus).

Ainult lihhenikoolseid liike hõlmava perekonna *Abrothallus* liikide piiritlemine on jäänud vaieldavaks, kuna autorid käsitlevad liike erinevas mahus kasutades erinevaid diagnostilisi tunnuseid. Käesolevas töös lähtuti tunnuste

analüüsimisel eeldusest, et nimetatud perekonna liigid on kohastunud kasvama kindlatel peremees samblikel. Ilmnes, et selline trend on olemas, kuid pole üldistatav kõigidele “taksonitele”. Hümeeniumi ülakihi värvus, rohelise härmakihi olemasolu, vegetatiivsete hüüfide reaktsioon Lugoli lahusega leiti olevat parimad taksoneid iseloomustavad tunnused. Näidati, et mõnedel juhtudel eristavad anamorfi tunnused taksoneid paremini kui teleomorfi tunnused.

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REFERENCES

Ahti, T., Hämet-Ahti, L. & Jalas, J. 1968: Vegetation zones and their sections in northwestern Europe. *Ann. Bot. Fenn.* 5: 169–211.

Aptroot, A., Czarnota, P., Jüriado, I., Kocourková, J., Kukwa, M., Lõhmus, P., Palice, Z., Randlane, T., Saag, L., Sérusiaux, E., Sipman, H., Sparrius, L. B., Suija, A. & Thüs, H. 2005: New or interesting lichens and lichenicolous fungi found during the 5th IAL Symposium in Estonia. *Folia Cryptog. Estonica* 41: 13–22.

Arvidsson, L. 1979: Svampangrepp pa lavar – en orsak till lavoken. Fungus attacks on lichens and lichen deserts in cities. *Svensk Bot. Tidskr.* 72: 285–292.

Ås, S., Bengtsson, J. & Eberhard, T. 1997: Archipelagos and the theories of insularity. *Ecol. Bull.* 46: 88–116.

Boulinier, T., McCoy, K. D. & Sorci, G. 2001: Dispersal and parasitism. *In: Clobert, J., Danchin, E., Dhondt, A. & Nichols, J. D. (eds.). Dispersal*, pp. 169–179. Oxford University Press, Oxford, UK.

Bruttan, A. 1870: Lichenen Est-, Liv- und Kurlands. *Arch. Naturk. Liv.- Est.- und Kurlands* ser. II, 7: 163–326.

Clauzade, G., Diederich, P. & Roux, C. 1989: Nelikenigintaj fungoj likenlogaj. Ilustrita determinlibro. *Bull. Soc. Linn. Provence, Numero Special* 1: 1–142.

Dietrich, M. & Scheidegger, C. 1997: Frequency, diversity and ecological strategies of epiphytic lichens in the Swiss Central Plateau and the Pre-Alps. *Lichenologist* 29(3): 237–258.

Edwards, T. C. Jr, Cutler, D. R., Geiser, L., Alegria, J. & McKenzie, D. 2004: Assessing rarity of species with low detectability: lichens in Pacific Northwest forests. *Ecol. Appl.* 14(2): 414–424.

Etayo, J. & Diederich, P. 1996: Lichenicolous fungi from the western Pyrenees, France and Spain. III. Species on *Lobaria pulmonaria*. *Bull. Soc. Naturalistes Luxemb.* 97: 93–118.

Gams, W., Diederich, P. & Põldmaa, K. 2004: Fungicolous fungi. *In: Mueller, G. M., Bills, G. F. & Foster, M. S. (eds.) Biodiversity of fungi. Inventory and Monitoring Methods,* pp. 343–392. Elsevier Academic Press.

Gilbert, F. M. 1980: The equilibrium theory of island biogeography: fact or fiction? *J. Biogeogr.* 7: 209–235.

Gilbert, G. S. 2002: Evolutionary ecology of plant diseases in natural ecosystems. *Annu. Rev. Phytopat.* 40: 13–43.

Gilbert, O. L. 1988: Studies on the destruction of *Lecanora conizaeoides* by the lichenicolous fungus *Athelia arachnoidea*. *Lichenologist* 20(2): 183–190.

Glenn, M. G., Gomez-Bolea, A. & Orsi, E. V. 1997: Effects of thallus damage on interactions of lichens with non-lichenized fungi under natural and laboratory conditions. *Lichenologist* 29(1): 51–65.

Gregory, R. D. 1990: Parasites and host geographic range as illustrated by waterfowl. *Funct. Ecol.* 4: 645–654.

Guegan, J.-F. & Hugueny, B. 1994: A nested parasite species subset pattern in tropical fish: Host as major determinant of parasite infracommunity structure. *Oecologia* 100(1–2): 184–189.

Guegan, J.-F., Morand, S. & Poulin, R. 2005: Are there general laws in parasite community ecology? The emergence of spatial parasitology and epidemiology. *In: Thomas, F., Renaud, F. & Guegan, J.-F. (eds). Parasitism and Ecosystems*. Oxford University Press, UK.

Hartley, S. & Kunin, W. E. 2003: Scale dependency of rarity, extinction risk, and conservation priority. *Conserv. Biol.* 17(6): 1559–1570.
Hawksworth, D. L. 1979: The lichenicolous Hyphomycetes. *Bull. Br. Mus. (Nat. Hist.), Bot.* 6: 183–300.
Hawksworth, D. L. 1981: The lichenicolous Coelomycetes. *Bull. Br. Mus. (Nat. Hist.), Bot.* 9: 1–98.
Hawksworth, D. L. 1982: Co-evolution and detection of ancestry in lichens. *J. Hattori Bot. Lab.* 52: 323–329.
Hawksworth, D. L. 1983: A key to the lichen-forming, parasitic, parasymbiotic and saprophytic fungi occurring on lichens in the British Isles. *Lichenologist* 15: 1–44.
Hawksworth, D. L. 1988: The variety of fungal-algal symbioses, their evolutionary significance, and the nature of lichens. *Bot. J. Linn. Soc.* 96(1): 3–20.
Hawksworth, D. L. 2003: The lichenicolous fungi of Great Britain and Ireland: an overview and annotated checklist. *Lichenologist* 35(3): 191–232.
Hawksworth, D. L. & Miadlikowska, J. 1997: New species of lichenicolous fungi occurring on *Peltigera* in Ecuador and Europe. *Mycol. Res.* 101: 1127–1134.
Hedenås, H., Lundin, K. & Ericson, L. 2002: The role of lichen parasites in conservation biology. *In: Hedenås, H. Epiphytic lichens on Populus tremula: Implications for Conservation.* Ph.D. dissertation, Umeå University.
Hilmo, O. 2002: Growth and morphological response of old-forest lichens transplanted into a young and an old *Picea abies* forest. *Ecography* 25(3): 329–335.
Jüriado, I. & Liira, J. Distribution, habitat ecology and conservation of lichen *Lobaria pulmonaria* in Estonia. Manuscript.
Jüriado, I., Lõhmus, P., Martin, J., Martin, L., Nilson, E., Piin, T., Randlane, T., Saag, A., Saag, L., Sarv, M., Suija, A., Temina, M. & Trass, H. 1999: Second checklist of lichenized, lichenicolous and allied fungi of Estonia. *Folia Cryptog. Estonica* 35: 1–132.
Jüriado, I., Lõhmus, P., Nilson, E., Randlane, T., Saag, A., Saag, L. & Suija, A. 2004: *Eesti Pisisamblikud* [*Estonian Microlichens*]. Tartu University Press. 583 pp.
Jüriado, I., Paal, J. & Liira, J. 2003: Epiphytic and epixylic lichen species diversity in Estonian natural forests. *Biodiver. Conservation* 12: 1587–1607.
Keissler, K. von 1930: *Die Flechtenparasiten Deutschlands, Österreichs und der Schweiz mit Berücksichtigung der übrigen Länder Europas sowie der angrenzenden Meeresgebiete*. 240 s.
Kirk, P. M., Cannon, P. F., David, J. C. & Stalpers, J. A. (eds.) 2001: *Ainsworth and Bisby's Dictionary of the Fungi.* 9th Edition. CABI Publishing. 650 pp.
Kondratyuk, S. Y. & Galloway, D. J. 1995: Lichenicolous fungi and chemical patterns in *Pseudocyphellaria*. *In: Knoph, J.-G., Schrüfer, K. & Sipman, H. J. M. (eds.): Studies in Lichenology with Emphasis on Chemotaxonomy, Geography and Phytochemistry. Festschrift Christian Leuckert. Biblioth. Lichenol.* 57: 327–345.
Kotte, I. 1909: Einige neue Fälle von Nebensymbiose (Parasymbiose). *Zentralbl. Bakteriol., Parasitenkd.* II 24: 74–93.
Kruys, N. & Jonsson, B. G. 1997: Insular patterns of calicioid lichens in a boreal old-growth forest-wetland mosaic. *Ecography* 20: 605–613.
Kull, T., Kukk, T., Leht, M., Krall, H., Kukk, Ü., Kull, K. & Kuusk, V. 2002: Distribution trends of rare vascular plant species. *Biodiver. Conservation* 11: 171–196.
Lawrey, J. D. 2000: Chemical interactions between two lichen degrading fungi. *J. Chem. Ecol.* 26(8): 1821–1831.
Lawrey, J. D. & Diederich, P. 2003: Lichenicolous fungi: interactions, evolution, and biodiversity. *Bryologist* 106(1): 81–120.

Lindsay, W. L. 1869: Enumeration of microlichens parasitic on other lichens. *Quarterly J. Microscop. Sci.* 9: 49–57, 135–147, 342–358.
Littell, R. C., Milliken, G. A., Stroup, W. W. & Wolfinger, R. D. 1996: SAS® system for mixed models. SAS Institute Inc., Cary, NC, US.
Lõhmus, P. 2003: Composition and substrata of forest lichens in Estonia: a meta-analysis. *Folia Cryptog. Estonica* 40: 19–38.
Lõhmus, P. & Lõhmus, A. 2001: Snags, and their lichen flora in old Estonian peatland forests. *Ann. Bot. Fenn.* 38: 265–280.
Lutzoni, F., Pagel, M. & Reeb, V. 2001: Major fungal lineages are derived from lichen symbiotic ancestors. *Nature* 411: 937–940.
Lücking, R. & Bernecker-Lücking, A. 2000: Lichen feeders and lichenicolous fungi: do they affect dispersal and diversity in tropical foliicolous lichen communities? *Ecotropica* 6: 23–41.
MacArthur, R. H. & Wilson, E. O. 1963: An equilibrium theory of island biogeography. *Evolution* 17: 373–387.
MacArthur, R. H. & Wilson, E. O. 1967: The theory of island biogeography. *Monographs in Population Biology 1*. Princeton University Press, Princeton, New Jersey, US. 203 pp.
Morton, A. 1999: DMAP for Windows ver. 7.0.
Nilson, E. & Piin, T. 1998: Lichens of the islets of Kolga Bay (Gulf of Finland, Estonia). Distribution and frequency of epiphytic lichen species. *Folia Cryptog. Estonica* 32: 57–62.
Nimis, P. L. 1993: *The Lichens of Italy*. Museo Regionale di Scienze Naturali, Torino. 897 pp.
Nuismer, S. L., Thompson, J. N. & Gomulkiewicz, R. 2003: Coevolution between hosts and parasites with partially overlapping geographic ranges. *J. Evol. Biol.* 16: 1337–1345.
Parmasto, E. 1998: *Athelia arachnoidea*, a lichenicolous basidiomycete in Estonia. *Folia Cryptog. Estonica* 32: 63–66.
Poulin, R. 1997: Species richness of parasite assemblages: evolution and patterns. *Annu. Rev. Ecol. Syst.* 28: 341–358.
Price, P. W. 1980: Evolutionary biology of Parasites. *Monographs in Population Biology 15*. Princeton University Press, Princeton, New Jersey. 237 pp.
Rabinowitz, D. 1981: Seven forms of rarity. *In: Synge, H. (ed). The biological aspects of rare plant conservation,* pp. 205–217. John Wiley and Sons, NY, US.
Randlane, T. 1986: Analysis of the lichen flora on Estonian western islands (in Russian). Ph. D. thesis, University of Tartu, Estonia.
Randlane, T. & Saag, A. 2000: Biogeographical survey of Estonian lichen flora, with reference to conservation strategies. *Forest, Snow and Landscape Research* 75(3): 381–390.
Randlane, T., Saag, A. & Suija, A. 2005: Lichenized, lichenicolous and allied fungi of Estonia. [http://www.ut.ee/lichens/fce.html] Last update: March 8, 2005.
Rebassoo, H.-E. 1972: *Laidude raamat* [*The Islets Book*]. Valgus, Tallinn. 107 pp.
SAS Institute Inc. 1989. SAS/STAT® user's guide. Version 6. 4th Edition, vol. 2. SAS Institute Inc., Cary, NC.
Suija, A. & Jüriado, I. 2002: Lichens and lichenicolous fungi of the Hiiumaa Islets Landscape Reserve (Estonia). *Folia Cryptog. Estonica* 39: 37–50.
Suija, A., Nõmm, M. & Boch, S. 2005: New Estonian records: lichens and lichenicolous fungi. *Folia Cryptog. Estonica* 41: 135–136.

Thomson, K., Gaston, K. J. & Band, S. R. 1999: Range size, dispersal and niche breath in the herbaceous flora of central England. *J. Ecol.* 87(1): 150–155.
Trass, H. 1970: The elements and development of the lichen-flora of Estonia (in Russian). *Papers on Bot., Trans. Tartu State Univ.* 9: 5–233.
Trass, H. & Randlane, T. 1994: *Eesti Suursamblikud* [*Estonian Macrolichens*]. Tartu University Press. 399 pp.
Tulasne, L.-R. 1852: Mémoire pour servir à l'histoire organographique et physiologique des lichens. *Ann. Sci. Nat.* 17: 5–128.
Vitikainen, O. 1994: Taxonomic revision of *Peltigera* (lichenized Ascomycotina) in Europe. *Acta Bot. Fenn*. 152: 1–96.
Wedin, M. 1994: New and noteworthy lichenicolous fungi from southernmost South America. *Lichenologist* 26(3): 301–310.

PUBLICATIONS

Suija, A. 2005a: Lichenicolous fungi and lichens in Estonia I. Ascomycota. *Nova Hedwigia* 80(1–2): 247–267.

Suija, A. 2005b: Lichenicolous fungi in Estonia II. Basidiomycota and conidial fungi. *Nova Hedwigia* 80(3): 349–366.

Suija, A. & Alstrup, V. 2004: *Buelliella lecanorae*, a new lichenicolous fungus. *Lichenologist* 36(3–4): 203–206.

Randlane, T., Saag, A. & Suija, A. 2002: Biodiversity of lichenized taxa in Estonia: distribution of rare species. *Biblioth. Lichenol.* 82: 99–109.

Jüriado, I., Suija, A. & Liira, J. Biogeographical determinants of lichen species diversity on islets in West-Estonian Archipelago. Manuscript submitted to *J. Veg. Sci*.

Suija, A. Character study of some two-celled species of the lichenicolous genus *Abrothallus.* Manuscript submitted to *Ann. Bot. Fenn*.

BIOGEOGRAPHICAL DETERMINANTS OF LICHEN SPECIES DIVERSITY ON ISLETS IN THE WEST-ESTONIAN ARCHIPELAGO, ESTONIA

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ABSTRACT

Questions: Does lichen species richness follow the general principles stated by the theory of island biogeography? Are there any species- or ecological group-specific trends associated with islet area, number of biotopes and distance from mainland?

Locations: Islets of West-Estonian Archipelago, Estonia.

Methods: The species list was compiled for each islet and substrate type, and the relative abundance of each lichen species was estimated. A generalized linear model (GLIM) analysis was applied to test the effect of islet traits on the number of lichen species on islets and in substrate types. The occurrence predictability and abundance of each species on an islet according to islet parameters was tested with GLIM and general linear mixed analysis (MIXED-model).

Results: The lichen flora of 32 islets consisted of 326 taxa. The number of species was positively correlated with the islet area and with the number of biotopes, and negatively correlated with distance from the mainland. The substrate-type-specific variations were observed. The effect of islet area was evident in only a few selected substrate types, while the effect of biotope diversity and distance from the mainland was significant for species richness in most substrate types. The islet traits predicted species occurrence and abundance according to the pattern of species richness in substrate types.

Conclusion: The lichen species and ecological groups on the studied islets do not correspond consistently to the islet area, biotope diversity and isolation, even if the general trends of species richness are obvious.

Keywords: Area; Biotope diversity; Dispersal strategy; Distance; Growth form; Island biogeography; Rare species; Species richness; Substrate type.

Nomenclature: Randlane & Saag (1999, 2004); Santesson et al. (2004).

INTRODUCTION

Biogeography and biodiversity of islands has received considerable attention because of the unique combination of climatic, geographic and topographic factors affecting island biota. A traditional approach to the studies of biodiversity on islands emphasises the role of island area and isolation on species richness – the number of species in an area tends to increase with its size and decrease with distance from the mainland. A lot of discussions have concentrated on possible reasons for such a pattern (e.g. MacArthur & Wilson 1963, 1967; Simberloff 1974; Gilbert 1980; McGuiness 1984; Ås et al. 1997). Two main mechanisms have been proposed to explain the island area phenomenon: direct effect, through the increase of area by itself (e.g. Preston 1960; MacArthur & Wilson 1967; Whitehead & Jones 1969; Connor & McCoy 1979; Lomolino & Weiser 2001), and indirect area effect, through the increase of diversity of habitats on larger islands – the habitat diversity hypothesis (e.g. Williams 1943; Kelly et al. 1989). However, the debate on the area *per se* vs. the habitat diversity effect has been ongoing for decades, because these two effects are difficult to distinguish. This is due to the fact that they are not mutually exclusive, but mutually additive (see for discussion Kohn & Walsh 1994; Rosenzweig 1995; Triantis et al. 2003). A smaller species number on (equal-sized) islands at a greater distance (isolation) from the mainland (e.g. MacArthur & Wilson 1967; Williams 1982) is mostly explained by the dispersal limitation of species (e.g. Diamond et al. 1976; Gilpin & Diamond 1976; Moody 2000). Additionally to the general patterns described, the importance of the influence of area, habitat diversity, and distance is largely dependent on the group of studied organisms (e.g. Nilsson et al. 1988; Ricklefs & Lovette 1999).

Most island biogeography studies have focussed on the species richness of vertebrates (e.g. Haila 1983; Heaney 1984; Nilsson 1986), vascular plants (e.g. Nilsson & Nilsson 1982; Deshaye & Morisset 1988; Rydin & Borgegård 1988; Kohn & Walsh 1994) and arthropods (e.g. Niemelä 1988; Kotze et al. 2000). Only a few papers deal with the island biogeography of cryptogams: bryophytes (Tangney et al. 1990), and lichenized fungi (Hayward & Hayward 1986; Seaward & Aptroot 2000). More often cryptogamic studies focus on island-type fragmented communities such as isolated forest patches (e.g. Kruys & Jonsson 1997; Berglund & Jonsson 2001; Mills & McDonald 2004) or rock surfaces in a landscape (e.g. Slatter 1990; Lawrey 1991b, 1992; Kimmerer & Driscoll 2000).

Lichenized fungi (lichens) are organisms that are able to colonize a wide range of substrata even in rather harsh environmental conditions unsuitable for most other organisms. Lichens are one of the first organisms capable of establishing in open habitat in the early stages of succession and also of surviving in late successional communities (Lawrey 1991a). Most lichens grow slowly, disperse passively, and are adapted to certain substrate types (tree bark, rock, soil, dead wood) (e.g. Armstrong 1988; Lawrey 1984, 1991a; Nash 1996). Lichens on islands and on the seashore tolerate salinity, a repeating drying and wetting cycle, and high light intensity (Lawrey 1984). Such a unique

combination of properties makes lichenized fungi an interesting group for island biogeographical studies.

Lichen flora on the Baltic Sea islands along the western and northern coast of Estonia is relatively well studied (e.g. Randlane 1986; Nilson & Piin 1998; Martin et al. 2000; Suija & Jüriado 2002). Nevertheless, the proportional importance of factors affecting the distribution pattern of lichens on islets still needs to be quantified. The aim of this paper is to clarify and quantify the limiting factors behind the species richness of lichens on islets. We hypothesize that islet area, biotope diversity, and islet isolation have a general impact on species number, but that this should be ecological-group-specific, because there are species-specific effects on the arrival and establishment of lichen species.

STUDY AREA

Estonia is a small country in Northern Europe with an area of 45 227 km^2 (the land area is 43 211 km^2). About 10% (4133 km^2) of the territory consists of the islands in the Baltic Sea (Raukas 1995). The majority of islands belong to the West-Estonian Archipelago, with the biggest islands being Saaremaa (2671 km²), Hiiumaa (989 km²), Muhu (198 km²) and Vormsi (93 km²). More than 1000 islands and islets lie near those large islands (Loopmann 1996). The islets are relatively young; their rise from the sea started about 2000 years ago, during the Limnea stage of the Baltic Sea (Kessel 1961). The islets' formation and disappearance, amalgamation with each other or merging with the mainland continues nowadays due to the constant and relatively rapid (2–3 mm per year) uplift of the earth (Sepp 1970; Raukas 1995).

The investigated islets (32 islets with pooled land area 4.15 km²) are located in southeastern and eastern direction from the island Hiiumaa and around the island of Vormsi in the Väinameri sea (Fig. 1; Table 1). Most of the islets consist of moraine, which was formed as a result of the action of the last glaciations. The main landforms on islets are beach barriers that surround plains rising slowly towards the centre (maximum 9 m a.s.l.) (Sepp 1974). The dominating coastal types of the studied islets belong either to the moraine, shingle or turf type. The abundance of erratic blocks (granite), scattered on the islets or forming capes, is also characteristic to these islets (Leito & Leito 1991).

Estonia belongs to the temperate zone, which is characterized by warm summers and moderately mild winters (Jõgi & Tarand 1995). The climate of the archipelago is milder than on the Estonian mainland because of the impact of the sea. On islands, the mean yearly air temperature is 6.1ºC and the calculated mean relative humidity is 81.5%. Winds from the south and southwestern directions are prevailing (Estonian Meteorological and Hydrological Institute, unpubl.). The action of ice and waves is especially obvious for the smallest periodically inundated islets (area up to 0.1 ha), also for some medium-sized distant islets (e.g. Langekare, Anerahu). The small islets closer to the mainland

(e.g. Auklaid) are more sheltered by the other islets or large islands and therefore less influenced by the action of the sea.

In general, the vegetation on the studied islets is mostly early successional. The vegetation of the smallest islets is especially poor and consists of only a few coastal plants. The vegetation of the intermediate-sized islets consists of coastal meadows, shrub-lands and sometimes of few solitary deciduous trees. Large islets have more complex vegetation including, for instance, suprasaline grasslands, wooded meadows and different forest types. Granite and limestone rocks are found in all habitats, from the seashore to the closed forest.

Direct anthropogenic impact is evident only on some large or intermediate-sized islets due to permanent inhabitancy until the beginning of the 1970's (Saarnaki, Hanikatsi) and the activity of the border guard until the 1990's (Harilaid). Nowadays, hay mowing and sheep grazing are organized by the administration of the Hiiumaa Islets Landscape Reserve to preserve semi-natural meadow communities.

METHODS

Sampling

The lichen floristic work was conducted in the years from 2001 to 2004. Species lists were compiled for every islet (Nilson & Jüriado 2001; Suija & Jüriado 2002). Species observed only in previous expeditions have also been taken into account (Sander 1974; Randlane 1986; Püttsepp 1986; unpubl.). The number of lichen species on different substrate types was registered on each islet. Five ecological groups (epiphytic, epixylic, epilithic, epigeic lichens, and lichenicolous fungi) were studied on seven substrate types: (1) Coniferous trees – coniferous trees (*Pinus sylvestris*, *Juniperus communis*); (2) Deciduous trees – deciduous trees (*Acer platanoides*, *Betula pendula*, *Fraxinus excelsior*, *Quercus robur*, *Sorbus aucuparia*, *Tilia cordata*, *Ulmus glabra* etc.) and bushes (*Lonicera xylosteum*, *Rhamnus catharctica*, *Ribes alpinum*, *Rosa* spp. etc.); (3) Dead wood – driftwood, wooden buildings and fences; (4) Granite – erratic blocks and granite shingle; (5) Limestone – calcareous rocks, limestone shingle, concrete stakes and tiles; (6) Soil – mineral soil, ground mosses; (7) Lichens – lichenicolous fungi and lichens growing on other lichens. The relative abundance of every lichen species was evaluated on a four-point abundance scale: 1 – one specimen per islet; 2 – up to ten specimens; 3 – sporadically, found only in some places or on particular substrate; 4 – numerous. Sampling of lichens was carried out in all habitats and biotopes suitable for lichen growth on the islets.

The collected specimens (about 1000 specimens) are kept in the lichenological herbarium at the University of Tartu (TU). For identification of lichens in the laboratory the stereomicroscope, light microscope, "spot tests", UV light, and standardized thin-layer chromatography (TLC) methods were used.

Randlane et al. (2002, 2004) is considered for estimating regional species pool size and the number of rare lichen species in Estonia. The share of the forest lichens in Estonia follows Lõhmus (2003).

Islet traits

The environmental conditions on islets were characterised using the area of the islet (ha), the number of biotopes per islet, and islet distance from mainland (km) (Table 1). The data about islet areas was taken from the database of Estonian marine islands (Loopmann 1996) or was supplied by the administration of Hiiumaa Islets Landscape Reserve. The number of biotopes was calculated using a modified system of Leito & Leito (1991), produced for the islets of the Hiiumaa Islets Landscape Reserve. Islet isolation was measured as the nearest distance to the mainland coastline (km) on a digital map from the Regio Estonian Road Atlas (Regio 1999). The 'mainland' was defined as Hiiumaa or Vormsi islands or continental Estonia, depending on which one was closest.

Analytical methods

A generalized linear model (GLIM) analysis with Poisson error distribution, implemented in the program package Statistica 6.5 (Statsoft Inc.), was applied to study the effect of islet traits (islet area, number of biotopes, and distance from mainland) on the number of lichen species on the islet. Number of lichen species was estimated at two levels: (1) the total number of lichen species on an islet, and (2) the number of lichen species on an islet by substrate type. Substrate types were 'Coniferous trees', 'Deciduous trees', 'Dead wood', 'Granite', 'Limestone', 'Soil' and 'Lichens'. In models, all continuous environmental variables were log-transformed. Akaike's information criterion (AIC; Akaike 1973) was used to find the optimal model according to predictive power and to avoid over-parameterisation (Shao 1997). Factor effect profile method, using semi-residuals of the model, was used for graphical presentation of factor effect on species richness. Semi-residuals for the factor of interest in the built model were estimated by summing the factor effect (the factor related model term multiplied by respective slope value) and the model residuals. It is important to note that slope parameter values of factors were taken from the model built for factor testing. Use of the semi-residuals makes it possible to illustrate observed relationships in the GLIM model, i.e. to illustrate the response of species richness along the gradient of one factor out of three, while the effect of the other two factors has been taken into account. The alternative method, prediction profiles of factor effects, where values of other factors are fixed at selected level, does not allow the original variation of data to be presented, in conditions where certain correlation between factors can be expected.

Frequently registered species, observed on at least six islets (20%, all together 104 taxa), were used to explain species-specific trends of dispersal and

colonization. The occurrence predictability of each lichen species on an islet according to islet parameters (area, number of biotopes and distance from mainland) was tested with logistic regression analyses in GLIM analysis (Binomial error distribution, logit link-function) (proc GENMOD, SAS Institute Inc. 1989). The presence of species-specific behaviour was tested as the significance of the interaction term between the discrete factor 'Species' and each continuous trait of islet. Substrate group specific pattern was also tested, but, as it was not significant, the results are not presented. The MIXED model analysis (Littell et al. 1996) was built with fixed factor 'Species' and random factor 'Islet' to evaluate the species-specific relation of abundance of lichen species to the islet area, number of biotopes, and distance from mainland.

RESULTS

The species richness

The species list of the 32 islets studied consists of 326 lichenized, lichenicolous and allied fungi (below considered as 'lichens') (App. 1). The most species-rich substrate types on islets were woody substrates (deciduous trees, dead wood and coniferous trees) and granite rocks (Table 2). Half of the Estonian lichen species growing on granite or coniferous trees (respectively 93 and 75 species) have been recorded on these islets. 86 species were registered on dead wood, which constitutes to 59% of the epixylic lichen flora of Estonia. The least abundantly represented groups on the islets were lichenicolous fungi (fungi growing on lichens) and ground layer lichens (21–24% of the regional species pool) (Table 2). It is noteworthy that, from the species pool of forest lichens (481 species), only 11 calicioid, 11 cyanobacterial (mainly species from genus *Peltigera*), and five pendulous lichens were found. On the islets, 86 rare lichen species (up to ten localities in Estonia), 13.4% of the total of 639 rare species in Estonia were recorded. The highest numbers of rare species were recorded in the groups of lichenicolous fungi (25 species) and epilithes on granite (23); the lowest proportion of rare lichens was found on trees and soil (Table 2).

The number of lichen species on islets varied from 2 to 197 species, from the smallest to the largest islets respectively (Table 1). The total number of lichen species on an islet increased logarithmically with islet area and number of biotopes, and decreased with the islet distance from the mainland (Figs. 2–4; Table 3).

The number of lichen species on substrate types was significantly determined by the islet area, the number of biotopes, and distance from mainland (Table 4). As observed in the general model, number of species increased with the islet area and with the number of biotopes, while it decreased with increasing islet distance from mainland (Table 4). However, substrate-group-specific variations were observed (interaction terms significant, Table 4) i.e. the general trends cannot be generalized to each substrate group.

The effect of islet area on species richness on various substrates was found to be important only for three groups: species on coniferous trees, on dead wood, and on soil (Fig. 5; Table 5). For species numbers in the other groups, the model failed to show the significant effect of area, even if the regression slope parameter was estimated to be a positive value (Table 5). The number of species in most of the substrate groups (except species on dead wood) was correlated with the number of biotopes on the islet (Fig. 6). The significant negative effect of distance from mainland on the number of lichen species on the selected substrates was detected for five substrate groups out of seven (Fig. 7). In other words, all three factors were significant predictors of the number of lichen species on coniferous trees and soil. Two substrate groups have only one significant environmental predictor of species richness – the number of species on deciduous trees and on limestone was determined only by the number of biotopes on the islet.

Theory predicts a certain collinear effect of islet area and number of biotopes. However, one can observe the full spectrum of these effects. Area and the number of biotopes both have an important effect on the number of lichens on coniferous trees and on soil. The effect of area was significant for the number of lichen species on dead wood, while, on the contrary, for the species on deciduous trees, on granite, on limestone, and also for lichenicolous fungi, the number of biotopes was more important than the size of the islet (Table 5).

The occurrence probability and the abundance of lichen species

All three biogeographic traits of islets affect the occurrence and abundance of lichen species on islets, but this effect is species dependent (Table 6 and 7). According to the results of logistic regression and MIXED model analyses, 78 out of 104 more-or-less common lichen taxa showed a significant relationship to one or two (in a few cases three) of the studied traits of the islets (Table 8). Significant effects of the islet traits were observed in 46 epiphytic and epixylic species (deciduous trees, coniferous trees, dead wood), 41 epilithic species (mainly on granite), and four epigeic species (on soil) (Table 8).

Results of the GLIM analysis on presence/absence data revealed that the occurrence of 12 species on the studied islets was affected by islet area, 32 species depended on the number of biotopes and 15 species showed significant distance limitation (Table 6 and 8). Most of those species had similar regression trends, increasing odds of presence/absence on large and more biotope rich islets or decreasing success of establishment with distance (Table 8). According to the model parameter solution, there was one exceptional species, *Rinodina gennarii*, the occurrence of which increased with distance from mainland.

In general, the abundance of lichen species depended non-linearly on islet area and the number of biotopes on the islet (Table 7). Both factors had a clear positive effect on the abundance of all species (main effects significant; Table 7 and 8). The area of the islet only had a significant main effect in the results of the MIXED model, without clear indication to species-specific patterns (Table 7). This positive effect was particularly clear for 41 taxa from various

substrates. Taxa for which the area effect was most evident were mainly from woody substrates and granite, though species from limestone and soil were also represented (Table 8). The abundance of 31 taxa increased significantly with an increasing number of biotopes (Table 8). However, the variable 'Distance' affected the general abundance of lichen species on islets, as revealed for 18 taxa from MIXED model analyses (Table 8). The species abundance on islets increased with distance from mainland for eight species; a negative impact of distance was detected for ten taxa.

DISCUSSION

The total area of the 32 studied islets is 4.15 km^2, which constitutes ca 0.01% of the Estonian land area. However, from this small and fragmented land, 32% of the lichen species known in Estonia were found. For example, on the studied islets, the species on woody substrates (deciduous and coniferous trees, dead wood) constitute almost half of the epiphytic and epixylic lichens known from Estonia (Randlane et al. 2002). Despite of the good representation of the regional species pool, only a few of the species found in the islets are characteristic of natural old forests with long ecological continuity. (Trass et al. 1999; Coppins & Coppins 2002). The list of species of Estonian lichens recorded in forests (Lõhmus 2003) includes many habitat specialists (calicioid, cyanobacterial and pendulous lichens), which are almost absent on studied islets. The absence of habitat specialists might be due to the short historical continuity of the forests. The larger islets were for centuries used as pastures, where tree cover existed, but as fragmented patches (Rebassoo 1972). The small proportion of forest habitat specialists and rare species in a group of epiphytic lichens also indicates dispersal limitation (Dettki & Esseen 1998; Hilmo & Såstad 2001).

The proportion of rare lichen species on the studied islets is rather low (13.4%) compared with the proportion of rare species in the whole of the Estonian lichen flora (64%) (Randlane et al. 2002). On islets, we found the largest proportion of rare species among lichenicolous fungi and epilithic lichens on granite. Both groups are relatively rare also in the rest of Estonia. One of the reasons, as pointed out earlier (Randlane et al. 2002), is the insufficient knowledge about the occurrence and distribution of these groups in Estonia. However, as most rare epilithic species belong to geographical elements that are atypical for local flora (arctic-alpine or hypo-arctic-montane), then this could be an additional reason explaining the high share of rare species on islets compared to the Estonian lichen flora (Randlane et al. 2002).

Distance

It has been pointed out that remote islands support fewer species than equal-sized islands close to the nearest colonization source (MacArthur & Wilson 1967). The biota of islands is formed by long-distance dispersal (Ås et al. 1997), and for successful colonization, both dispersal capability and diaspore

viability are important (Armstrong 1988). Lichens have two basic modes of reproduction and dispersal: sexual via ascospores, and asexual via soredia, isidia or thallus fragments. Asexual reproduction has several advantages over sexual reproduction for lichens, mostly because asexual diaspores ensure dispersal of both symbiontic partners, a heterotrophic fungus and an autotrophic alga (or cyanobacterium) simultaneously (Nash 1996). Although knowledge about the dispersal efficiency of different propagule types is still limited, there are indications of the prevalence of ascospores in long-distance dispersal while asexual diaspores are important in short distance dispersal within a community (Bailey 1976; Hedenås & Ericson 2000).

The results of our study show that the number of lichen species on islets is affected by distance from their source; this can be a result of the different reproductive and dispersal potentials of species. The negative relationship between distance and species richness of almost all substrate groups of lichens is obvious. However, on the level of individual species, species-specific effects were observed. Most of the species whose probability of occurrence on the islet increased with increasing distance from mainland are typical early colonizers of rocky places (*Caloplaca citrina*, *Lecanora helicopis*, and *Rinodina gennarii*), as well as woody substrate (*Physcia stellaris* and *Physconia distorta*) (Degelius 1964; Fletcher 1973). They are characterised by the tightly attached, flattened, either crustose or foliose thallus, and they disperse merely with ascospores, except *Caloplaca citrina*, which reproduces sexually and asexually. In addition, among the species with good dispersal ability, there are two crustose and exclusively sorediate lichens, *Lepraria incana* and *Phlyctis argena*. The extensive production of vegetative diaspores seems to be a mechanism that ensures the distribution of these species over wide distances. It has been noted that *Lepraria incana* prefers maritime conditions (Brown & Di Meo 1972; Tønsebrg 1992), and that it is one of the first colonizers on islands (Kristinsson 1974).

Species whose distribution show a negative correlation with distance, are characterised by the limited production of soredia in soralia and also by more loosely attached thallus (e.g. *Hypogymnia physodes*, *H. tubulosa*, *Parmelia sulcata*, *Parmeliopsis ambigua*, *Physcia dubia*, *Tuckermannopsis chlorophylla*). Disturbances on distant islets at open seas are more intense than on the islets near mainland coasts. The loosely attached growth form is a disadvantage in conditions of the destructive influence of wind and waves (Fletcher 1973). There are also several crustose species (e.g. *Acarospora veronensis*, *Amandinea punctata*, *Lecanora pulicaris*, *L. varia*, *Scoliciosporum chlorococcum*), which reproduce only sexually. However, a clear explanation for the reasons of long-distance dispersal disability is lacking.

Area

The general principles of species-area correlation and the specific trends for islands have been analysed and discussed widely in literature (e.g. Arrhenius 1921; MacArthur & Wilson 1963, 1967). We also found a direct positive

relationship between species richness of lichens and islet area, but the shape of the relationship was dependent on a particular species group. After the removal of the effects of biotope diversity and distance, a statistically significant area effect was detected for richness of lichens growing on soil, dead wood, and conifers. Only epixylic species showed a direct correlation with area, without additional significant influence by biotope diversity.

Larger islands provide a more stable environment than smaller islands, i.e. the probability of stochastic events, especially wave and wind disturbances that have a destructive influence on soil erosion, is smaller. It has been shown that ground lichens establish in a community only after the soil surface has been stabilized (Belnap & Eldridge 2003). The later composition of lichen flora is basically dependent on soil characteristics, especially on the soil texture, chemistry, and water holding capacity (Rosentrater & Belnap 2003). We propose that the species richness of epigeic lichens on islets is determined by the extent of disturbance and by the differentiation of soils. For instance, the larger islets support a higher abundance of lichens typical of dry soils in light-exposed habitats (*Cetraria islandica*, *Cladonia furcata*, *C. subrangiformis*, *Peltigera rufescens*).

Driftwood transported onto islands by the sea is natural habitat for epixylic species (Himelbrant & Kuznetzova 2002). The colonization of driftwood by lichens assumes the stable persistence of driftwood, which is more likely on larger areas. In addition to driftwood, older wooden buildings (farm houses, wooden quays, wooden windmills, fences) on larger islets serve as suitable substrates for many epixylic species, and therefore increase the species richness on these islets. We detected that the abundance of two common epixylic species (*Lecanora varia* and *Trapeliopsis flexuosa*) increased with area. These species are able to grow on worked timber as well as on natural lignum (Randlane & Saag 2004), and their higher abundance might be related to the sufficient amount of suitable substrates.

Some ecological groups of lichens are clearly limited by substrate availability, for example, by the presence of coniferous trees. As a rule, the pioneers in early stages of vegetation development on islets are certain deciduous trees and bushes. Conifers establish only in later stages of land-lift and vegetation succession, i.e. only on intermediate and large islets (Rebassoo 1972; Svennson & Jeglum 2003). The main conifer on the studied islets is *Juniperus communis*, which often forms extensive brushwood. *Pinus sylvestris* occurs only in forest patches on large islets. We found that the abundance of several foliose and fruticose lichen species, mainly confined to conifers, was determined only by islet area (*Cladonia coniocraea*, *C. fimbriata*, *Parmeliopsis ambigua*, *Pseudevernia furfuracea*, *Tuckermannopsis chlorophylla*, *Vulpicida pinastri*). These are species that disperse mainly with asexual diaspores and prefer to grow in a more terrestrial environment. It has been demonstrated that the abundance of species with dominating asexual propagules increases in habitats with small-scale disturbances and in later stages of community succession (Kiss 1988; Dietrich & Scheidegger 1996).

Number of biotopes

We found that the total lichen species richness is higher on islets with a higher number of biotopes. It has been shown in several studies that the number of species for a given area correlates with biotope diversity because the number of biotopes determines the diversity of environmental niches (Williams 1943; Kelly et al. 1989). The relative importance of biotope diversity on the formation of lichen flora of islands has been highlighted in a few studies (Sipman & Raus 1999; Seaward & Aptroot 2000).

The uplift of the islets and the succession of the vegetation alter the environment, especially local light and moisture conditions, and diminish the disturbance impact by the sea and winds. Habitat change affects the formation of specific lichen communities (Longton 1992), due to the ability of lichens to use finely differentiated niches originating from small changes in environmental conditions (Barkman 1958; Ott et al. 1996a, 1996b). The higher number of biotopes provides a higher number of niches that can be colonized by lichen species with narrow ecological adaptations, and thereby habitat diversity supports species richness on islets.

The effect of biotope diversity on species richness of lichens varies between substrate types. It is important for lichens on some substrates such as deciduous trees, granite and limestone, and also for lichenicolous fungi. Beside the significant effect of biotope diversity on lichen richness on conifers and on soil, the additional effect of area was also evident.

Results of the species data analyses revealed that the abundance of several epilithes (both granite and limestone species) and epiphytes on islets is positively correlated with the number of biotopes. The biotope diversity dependent epilithic species (*Candelariella coralliza*, *Neofuscelia loxodes*, *Tephromela atra*, *Xanthoparmelia conspersa*, *Lecanora albescens*, *Lecidella stigmatea* etc.) grow preferably in the xeric supralittoral or in the terrestrial zone.

Most of the epiphytes that benefit from a higher number of biotopes have wide ecological amplitude and are able to establish on the bark of trees and shrubs in various biotopes. Within these species, some of them (e.g. *Evernia prunastri*, *Hypogymnia physodes*, *Phlyctis argena*, *Ramalina farinacea*) are not specialized and grow in various habitats on both deciduous and coniferous trees, while other species (e.g. *Lecanora carpinea*, *Physcia stellaris*, *P. tenella*) are specialized to deciduous trees with smooth bark. However, the smooth barked trees (e.g. *Sorbus aucuparia, Rhamnus cathartica* or *Viburnum opulus*) are habitat generalists and therefore support the presence and abundance of lichen species on biotope-rich islets.

It has been hypothesized that, during natural community succession, the diversity of lichen parasites (lichenicolous fungi) increases together with the increasing number of host lichen species (Lawrey & Diederich 2003). Therefore, the biotope effect on the diversity of lichenicolous fungi can be solely the effect of the variety of host species.

CONCLUSIONS

Our study does not seek to test any of the specific theories or hypotheses proposed to explain the relationship of species richness with islands features, which have been discussed for decades (see for reviews Gotelli & Graves 1996; Whittaker 1998), but to describe the various patterns of species richness on islets and to analyse the species-specific reasons for observed patterns of species richness. The results of our study revealed that lichenized fungi do not respond consistently to islet area, biotope diversity, and isolation, even if the general pattern of species richness is obvious. The effect of islet area on the species richness of lichens was evident only in a few selected substrate types, while the effect of biotope diversity and distance from the mainland was significant for species richness in most of the ecological groups. However, the effect of islet traits at species level is even more puzzling, as the species presence and abundance is a complex combination of dispersal strategy, growth form and ecological requirements of the individual species. Besides natural factors, anthropogenic activities, such as the creation of new habitats (e.g. wooded meadows and shrub lands) or substrates (e.g. wooden buildings), sometimes also have a positive impact on lichen growth.

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REFERENCES

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. In: Petrov, B.N. & Csaki, F. (eds.) *2nd International Symposium on Information Theory*. Akademiai Kiado. Budapest, Hungary.

Armstrong, R.A. 1988. Substrate colonization, growth, and competition. In: Galun, M. (ed.) *CRC Handbook of Lichenology*. Vol. II, pp. 3–16. CRC Press, Inc., Boca Raton.

Arrhenius, O. 1921. Species and area. *J. Ecol.* 9: 95–99.

Ås, S., Bengtsson, J. & Eberhard, T. 1997. Archipelagoes and the theories of insularity. *Ecol. Bull.* 46: 88–116.

Bailey, R.H. 1976. Ecological aspects of dispersal and establishment in lichens. In: Brown, D.H., Hawksworth, D.L. & Bailey, R.H. (eds.) *Lichenology: Progress and Problems*: 215–247. Academic Press, London, UK.

Barkman, J.J. 1958. *Phytosociology and Ecology of Cryptogamic Epiphytes*. Van Gorcum and Co., Assen, the Netherlands.
Belnap, J. & Eldridge, D.J. 2003. Disturbance and Recovery of Biological Soil Crusts. In: Belnap, J. & Lange, O.L. (eds.) *Biological Soil Crusts: Structure, Function and* management. Ecological Studies 150: 363–383. Springer-Verlag Berlin Heidelberg New York.
Berglund, H. & Jonsson, B.G. 2001. Predictability of plant and fungal species richness of old-growth boreal forest islands. *J. Veg. Sci.* 12: 857–866.
Brown, D.H. & Di Meo, J.A. 1972. Influence of local maritime conditions on the distribution of two epiphytic lichens. *Lichenologist* 5: 305–310.
Connor, E.F. & McCoy, E.D. 1979. The statistics and biology of the species-area relationships. *Am. Nat.* 113: 791–833.
Coppins, A.M. & Coppins, B.J. 2002. *Indices of ecological continuity for Woodland Epiphytic Lichen Habitats in the British Isles.* British Lichen Society, Wimbledon, UK.
Degelius, G. 1964. Biological studies of the epiphytic vegetation on twigs of *Fraxinus excelsior*. *Acta Horti Gothob.* 27(3): 1–55.
Deshaye, J. & Morisset, P. 1988. Floristic richness, area, and habitat diversity in a hemiarctic archipelago. *J. Biogeogr.* 15: 747–757.
Dettki, H. & Esseen, P.-A. 1998. Epiphytic macrolichens in managed and natural forest landscapes: a comparison at two spatial scales. *Ecography* 21: 613–624.
Diamond, J.M., Gilpin, M.E. & Mayr, E. 1976. Species-Distance Relation for Birds of the Solomon Archipelago, and the Paradox of the Great Speciators. *Proc. Natl. Acad. Sci.* 73(6): 2160–2164.
Dietrich, M. & Scheidegger, C. 1996. The importance of sorediate crustose lichens in the epiphytic lichen flora of the Swiss Plateau and the Pre-Alps. *Lichenologist* 28(3): 245–256.
Fletcher, A. 1973. The ecology of maritime (supralittoral) lichens on some rocky shores of Anglesey. *Lichenologist* 5: 401–422.
Gilbert, F.M. 1980. The equilibrium theory of island biogeography: fact of fiction? *J. Biogeogr.* 7: 209–235.
Gilpin, M.E. & Diamond, J.M. 1976. Calculation of immigration and extinction curves from the species-area-distance relation. *Proc. Natl. Acad. Sci.* 73(11): 4130–4134.
Gotelli, N.J. & Graves, G.R. 1996. *Null models in ecology*. Smithsonian Institution Press, Washington, DC, US.
Haila, Y. 1983. Land birds on northern islands: a sampling metaphor for insular colonization. *Oikos* 41: 334–349.
Hayward, B.W. & Hayward, G.C. 1986. Lichen flora of the offshore islands of northern New Zealand. *The offshore islands of northern New Zealand Department of Lands and Survey Information Series* 16: 153–160.
Heaney, L.R. 1984. Mammalian species richness on islands on the Sunda shelf, southeast Asia. *Oecologia* 61: 11–17.
Hedenås, H. & Ericson, L. 2000. Epiphytic macrolichens as conservation indicators: successional sequence in *Populus tremula* stands. *Biol. Conservation* 93: 43–53.
Hilmo, O. & Såstad, S.M. 2001. Colonization of old-forest lichens in a young and an old boreal *Picea abies* forest: an experimental approach. *Biol. Conservation* 102: 251–259.
Himelbrant D. & Kuznetsova E. 2002. Lignicolous lichens on driftwood of the Keret' archipelago (White Sea). *Botanica Lithuanica* 8(4): 349–355.

Jõgi, J. & Tarand, A. 1995. Climate. In: Raukas, A. (ed.) *Estonian Nature*: 183–216. (in Estonian, English summary). Valgus & Estonian Encyclopedia Publishers, Estonia.
Kelly, B.J., Wilson, J.B. & Mark, A.F. 1989. Causes of the species-area relation: a study of islands in Lake Manapouri, New Zealand. *J. Ecol.* 77: 1021–1028.
Kessel, H. 1961. Über die Entwicklung der Ostsee im Bereich des Territoriums der Estnischen SSR im Holozän. (In Estonian, German summary). *ENSV TA Geoloogia Instituudi Uurimused VII*: 167–185.
Kimmerer, R.W. & Driscoll, M.J.L. 2000. Bryophyte species richness on insular boulder habitats: the effect of area, isolation and microsite diversity. *Bryologist* 103: 748–756.
Kiss, T. 1988. Dispersal and growth forms: an approach towards an understanding of the life-strategy concept in lichenology. *Acta Bot. Hung.* 34(1–2): 175–191.
Kohn, D.D. & Walsh, D.M. 1994. Plant Species Richness – The Effect of Island Size and Habitat Diversity. *J. Ecol.* 82(2): 367–377.
Kotze, D.J., Niemelä, J. & Nieminen, M. 2000. Colonization success of carabid beetles on Baltic islands. *J. Biogeogr.* 27: 807–820.
Kristinsson, H. 1974. Lichen colonization in Surtsey 1971–1973. *Surtsey Res. Progr. Rept. [Reykjavik]* 7: 9–16.
Kruys, N. & Jonsson, B.G. 1997. Insular patterns of calicioid lichens in a boreal old-growth forest-wetland mosaic. *Ecography* 20: 605–613.
Lawrey, J.D. 1984. *Biology of Lichenized Fungi*. Praeger Publishers, NY, US.
Lawrey, J.D. 1991a. Biotic interactions in lichen community development: a review. *Lichenologist* 23(3): 205–214.
Lawrey, J.D. 1991b. The species-area curve as an index of disturbance in saxicolous lichen communities. *Bryologist* 94(4): 377–382.
Lawrey, J.D. 1992. Natural and randomly-assembled lichen communities compared using the species area curve. *Bryologist* 95(2): 137–141.
Lawrey, J.D. & Diederich, P. 2003. Lichenicolous fungi: interactions, evolution, and biodiversity. *Bryologist* 106(1): 81–120.
Leito, A. & Leito, I. 1991. *Hiiumaa Islets State Landscape Reserve* (in Estonian). Kärdla, Estonia.
Littell, R.C., Milliken, G.A., Stroup, W.W. & Wolfinger, R.D. 1996. SAS® system for mixed models. SAS Institute Inc., Cary, NC, US.
Lomolino, M.V. & Weiser, M.D. 2001. Towards a more general species-area relationship: diversity on all islands, great and small. *J. Biogeogr.* 28(4): 431–445.
Longton, R.E. 1992. The role of bryophytes and lichens in terrestrial ecosystems. In*:* Bates, J.W. & Farmer, A.M. (eds.) *Bryophytes and Lichens in a Changing Environment*: 32–76. Clarendon Press, Oxford, UK.
Loopmann, A. 1996. *List of Estonian sea islands* (in Estonian). Tallinn, Estonia.
Lõhmus, P. 2003. Composition and substrata of forest lichens in Estonia: a meta-analysis. *Folia Cryptog. Estonica* 40: 19–38.
MacArthur, R.H., & Wilson, E.O. 1963. An equilibrium theory of island biogeography. *Evolution* 17: 373–387.
MacArthur, R.H. & Wilson, E.O. 1967. *The theory of island biogeography*. *Monographs in Population Biology 1*. Princeton University Press, Princeton, New Jersey, US.
Martin, L., Randlane, T. & Martin, J. 2000. Lichens of Vormsi island. *Folia Cryptog. Estonica* 36: 65–81.
McGuiness, K.A. 1984. Equations and explanations in the study of species-area curves. *Biol. Rev.* 59: 423–440.

Mills, S.E. & McDonald, S.E. 2004. Predictors of moss and liverwort species of microsites in conifer dominated boreal forest. *J. Veg. Sci.* 15: 189–198.
Moody, A. 2000. Analysis of plant species diversity with respect to island characteristics on the Channel Islands, California. *J. Biogeogr.* 27(3): 711–723.
Nash, T.H. III (ed.) 1996. *Lichen Biology*. Cambridge University Press, Cambridge, UK.
Niemelä, J. 1988. Habitat occupancy of carabid beetles on small islands and adjacent Åland mainland. *Ann. Zool. Fennici* 25: 121–131.
Nilson, E. & Jüriado, I. 2001. Lichens of Harilaid Island (West-Estonian Archipelago). *Folia Cryptog. Estonica* 38: 47–50.
Nilson, E. & Piin, T. 1998 Lichens of the islets of Kolga Bay (Gulf of Finland, Estonia). Distribution and frequency of epiphytic lichen species. *Folia Cryptog. Estonica* 32: 57–62.
Nilsson, I.N. & Nilsson, S.G. 1982. Turnover of vascular plant species on small islands in Lake Möckeln, South Sweden 1976–1980. *Oecologia* 53: 128–133.
Nilsson, S.G. 1986. Are bird communities in small biotope patches random samples from communities in large patches? *Biol. Conservation* 38: 179–204.
Nilsson, S.G., Bengtsson, J. & Ås, S. 1988. Habitat diversity or Area *per se*? Species Richness of Woody plants, Carabid Beetles and Land Snails on Islands. *J. Anim. Ecol.* 57(2): 685–704.
Ott, S., Burger, E., Schuster, G. & Jahns, H.M. 1996a. Distribution of lichens on rock. *Herzogia* 12: 171–198.
Ott, S., Elders, U., Jahns, H.M. 1996b. Vegetation of the rock-alvar of Gotland. I. Microhabitats and succession. *Nova Hedwigia* 63(3–4): 433–470.
Preston, F.W. 1960. Time and space and the variation of species. *Ecology* 41: 611–627.
Randlane, T. 1986. Analysis of the lichen flora on Estonian western islands (in Russian). Candidate's dissertation, University of Tartu, Estonia.
Randlane, T. & Saag, A. (eds.) 1999. Second checklist of lichenized, lichenicolous and allied fungi of Estonia. *Folia Cryptog. Estonica* 35: 1–132.
Randlane, T. & Saag, A. (eds.) 2004. *Estonian Microlichens* (in Estonian). Tartu University Press, Estonia.
Randlane, T., Saag, A. & Suija, A. 2002. Biodiversity of lichenized taxa in Estonia: distribution of rare species. *Biblioth. Lichenol.* 82: 99–109.
Randlane, T., Saag, A. & Suija, A. 2004. Lichenized, lichenicolous and allied fungi of Estonia. URL: http://www.ut.ee/lichens/fce.html [Estonian Lichenology].
Raukas, A. (ed.) 1995. *Estonian Nature* (in Estonian, English summary). Valgus & Estonian Encyclopedia Publishers, Estonia.
Rebassoo, H.-E. 1972. *The Islets Book* (In Estonian). Valgus, Tallinn, Estonia.
Regio 1999. Regio Estonian CD Atlas.
Ricklefs, R.E. & Lovette, I.J. 1999. The roles of island area *per se* and habitat diversity in the species-area relationships of four Lesser Antillean faunal groups. *J. Anim. Ecol.* 68: 1142–1160.
Rosenzweig, M.L. 1995. *Species diversity in space and time*. Cambridge University Press, NY, US.
Rosentrater, R. & Belnap, J. 2003. Biological Crusts of North America. In: Belnap, J. & Lange, O.L. (eds.) *Biological Soil Crusts: Structure, Function and* management. Ecological Studies 150: 31–50. Springer-Verlag Berlin Heidelberg New York.
Rydin, H. & Borgegård, S.-O. 1988. Plant species richness on islands over a century of primary succession: Lake Hjälmaren. *Ecology* 69: 916–927.

Santesson, R. Moberg, R., Nordin, A., Tønsberg, T. & Vitikainen, O. 2004. *Lichen-forming and Lichenicolous Fungi of Fennoscandia*. Museum of Evolution, Uppsala University, Uppsala, Sweden.

SAS Institute Inc. 1989. SAS/STAT® user's guide. Version 6. Fourth Edition. Volume 2. SAS Institute Inc., Cary, NC.

Seaward, M.R.D. & Aptroot, A. 2000. The lichen flora of the Chagos Archipelago, including a comparison with other island and coastal tropical floras. *Tropical Bryology* 18: 185–198.

Sepp, U. 1970. The Väinameri Islands (In Estonian, English summary). In: Kumari (ed.). *Nature in the West-Estonian Coastal Areas,* pp. 17–26. Valgus, Tallinn, Estonia.

Sepp, U. 1974. *The landscape characteristics of Hiiumaa* (In Estonian, English summary). Valgus, Tallinn, Estonia.

Shao, J. 1997. An asymptotic theory for linear model selection. *Statistica Sinica* 7: 221–264.

Simberloff, D.S. 1974. Equilibrium Theory of Island Biogeography and Ecology. *Ann. Rev. Ecol. Syst.* 5: 161–182.

Sipman, H. & Raus, T. 1999. A lichenological comparison of the Paros and Santorini island groups (Aegean, Greece), with annotated checklist. *Willdenowia* 29: 239–297.

Slatter, R.J. 1990. Limestone communities and island biogeography. *Journal of Biological Education* 24(2): 87–91.

Suija, A. & Jüriado, I. 2002. Lichens and lichenicolous fungi of the Hiiumaa Islets Landscape Reserve (Estonia). *Folia Cryptog. Estonica* 39: 37–50.

Svennson, J.S. & Jeglum, J.J. 2003. Spatio-temporal properties of tree species belts during primary succession on rising Gulf of Bothnia coastlines. *Ann. Bot. Fennici* 40: 265–282.

Tangney, R.S., Wilson, J.B. & Mark, A.F. 1990. Bryophyte island biogeography: a study in Lake Manapouri, New Zealand. *Oikos* 59: 21–26.

Tønsberg, T. 1992. The sorediate and isidiate, corticolous, crustose lichens in Norway. *Sommerfeltia* 14: 1–331.

Trass H., Vellak, K. & Ingerpuu, N. 1999. Floristical and ecological properties for identifying of primeval forests in Estonia. *Ann. Bot. Fennici* 36: 67–80

Triantis, K.A., Mylonas, M., Lika, K. & Vardinoyannis, K. 2003. A model for the species-area-habitat relationship. *J. Biogeogr.* 30: 19–27.

Whitehead, D.R. & Jones, C.E. 1969. Small islands and the equilibrium theory of insular biogeography. *Evolution* 23:171–179.

Whittaker, R.J. 1998. *Island Biogeography: ecology, evolution and conservation*. Oxford University Press, Oxford, UK.

Williams, C.B. 1943. Area and number of species. *Nature* 152: 264–267.

Williams, G.R. 1982. Species-area and similar relationships of insects and vascular plants on the southern out lying islands of New Zealand. *New Zealand Journal of Ecology* 5: 86–96.

Table 1. Islet area, number of biotopes on islet, distance to the mainland, and the number of lichen and lichenicolous fungi species on studied islets. The islets are sorted by area and number of biotopes.

No.	Islets	Area (ha)	No. of Biotopes	Distance (km)	No. of. Species
1	Kivirahu	0.1	1	0.7	2
2	Pähkrahu	0.1	1	2.1	2
3	Säinarahu	0.1	1	2.1	2
4	Hoburahu	0.1	2	0.7	10
5	Luigerahu	0.1	2	14.0	4
6	Oorahu	0.1	2	5.1	6
7	Kajakarahu	0.1	3	2.1	18
8	Palgirahu	0.1	3	2.1	27
9	Sitakare	0.1	3	0.7	14
10	Valgekare	0.2	2	0.9	7
11	Väike-Pihlakare	0.2	4	1.2	26
12	Ankrurahu	0.3	3	14.0	14
13	Suur-Pihlakare	0.3	4	1.3	25
14	Anerahu	1.2	4	12.5	28
15	Langekare	1.2	4	11.2	27
16	Auklaid	1.2	5	0.7	77
17	Uuemererahu	2.3	2	1.7	9
18	Kakralaid	3	1	4.7	3
19	Eerikulaid	4	2	5.3	8
20	Öakse	7.6	6	1.5	101
21	Rukkirahu	7.8	3	3.7	17
22	Uusmererahu	11	4	2.6	80
23	Hellamaa rahu	14	4	0.8	70
24	Harilaid	15	5	3.8	118
25	Kõrgelaid	16	7	11.6	101
26	Ahelaid	17	7	14.2	93
27	Kadakalaid	19	7	3.3	142
28	Hõralaid	20	6	2.0	97
29	Kõverlaid	20	7	15.1	85
30	Vareslaid	31	7	10.2	101
31	Hanikatsi	82	7	7.9	197
32	Saarnaki	140	7	4.2	164

Table 2. Number of lichen species in the regional species pool (Estonia); number of lichen species on islets, and the proportion of the regional species pool represented; the number of rare lichen species on islets according to substrate type.

Substrate type	Regional species pool size	Observed number (proportion) of species		Number of rare species
Coniferous trees	151	75	(50%)	4
Deciduous trees	298	114	(38%)	9
Dead wood	145	86	(59%)	13
Granite	183	93	(51%)	23
Lichens	130	28	(21.5%)	25
Limestone	139	47	(34%)	12
Soil	144	35	(24%)	2
Species pool	1002	326		

Table 3. Results of GLIM analysis on the effect of the islet area, number of biotopes and distance on the number of lichen species on an islet. GLIM model specifications are: Poisson error distribution, log-link function and Pearson correction-coefficient for overdispersion. 'Area', 'No. of biotopes' and 'Distance' are log-transformed. Estimated slope parameter with standard error is presented.

Variable	df	Wald statistic	*p*	Slope (±SE)
Intercept	1	1.52	0.2170	0.510 (±0.413)
Area	1	18.99	**0.0001**	0.393 (±0.090)
No. of biotopes	1	64.20	**0.0001**	2.112 (±0.264)
Distance	1	15.95	**0.0001**	–0.671 (±0.168)

Table 4. Results of GLIM analysis on the effect of the islet area, number of biotopes and distance on the number of lichen species on substrate types. GLIM model specifications are: Poisson error distribution, log-link function and Pearson correction-coefficient for overdispersion. 'Area', 'No. of biotopes' and 'Distance' are log-transformed.

Variable	df	Wald statistic	*p*
Intercept	1	14.19	**0.0001**
Area	1	40.15	**0.0001**
No. of biotopes	1	56.07	**0.0001**
Distance	1	37.74	**0.0001**
Substrate type	6	34.71	**0.0001**
Substrate type*Area	6	29.53	**0.0001**
Substrate type*No. of biotopes	6	26.03	**0.0002**
Substrate type*Distance	6	41.68	**0.0001**

Table 5. Slope estimates of Poisson regression of lichen species number on different types of substrates depending on log-transformed variables of 'Area', 'No. of biotopes' and 'Distance'. The significance test of slope: * ($p<0.05$), ** ($p<0.01$), *** ($p<0.0001$), ns – non significant.

Substrate type	Area		No. of biotopes		Distance	
Coniferous trees	0.382	*	2.600	***	–0.683	***
Deciduous trees	0.091	ns	2.347	***	0.132	ns
Dead wood	1.644	***	0.081	ns	–0.394	*
Granite	0.237	ns	1.261	***	–0.176	*
Limestone	0.331	ns	1.790	***	–0.239	ns
Lichens	0.675	ns	3.695	**	–0.866	**
Soil	0.927	**	3.712	**	–0.500	*

Table 6. The test results of the logistic regression analysis (in GLIM) on the dependence of species occurrences on log-transformed islet traits. Species occurring on at least 20% of islets were included in the analysis.

Variable	df	Wald statistic	*p*
Area	1	5.26	**0.0218**
No. of biotopes	1	67.39	**0.0001**
Distance	1	9.71	**0.0018**
Species	74	179.06	**0.0001**
Species*Area	74	102.16	**0.0167**
Species*No. of biotopes	74	156.93	**0.0001**
Species*Distance	74	137.70	**0.0001**

Table 7. The test of species-specific relations of species abundances to the islet traits in the MIXED model analysis. Islet parameters are log-transformed as independent variables. 'Species' was treated as a fixed factor and 'Islet' as random factor in the model. Species occurring on at least 20% of islets were included in the analysis.

Variable	df	*F*	*p*
Area	1; 2715	39.07	**0.0001**
No. of biotopes	1; 2715	46.15	**0.0001**
Distance	1; 2715	0.31	0.5765
Species	99; 2715	1.22	0.0708
Species*Area	99; 2715	1.19	0.1023
Species*No. of biotopes	99; 2715	2.37	**0.0001**
Species* Distance	99; 2715	2.27	**0.0001**

Table 8. The significant relationships ($p<0.05$) between species occurrence and abundance and islet traits, according to the results of logistic regression in GLIM and MIXED model (see Table 6 and 7). A statistically significant effect is denoted by a sign of a slope parameter in a model. Abbreviations of factors: 'Area' – area, 'Biot.' – number of biotopes, 'Dist.' – distance from the mainland. Abbreviations of substrate types: 'D' – Deciduous trees, 'C' – Coniferous trees, 'G' – Granite, 'L' – Limestone, 'S' – Soil, 'W' – Dead wood.

Lichen taxa	Logistic regression analysis (in GLIM)			MIXED model analysis			Substrate type
	Area	Biot.	Dist.	Area	Biot.	Dist.	
Acarospora veronensis			–			–	G
Amandinea coniops			–				G
A. punctata		+	–		+	–	D, C, G, W
Aspicilia cinerea		+		+	+		G
A. contorta spp. *hoffmanniana*		+	–				L
Buellia griseovirens				+	+		D, C, W
Caloplaca citrina						+	G, L, W
C. holocarpa		+			+		G, L
Candelariella aurella	+			+			L
C. coralliza	+			+	+		G
C. vitellina		+		+			L
Cetraria islandica				+			S
C. sepincola				+			D, C, W
Cladonia coniocraea				+			W
C. fimbriata				+			W, S
C. furcata				+			S
C. subrangiformis				+			S
Evernia prunastri				+	+		D, C
Hypogymnia physodes				+	+	–	D, C, G, W
H. tubulosa				+		–	D, C, W
Lecanora albescens		+					L
L. andrewii		+					G, W
L. carpinea		+			+	+	D, C
L. cenisia		+					G
L. chlarotera					+		D, C
L. dispersa	+			+			L
L. hagenii	+			+			D, C, W
L. muralis					+		G
L. helicopis						+	G
L. leptyrodes		+					D
L. polytropa		+					G
L. pulicaris		+		+	+	–	D, C, W
L. rupicola				+	+		G
L. saligna							W, D
L. sulphurea		+			+		G

L. symmicta				+			D, C, W
L. varia	+		–	+			D, C, W
Lecidea fuscoatra				+			G
L. lapicida var. *pantherina*		+	–		+		G
Lecidella elaeochroma					+		D, C, W
L. carpathica			–				G
L. stigmatea		+					L, G
Lepraria incana						+	D, C, G, W
Melanelia exasperata		+	–				D, C
M. fuliginosa		+		+	+		D, G
M. olivacea				+			D, C
Neofuscelia loxodes	+			+	+		G, W
N. pulla		+		+	+		G
Parmelia saxatilis		+	–	+	+		G, D, C
P. sulcata				+	+	–	D, C, W
Parmeliopsis ambigua				+		–	D, C, W,
Peltigera rufescens				+			S
Phaeophyscia orbicularis	+						D, G, L
Phlyctis argena		+			+	+	D, C
Physcia adscendens		+			+		D, C, W
P. caesia	+			+			G, L
P. dubia			–				D, C, G, W
P. stellaris		+			+	+	D, C
P. tenella var. *marina*			–			–	G
P. tenella var. *tenella*	+	+		+	+		D, C
Physconia distorta						+	D
Pseudevernia furfuracea				+			D, C, W
Ramalina farinacea				+	+		D, C
R. fastigiata	+			+	+		D, C
R. fraxinea		+			+		D, C
Rhizocarpon distinctum		+			+		G
Rinodina gennarii			+			+	G
R. sophodes		+	–				D, C
Scoliciosporum chlorococcum			–				D, C, W
Tephromela atra		+		+	+		G, D
Trapeliopsis flexuosa	+			+			W, C
Tuckermannopsis chlorophylla				+		–	D, C, W
Verrucaria muralis		+					L
V. nigrescens		+		+			L
Vulpicida pinastri				+			W, C
Xanthoria candelaria	+	+	–	+	+	–	G, W
X. polycarpa		+					D, C
Xanthoparmelia conspersa		+		+	+		G

Fig. 1. Location of studied islets in the West-Estonian Archipelago, Estonia. Some islets are noted with numbers: 1 – Kivirahu, Hoburahu, Sitakare, Valgekare, Väike-Pihlakare, and Suur-Pihlakare; 2 – Pähkrahu, Säinarahu, Kajakarahu, and Palgirahu; 3 – Luigerahu.

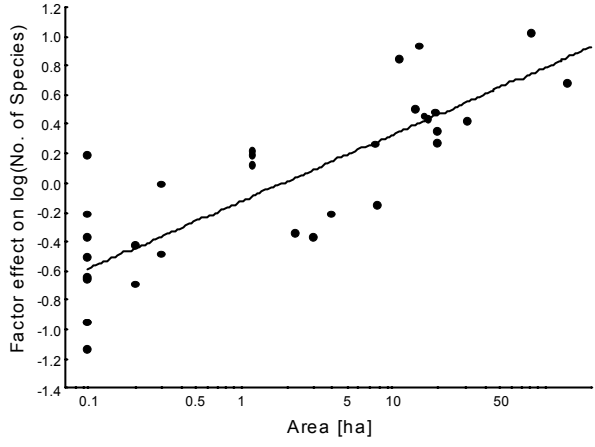

Fig. 2. The effect of islet area on log-number of species on islet, presented as model semi-residuals of species richness conditioning on the other two factors in the model (see Table 3).

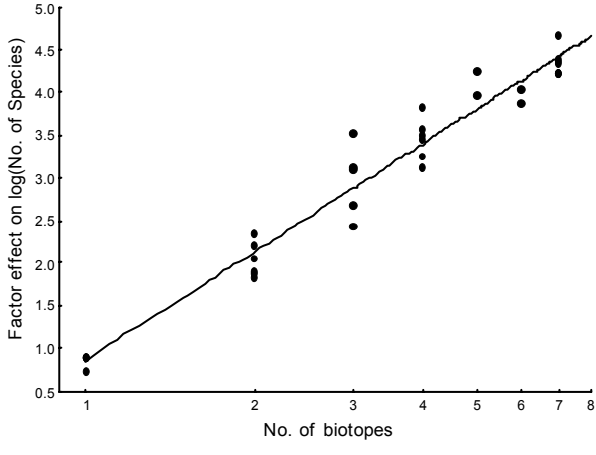

Fig. 3. The effect of number of biotopes on log-number of species on islet, presented as model semi-residuals of species richness conditioning on the other two factors in the model (see Table 3).

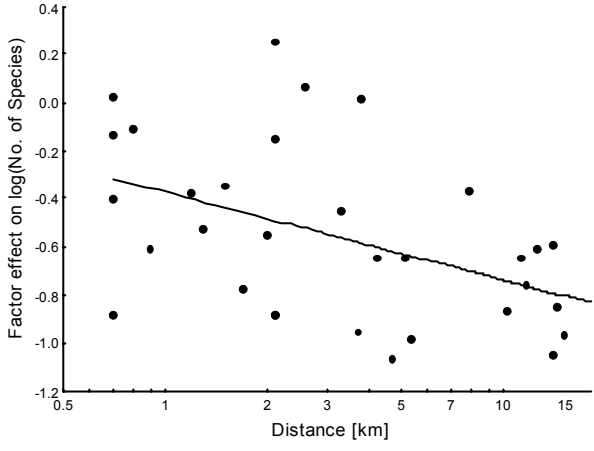

Fig. 4. The effect of distance on log-number of species on islet, presented as model semi-residuals of species richness conditioning on the other two factors in the model (see Table 3).

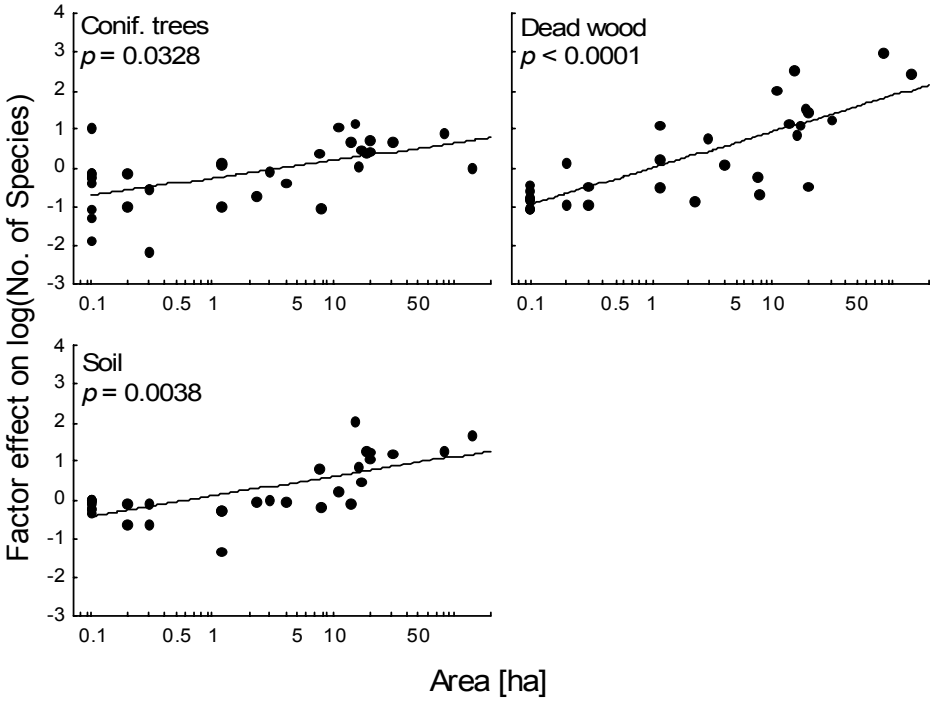

Fig. 5. The effect of islet area on log-number of species in substrate types, presented as model semi-residuals of species richness conditioning on the other two factors in the model GLIM analysis (see Table 4 and 5). Figures are presented only for substrate types where the relationship was significant. Abbreviation of substrate type: 'Conif. trees' – Coniferous trees.

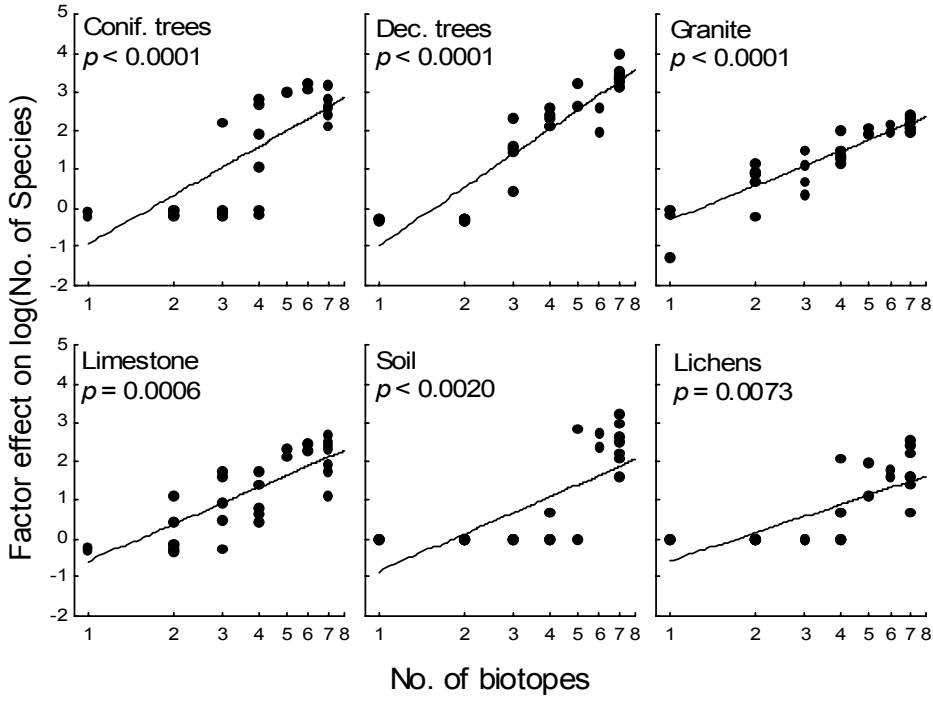

Fig. 6. The effect of the number of biotopes on log-number of species in substrate types, presented as model semi-residuals of species richness conditioning on the other two factors in the model GLIM analysis (see Table 4 and 5). Figures are presented only for substrate types where the relationship was significant. Abbreviations of substrate types: 'Dec. trees' – Deciduous trees, 'Conif. trees' – Coniferous trees.

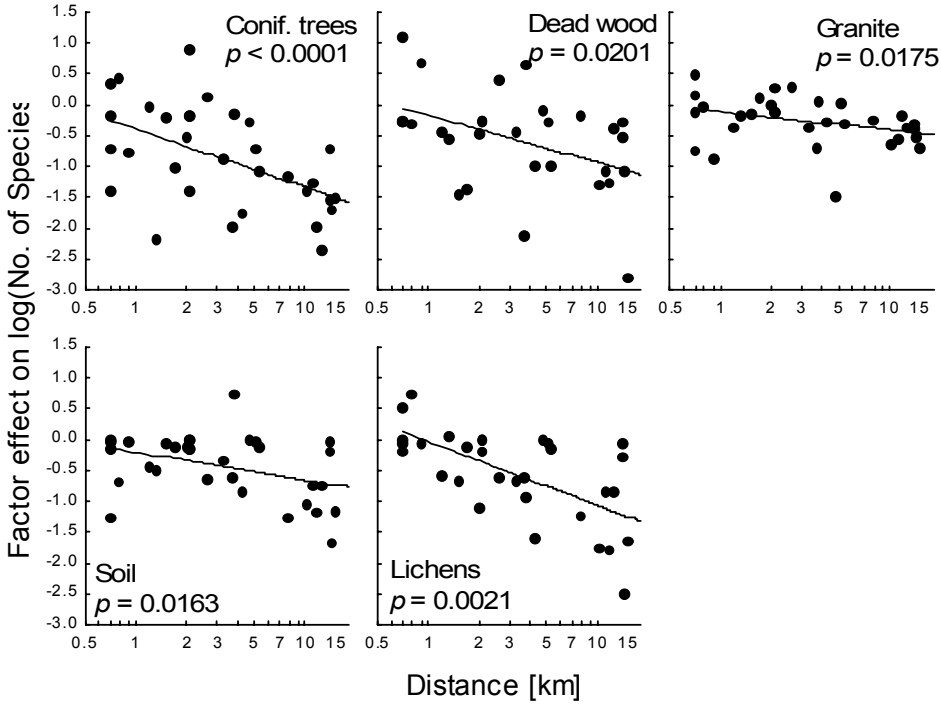

Fig. 7. The effect of the distance on log-number of species in substrate types, presented as model semi-residuals of species richness conditioning on the other two factors in the model GLIM analysis (see Table 4 and 5). Figures are presented only for substrate types where the relationship was significant. Abbreviation of substrate type: 'Conif. trees' – Coniferous trees.

CHARACTER STUDY OF SOME TWO-CELLED SPECIES OF THE LICHENICOLOUS GENUS *ABROTHALLUS*

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Abstract: The variation of 68 samples of the exclusively lichenicolous genus *Abrothallus* De Not. was studied by means of multivariate statistical approach (discriminant analysis). The samples were analysed in order to estimate the possible taxonomic implications of frequent in literature used. The colour of the crystalline layer above the hymenium, pruinosity of the ascomata and Lugol reaction of the hyphae appeared to be the most reliable features for "species" recognition. For some taxa, the measurements of ascospores and conidia were also important.

Key words: *Abrothallus*, character, host specificity

1. INTRODUCTION

The ascomycetous genus *Abrothallus* was introduced by G. de Notaris (1845) to accommodate a single species, *Abrothallus bertianus*. However, the genus was originally described as a lichen genus because of the misinterpretation of the host thallus. A few years later it was confirmed to be a lichenicolous fungus (Montagne 1851). Still, even in the subsequent studies, *Abrothallus* was included either in *lichenes athallii* (Tulasne 1852) or *microlichens* (Lindsay 1857, 1869).

The question about the systematic position of *Abrothallus* has remained unclear due to the fact that the genus has no coherent affinities to other genera. The relationship to family Phacidiaceae (Saccardo 1889) or to orders Arthoniales (Jatta 1911; Bellemere et al. 1986) and Patellariales (Keissler 1929; Nannfeldt 1932) has been proposed. Still, in the modern classification systems of Ascomycota (Kirk et al. 2001; Eriksson et al. 2004), the position of the *Abrothallus* remains uncertain.

Various taxa have been introduced within the genus, many of which have later been transferred to other genera, for example to *Arthonia*, *Clypeococcum*, *Dactylospora*, *Phacopsis*, etc. (e.g. Zahlbruckner 1924, 1931; Hawksworth 1977; Hafellner 1979; Triebel & Rambold 1988). According to the current circumscription, the genus comprises 21 species (Table 1), known on a wide range of hosts, especially on Parmeliaceae (e.g. *Melanelia*, *Parmelia*, *Platismatia, Usnea,* etc.), but also Lobariaceae (*Sticta*, *Nephroma, Pseudo-*

cyphellaria), Ramalinaceae (*Ramalina*), Stereocaulaceae (*Stereocaulon*) and Cladoniaceae (*Cladonia*). The genus is cosmopolitan, known in the Arctic (Alstrup & Hawksworth 1990) as well as in the tropical regions (Wedin 1994; Etayo 2002).

The genus is rather well defined by its morphological characters: (1) globose or almost globose immarginate ascomata, sometimes with green pruina; (2) bitunicate asci with eight ascospores; (3) brown, 2- to 4-celled, warted asymmetric ascospores; (4) ramified-anastomosed paraphyses and (5) coloured, crystalline layer above the hymenium which dissolves in potassium hydroxide (KOH) (Figs. 1–3). In many cases, pycnidia of the *Vouauxiomyces*-type have been found mixed with the ascomata. Already in 1852 L.-R. Tulasne proposed that the pycnidia represent an imperfect state of the *Abrothallus*.

Despite the clear distinction of the genus, the subgeneric division has been a subject of dispute (Lindsay 1857; Kotte 1909; Keissler 1929; Santesson 1960) and of different interpretation (Hawksworth 1983; Clauzade et al. 1989; Santesson 1993; Santesson et al. 2004) for a long time: both broad (e.g. Keissler 1929; Hawksworth 1983; Santesson 1993) and narrow approach for species' distinction has been used (e.g. Kotte 1909; Clauzade et al. 1989; Santesson et al. 2004). The confusion is caused by different level of significance attributed to relevant characters by various authors. For example, I. Kotte (1909) emphasized the importance of iodine reaction of the vegetative hyphae, dimensions of ascospores and conidia as well as the preference to certain host as diagnostic features for species delimitation. In contrast, K. Keissler (1929) denied the relevancy of iodine reaction and host preference, using characters like presence of greenish pruina over the ascomata, colour of the epithecium and reaction of hymenium with KOH instead. In the most recent complex treatment of lichenicolous fungi (Clauzade et al. 1989), the authors returned to the narrow concept of species proposed by I. Kotte (1909), applying however, some additional characters used by K. Keissler (1929) as pruinosity of the ascomata, hymenium reaction with KOH, etc.

This study is a first step towards the assessment of the status of some 2-celled species of *Abrothallus* as to the characters and their relative importance in the studied genus. The aim of the present study is to elucidate the value of the frequently used characters of the genus.

2. MATERIALS AND METHODS

2.1. Materials

Dried herbarium specimens (C, H, S, TU, UPS, UGDA-L) were used for the analysis of morphological features. The quantity of the material from different hosts and the availability of healthy specimens were the main criteria for material selection. In the final analysis, 68 specimens from eight different hosts were exploited. The main criterion for group separation was host specificity: (1)

specimens on *Hypogymnia physodes* (in the further text *Hyp)*; (2) on *Melanelia* spp. (*Mel*); (3) on *Parmelia* spp. (*Par*); (4) on *Platismatia* spp. (*Pla*); (5) on *Sticta* spp. (*Sti*); (6) on *Usnea* spp. *(Usn);* (7) on *Vulpicida* spp. (*Vul*); (8) on *Xanthoparmelia* spp. *(Xan*).

2.2. Microscopy

The character examination was carried out with the stereomicroscope TECHNIVAL 2 (Carl Zeiss Jena) (magnifications –x50) and with a light microscope Olympus CX41 (magnifications –x1200). Routine methods of light microscopy were used: cross-sections were made with the razor blade, at first the sections were mounted in tap water and later in ca 10% KOH (K) or Lugol's solution (I; Fluka 62650). All measurements were implemented in the water medium. Photographs were taken with an Olympos Camedia Z4040 digital camera.

2.3. Characters

Morphological characters for the analysis were selected according to the of diagnostic characters proposed in the earlier studies (Kotte 1909; Hawksworth 1983; Diederich 1989; Clauzade et al. 1989). The number of characters was higher initially but some of them (ascus dimensions, hymenium height) were not used later. The reaction with K, which has been considered to be important in species delimitation, was excluded because of the rather constant positive reaction shown on most of the studied specimens. The only difference was observed in its intensity (comments also in Calatayud & Barreno 1995). In addition, the microscopical characters of the coniodiomata have not been taken into account as the pycnidia appeared rather scanty or the conidiomata were mostly empty in older herbarium specimens. Still, the exception was made for *Vul* and *Xan*, on which the conidiomata appeared rather constantly. The shape of the ascomata was visually appraised by the dominance of either flattened or globose type. For every specimen, the ascomata, ascospores and conidia were measured at least in ten replications. The width of the ascospores was measured from two points and treated as two separate characters. Altogether four quantitative and six qualitative characters and one calculated ratio were finally used. In addition, the character "Host" (for abbreviations see "Materials") was used as a grouping variable in the further analysis.

List of the characters used and their abbreviations:

1. ASCD – diameter of the ascoma (mm)
2. ASLEN – length of ascospore (μm)
3. ASWI1 – width of the upper cell of the ascospore (μm)
4. ASWI2 – width of the lower cell of the ascospore (μm)
5. ASRA – the ratio of the ascospore length and upper cell width
6. HYMCO – colour of the crystalline layer above the hymenium (0 – red; 1 – brown)

7. LUG – reaction with the Lugol's solution (0 – reaction negative; 1 – reaction positive)
8. CONID – absence or presence of the conidomata (0 – absence; 1 – presence)
9. ASCP – pruinosity of the ascomata (0 – without green pruina; 1 – with green pruina)
10. HYPCOL – colour of the hypothecium (0 – dark brown; 1 – brown; 2 – light brown)
11. ASCS – shape of the ascomata (0 – globose; 1 – flattened)

2.4. Statistical methods

In order to test the concordance of the conventional and predicted identification of individuals, the classificatory discriminant analysis (CDA) with direct method was implemented with Statistica 6.5 (Statsoft Inc. 2003). In CDA, the character "Host" was chosen as a grouping variable. The descriptive statistics (mean, minimum and maximum values and standard deviation) were calculated for each specimen and for each quantitative character. The Student's t-test was applied for comparison of mean values of quantitative characters.

3. RESULTS

The distribution of qualitative characters is presented in Table 2 and descriptive statistics (mean, minimum and maximum values and standard deviation) of quantitative characters in Table 3.

The results of the classificatory discriminant analysis (CDA) showed a classification accuracy of 79.4% (Table 4). According to the CDA, 12 of the total 68 individuals were re-classified into another species. The lowest share of the classification accuracy was observed at *Pla* (60%), of which two misclassified specimens were mixed with the *Par* and the other two with *Vul* and *Hyp.* The two misclassified specimens of *Vul* fell into the *Xan* and *vice versa*. On the contrary, the distinction of *Hyp*, *Mel*, *Usn* and *Sti* from the rest was obvious: the proportion of the correctly classified specimens was from 90% (*Mel*) to 100% (*Usn, Hyp*, *Sti*).

Five characters out of the eleven used appeared to be the most reliable in distinguishing taxa of *Abrothallus*. The most important features (listed with descending order) in taxon separation were HYMCO (colour of the crystalline layer above hymenium), LUG (Lugol reaction), ASCP (pruinosity of ascomata), HYPCOL (colour of hypothecium) and ASCS (shape of the ascomata) (Table 5). According to the CDA results, the quantitative characters were not statistically significant for taxon separation (Table 5).

The colour of the crystalline layer above hymenium (HYMCO) had the highest discriminative ability. This two-mode appraised character showed almost no variation within species: the reddish colour of the layer occurred in

all specimens of *Usn* and *Hyp*, separating them from the rest possessing brownish layer (Table 2).

Another character with a high discriminative power was the presence or absence of green pruina (ASCP). Four groups (*Hyp*, *Usn*, *Vul* and *Xan*) out of the eight were characterized by the absence and one group (*Sti*) by the presence of this character (Table 2). Still, the situation was more complicated with *Mel*, *Par* and *Pla* on which the pruinose ascomata were usual, however, not constantly observed. It is notable that the greenish pruina was best developed on the younger ascomata and could not always be observed on the older ones.

The reaction of vegetative hyphae with Lugol reactive (LUG) has been widely used as a taxonomic character. The clear presentation of this feature was obvious also in this study: the positive reaction was always noticed by *Sti*, *Usn*, *Vul* and *Xan*, but never by *Hyp.* However, there was not so clear distinction by *Mel*, *Pla* and *Par*: the hyphae of most *Mel* and *Pla* specimens and only half of *Par* reacted with the Lugol reagent (Table 2).

The shape of the ascomata (ASCS), which was estimated to be either flattened or globose, showed significant variation within the groups. Still, at least in some cases, there were clear tendencies towards having either one or another type: only flattened ascomata by *Sti* and *Pla* and only globose by *Usn* (Table 2).

Finally, the intensity of hypothecium pigmentation (HYPCOL) varied also between and within the groups. Still, there were two taxa on which the share of pigmentation was obvious: *Xan* with remarkably dark hypothecium and *Pla* with light hypothecium.

According to CDA, quantitative characters such as size of ascomata, ascospore length and width were not useful for taxon separation because of the clear overlapping in their ranges (Table 3). Still, for some taxa the Student's t-test showed a statistically significant ($p < 0.05$) distinction (Table 7). The specimens of *Sti* differed from all others according to all quantitative characters: the mean values of both ascomata and ascospores were larger than those on the rest of taxa (Table 3). There was also an intrinsic differentiation of *Usn* and *Vul* by ascospore dimensions: the ascospores were on average smaller than those in other species (Table 6), but, there was no significant distinction between *Vul* and *Usn* revealed.

Although the size of conidia has been considered to be a distinctive character at least for some taxa, in the studied material, only *Vul* and *Xan* possessed enough mature conidiomata to test their discrepancy. According to the t-test, the differentiation of the conidia between these two groups was statistically significant: the conidia of *Xan* were longer and slender in contrast to *Vul*, on which the conidia were shorter and thicker (Table 7).

4. DISCUSSION

The genus *Abrothallus* containing exclusively lichenicolous taxa is a rather well known and widespread genus which shows almost no phylogenetic affinities to other taxonomic entities. Despite the distinctness of the genus, the species delimitation is still a subject of interpretation. For this preliminary study, eight conventionally identified taxa were tested to estimate the value of characteristics used in previous studies (Kotte 1909; Keissler 1929; Hawksworth 1983; Clauzade et al. 1989; Diederich 1989). Host species served as a diagnostic character of crucial importance.

The statistical analyses demonstrated that at least six groups (*Usn*, *Sti*, *Mel, Hyp, Vul* and *Xan*) out of the eight studied can be well defined by the proposed characters. On the contrary, the separation of *Pla* and *Par* is more complicated and further examination is needed.

Two of the characters, the presence of the green pruina over the ascomata and the amyloid reaction of vegetative hyphae which are considered in most of the studies (e.g. Kotte 1909; Keissler 1929; Hawksworth 1983; Clauzade et al. 1989) showed more variation as expected prior to the study. The presence of the greenish pruina which has been considered to be one of the main diagnostic characteristics in *Abrothallus* (Keissler 1929; Hawksworth 1983; Clauzade et al. 1989), seems to be mainly applicable to younger ascomata (see note in Hawksworth 1983). In addition, on older herbarium specimens, the pruina might be swept off in the course of time. The problems with pruina as a taxonomic character have also been pointed out in lichenized fungi studies (Heidmarsson 1996). Hence, even if the character itself seems to be advantageous, one has to be careful when applying it.

The colour reactions with iodine solutions as diagnostic markers has been routinely used in systematics of non-lichenized and lichenized fungi (reviews in Baral 1987; Common 1991). In *Abrothallus* systematics, the reaction of vegetative hyphae with Lugol reactive has been applied to subgeneric division since the dissertation by I. Kotte (1909). At the same time, the exploitation of the amyloid reaction in separation of *Abrothallus* species has been questioned in some earlier studies (Schaechtelin & Werner 1927; Keissler 1929), partly because of the difficulties in observation (Schaechtelin & Werner 1927). Considering the studied material, the presence or absence of the amyloid reaction seems to be an applicable feature in taxon delimitation. Still, there was one exception: *Par* included specimens with positive and negative reaction more or less equally, which may indicate that more than one *Abrothallus* species can grow on host genus *Parmelia.*

The data on the ascospore dimensions vary in literature because of the different concepts of species used (e.g. Kotte 1909; Hawksworth 1983; Diederich 1989) or overly generalized data (Clauzade et al. 1989). These reasons make the comparison of ascospores variation rates difficult or even impossible. According to the data presented, the length and width and the

length-width ratio of ascospores serve as good characters for some "species" (*Sti*, *Usn*, *Vul*).

It has been proposed, that the conidiomata referred to as anamorph-genus *Vouauxiomyces* represent an asexual stage of *Abrothallus* (Tulasne 1852; Kotte 1909; Galløe 1950; Nordin 1964; Hawksworth 1981; Wedin 1994). However, this evidence is based on the frequent co-occurrence of ascomata and conidiomata and has not yet proved by supplementary culture experiments. At the same time, the anamorph may also appear regularly without teleomorph (Hawksworth 1981; Kondratyuk 1996). Considering literature (Kotte 1909; Hawksworth 1981, 1983; Clauzade et al. 1989) and also the present data, the characters originating from the imperfect state of *Abrothallus* are also acceptable in delimitation of taxa. In the present study the distinction between *Vul* and *Xan* by the size (and shape) of conidia was more evident than by the characters of ascomata.

5. CONCLUSIONS

The present analysis based on 68 samples from eight host genera, showed a clear tendency towards the host-specificity in the exclusively lichenicolous genus *Abrothallus*. This resolution, however, was not so obvious for some "species" (*Par* and *Pla*).

The usefulness of several anatomical-morphological characters (i.e. pruinosity of ascomata, amyloid reaction of hyphae, colour of the layer above the hymenium) for taxon separation was supported by the discriminant analysis. In addition, for recognition of *Abrothallus* on *Sticta* spp., *Vulpicida* spp. and *Usnea* spp., the measurements and the shape of ascospores were significantly statistically important. For distinguishing between *Abrothallus* on *Vulpicida* spp. and on *Xanthoparmelia* spp., the anamorph characters appeared to be better indicators than the teleomorph characters.

The results obtained correspond well with the contemporary views of the high host-specificity of the lichenicolous fungi (Lawrey & Diederich 2003). However, for further details of the complicate taxonomy of *Abrothallus,* more material from different host lichens and more specific characters (e.g. DNA sequences, anamorph characteristics) as well as aspects of pathogenity should be applied.

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REFERENCES

Alstrup, V. & Hawksworth, D. L. 1990: The lichenicolous fungi of Greenland. *Meddel. Grønl., Biosci.* 31: 1–90.

Baral, H. O. 1987: Lugol's solution/IKI versus Melzer's reagent: hemiamyloidity, a universal feature of the ascus wall. *Mycotaxon* 29: 399–450.

Bellemere, A., Malherbe, M. C., Chacun, H. & Hafellner, J. 1986: Etude ultrastructurale des asques et des ascospores chez les especes lichenicoles non lichenisees *Abrothallus bertianus* de Not. et *A. parmeliarum* (Sommerf.) Nyl. *Cryptog., Mycol.* 7: 47–85.

Calatayud, V. & Barreno, E. 1995: Lichenicolous fungi from the Iberian Peninsula and the Canary Islands. II. *In:* Daniëls, F. J. A., Schulz, M. & Peine, J. (eds.): *Flechten Follmann. Contributions to lichenology in Honour of Gerhard Follmann*: 397–402. Geobotanical and Phytotaxonomical Study Group, Botanical Institute, University of Cologne, Cologne.

Clauzade, G., Diederich, P. & Roux, C. 1989: Nelikenigintaj fungoj likenlogaj. Ilustrita determinlibro. *Bull. Soc. Linn. Provence, Numero Special* 1: 1–42.

Cole, M. S. & Hawksworth, D. L. 2001: Lichenicolous fungi, mainly from the USA, including *Patriciomyces* gen. nov. *Mycotaxon* 77: 305–338.

Common, R. S. 1991. The distribution and taxonomic significance of lichenan and isolichenan in the Parmeliaceae (lichenized Ascomycotina), as determined by iodine reactions. I. Introduction and methods. II. The genus *Alectoria* and associated taxa. *Mycotaxon* 41(1): 67–112.

De Notaris, G. 1845: *Abrothallus* novum lichenum genus. *Mem. Reale Accad. Sci. Torino* ser. 2, 10: 351–355.

Diederich, P. 1989: *Les Lichens Epiphytiques et leurs Champignons Lichenicoles (Macrolichens Exceptes) du Luxembourg*. Travaux Scientifiques de Musee National d'Histoire Naturelle de Luxembourg, Ministere des Affairs Culturelles, Luxembourg.

Diederich, P. 1990: New or interesting lichenicolous fungi 1. Species from Luxembourg. *Mycotaxon* 37: 297–330.

Diederich, P. 2003: New species and new records of American lichenicolous fungi [Neue Arten und neue Funde von amerkanischen lichenicolen Pilzen]. *Herzogia* 16: 41–90.

Eriksson, O. E., Baral, H.-O., Currah, R. S., Hansen, K., Kurtzman, C. P., Rambold, G. & Laessøe, T. 2004: Outline of Ascomycota. *Myconet* 10, Feb. 26, 2004. http://www.umu.se/myconet/M10a.html

Etayo, J. 2002: *Aportación al Conocimiento de los Hongos Liquenícolas de Colombia*. *Biblioth. Lichenol*. 84, J. Cramer, Berlin, Stuttgart.

Galløe, O. 1950: *Natural History of the Danish Lichens. Part VIII*. E. Munksgaard, Copenhagen.

Hafellner, J. 1979: *Karschia*. Revision einer Sammelgattung an der Grenze von lichenisierten und nichtlichenisierten Ascomyceten. *Beih. Nova Hedwigia* 62: 1–248.

Hafellner, J. 1994: Beiträge zu einem Prodromus der lichenicolen Pilze Österreichs und angrenzender Gebiete. I. Einige neue oder seltene Arten [Contributions to a prodromus of the lichenicolous fungi of Austria and adjacent areas. I. Some new or rare species]. *Herzogia* 10: 1–28.

Hawksworth, D. L. 1977: Three new genera of lichenicolous fungi. *Bot. Jour. Linn. Soc.* 75: 195–209.

Hawksworth, D. L. 1981: The lichenicolous Coelomycetes. *Bull. Br. Mus. Nat. Hist.* 9(1): 1–98.

Hawksworth, D. L. 1983: A key to the lichen-forming, parasitic, parasymbiotic and saprophytic fungi occurring on lichens in the British Isles. *Lichenologist* 15: 1–44.

Hawksworth, D. L. 1990: Notes on British lichenicolous fungi: VI. *Notes Roy. Bot. Gard. Edinburgh* 46(3): 391–403.

Heidmarsson, S. 1996: Pruina as a taxonomic character in the lichen genus *Dermatocarpon*. *Bryologist* 99(3): 315–320.

Jatta, A. 1911: Lichenes (end). *Flora Italica Cryptogama, Firenze* Pars III, Fasc. 4–6: 461–958.

Keissler, K. 1930: D*ie Flechtenparasiten Deutschlands, Österreichs und der Schweiz mit Berücksichtigung der übrigen Länder Europas sowie der angrenzenden Meeresgebiete*.

Kirk, P. M., Cannon, P. F., David, J. C., Stalpers, J. A. (eds.) 2001: *Ainsworth and Bisby's Dictionary of the Fungi*, 9th Edition. CABI Publishing.

Kirschstein, W. 1935: Neue und seltene Ascomycten. *Ann. Myc*. 33, Berlin.

Kondratyuk, S. Y. 1996: New species of *Pronectria*, *Vouauxiomyces*, *Wentiomyces* and *Zwackhiomyces* from Australasia. *Muelleria* 9: 93–104.

Kotte, I. 1909: Einige neue Fälle von Nebensymbiose (Parasymbiose). *Zentralbl. Bakteriol., Parasitenkd. II* 24: 74–93.

Lawrey, J. D. & Diederich, P. 2003: Lichenicolous fungi: interactions, evolution, and biodiversity. *Bryologist* 106(1): 81–120.

Lindsay, W. L. 1857: Monograph of the genus *Abrothallus*. (De Notaris and Tulasne emend.). *Quarterly J. microscop. Sci.* 5: 27–63.

Lindsay, W. L. 1869: Enumeration of Micro-lichens on other lichens. *Quaterly J. Microsc. Sci* 9: 49–57.

Montagne, C. 1851: Cryptogamia Guyanensis seu plantarum cellularium in Guyana gallica annis 1835–1849 a cl. Leprieur collectarum enumeratio universalis. suite. *Ann. Sci. Nat.* 16: 47–81.

Nannfeldt, J. A. 1932: *Studien über die Morphologie und Systematik der Nicht-Lichenisieren inoperculaten Discomycetes*. Uppsala. Inaugural Dissertatsion.

Nordin, I. 1964: *Abrothallus suecicus*, a common lichenicolous fungus. *Svensk Bot. Tidskr.* 58(1): 225–232.

Rabenhorst, L. 1845: *Deutschlands Cryptogamen-Flora*. Leipzig

Saccardo, P. A. 1889: *Sylloge fungorum*.

Santesson, R. 1960: Lichenicolous fungi from Northern Spain. *Svensk Bot. Tidskr.* 54(4): 499–522.

Santesson, R. 1993: *The Lichens and Lichenicolous Fungi of Sweden and Norway*. SBT-förlaget, Lund.

Santesson, R., Moberg, R., Nordin, A., Tønsberg, T. & Vitikainen, O. 2004: *Lichen-forming and Lichenicolous Fungi of Fennoscandia*. Museum of Evolution, Uppsala University, Uppsala, Sweden.

Schaechtelin, J. & Werner, R. G. 1927: Développement et biologie de l'*Abrothallus parmeliarum* Smft. *Bull. Soc. Mycol. France* 42: 233–243.
Sommerfelt, S. C. 1826: *Supplementum Florae Lapponicae*. Christiania.
Stein, B. 1879: Flechten. *In*: *Kryptogamen-Flora von Schlesien*. Im Namen der Schles. Ges. f. vaterländ. Kultur herausgeg. v. Prof. Dr. Ferd. Cohn. *Jahresber. Schles. ges. f. vaterl. Cultur* 2: 1–400.
Triebel, D. & Rambold, G. 1988: *Cecidonia* und *Phacopsis* (Lecanorales): zwei lichenicole Pilzgattungen mit cecidogenen Arten. *Nova Hedwigia* 47(3–4): 279–309.
Tulasne, L.-R. 1852: Mémoire pour servir à l'histoire organographique et physiologique des lichens. *Ann. Sci. Nat.* 17: 5–128.
Wedin, M. 1994: New and noteworthy lichenicolous fungi from southernmost South America. *Lichenologist* 26(3): 301–310.
Zahlbruckner, A. 1925: *Catalogus Lichenum Universalis*. 2 Bd. Borntraeger, Leipzig.
Zahlbruckner, A. 1931: *Catalogus Lichenum Universalis*. 7 Bd. Borntraeger, Leipzig.

Table 1. Accepted species of the genus *Abrothallus* together with the references of the original species descriptions.

Taxon name	Reference
A. acetabuli Diederich	Diederich (1990)
A. bertianus De Not.	De Notaris (1845)
A. bryorianum Hafellner	Hafellner (1994)
A. caerulescens Kotte	Kotte (1909)
A. cetrariae Kotte	Kotte (1909)
A. cladoniae R. Sant. & D. Hawksw.	Hawksworth (1990)
A. granulatae Wedin	Wedin (1994)
A. hypotrachynae Etayo & Diederich	Etayo (2002)
A. microspermus Tul.	Tulasne (1852)
A. parmeliarum (Sommerf.) Nyl.	Sommerfelt (1826)
A. parmotrematis Diederich, ined.	Clauzade et al. (1989), not validly published
A. peyritschii (Stein) Kotte	Stein (1879)
A. pezizeicola Diedrich	Diederich (2003)
A. prodiens (Harm.) Diederich	Harmand (1898)
A. secedens Wedin & R. Sant.	Wedin (1994)
A. stereocaulorum Etayo & Diederich	Etayo (2002)
A. stictarum Etayo	Etayo (2002)
A. suecicus (Kirschst.) Nordin	Kirschstein (1935)
A. tulasnei M.S. Cole & D. Hawksw.	Cole & Hawksworth (2001)
A. usneae Rabenh.	Rabenhorst (1845)
A. welwitschii Mont.	Montagne (1851)

Table 2. Distribution of qualitative characters. Abbreviations of group names and characters see 'Materials and methods'; pos. – positive, neg. – negative, d. brown – dark brown, l. brown – light brown.

	HYMCO		LUG		CONID		ASCP		HYPCOL		ASCS	
Hyp												
(n=4)	red	4	neg.	4	absence	3	without	4	d. brown	2	globose	2
	brown	0	pos.	0	presence	1	with	0	brown	0	flattened	2
									d. brown	2		
Mel												
(n=10)	red	0	neg.	1	absence	2	without	7	d. brown	3	globose	9
	brown	10	pos.	9	presence	8	with	3	brown	1	flattened	1
									l. brown	6		
Par												
(n=18)	red	2	neg.	8	absence	11	without	14	d.brown	6	globose	2
	brown	16	pos.	10	presence	7	with	4	brown	5	flattened	16
									l. brown	7		
Pla												
(n=10)	red	3	neg.	1	absence	5	without	3	d. brown	0	globose	0
	brown	7	pos.	9	presence	5	with	7	brown	4	flattened	10
									l. brown	6		
Sti												
(n=4)	red	0	neg.	0	absence	2	without	0	d. brown	1	globose	0
	brown	4	pos.	4	presence	2	with	4	brown	2	flattened	4
									l. brown	1		
Usn												
(n=6)	red	6	neg.	0	absence	0	without	6	d. brown	4	globose	6
	brown	0	pos.	6	presence	6	with	0	brown	0	flattened	0
									l. brown	2		
Xan												
(n=7)	red	0	neg.	0	absence	1	without	7	d. brown	7	globose	0
	brown	7	pos.	7	presence	6	with	0	brown	0	flattened	7
									l. brown	0		

Table 3. Descriptive statistics (mean = arithmetic mean, min = minimal value; max = maximal value and SD = standard deviation; n = number of measurements).

Group	Character	mean	min	max	SD
Usn (n=60)	ASCD (mm)	0.26	0.1	0.5	0.11
	ASLEN (µm)	10.93	8.8	16.4	1.08
	ASWI1 (µm)	4.7	4	6.4	0.5
	ASWI2 (µm)	3.87	3.2	4.8	0.37
	ASRA	2.34	1.86	3.42	0.27
Hyp (n=40)	ASCD (mm)	0.24	0.13	0.43	0.07
	ASLEN (µm)	12.96	10.8	16	1.14
	ASWI1 (µm)	5.28	3.8	6.4	0.78
	ASWI2 (µm)	4.42	2.2	5.6	0.66
	ASRA	2.5	1.88	3.3	0.38
Mel (n=100)	ASCD (mm)	0.24	0.13	0.55	0.07
	ASLEN (µm)	12.32	8	18.3	1.65
	ASWI1 (µm)	4.68	3.6	6.4	0.58
	ASWI2 (µm)	3.94	2.9	5.4	0.55
	ASRA	2.66	1.43	3.56	0.38
Pla (n=100)	ASCD (mm)	0.31	0.13	3	0.29
	ASLEN (µm)	13.55	10.4	17.3	1.3
	ASWI1 (µm)	5.15	4	7.2	0.56
	ASWI2 (µm)	4.16	3.2	5.6	0.49
	ASRA	2.66	2	3.8	0.34
Sti (n=40)	ASCD (mm)	0.44	0.18	0.65	0.13
	ASLEN (µm)	15.14	12	19.2	1.44
	ASWI1 (µm)	6.19	5.2	8	0.63
	ASWI2 (µm)	5.12	4	6.4	0.54
	ASRA	2.46	2	3.14	0.24
Vul (n=90)	ASCD (mm)	0.23	0.13	0.43	0.06
	ASLEN (µm)	11.49	8	14.4	1.19
	ASWI1 (µm)	4.68	3.2	5.6	0.52
	ASWI2 (µm)	3.87	2.2	4.8	0.55
	ASRA	2.48	1.54	3.72	0.36
Xan (n=70)	ASCD (mm)	0.24	0.13	0.38	0.06
	ASLEN (µm)	13.7	9.7	17.6	1.46
	ASWI1 (µm)	5.36	4	7.2	0.63
	ASWI2 (µm)	4.46	3.2	5.6	0.6
	ASRA	2.58	1.75	4	0.38
Par (n=180)	ASCD (mm)	0.28	0.15	0.55	0.09
	ASLEN (µm)	14.16	9.7	19.2	1.49
	ASWI1 (µm)	5.39	4	7.2	0.69
	ASWI2 (µm)	4.4	3.2	7.2	0.68
	ASRA	2.67	1.83	4	0.42

Table 4. Classification Matrix. Rows: Observed classifications. Columns: Predicted classifications. The number in brackets after the group name corresponds to the number of specimens.

Group	% correct	*Hyp*	*Mel*	*Par*	*Pla*	*Sti*	*Usn*	*Vul*	*Xan*
Hyp (4)	100	4	0	0	0	0	0	0	0
Mel (10)	90	0	9	1	0	0	0	0	0
Par (18)	77.8	0	2	14	2	0	0	0	0
Pla (10)	60	1	0	2	6	0	0	1	0
Sti (4)	100	0	0	0	0	4	0	0	0
Usn (6)	100	0	0	0	0	0	6	0	0
Vul (9)	66.7	0	0	1	0	0	0	6	2
Xan (7)	71.4	0	0	0	0	0	0	2	5
Total	79.4	5	11	18	8	4	6	9	7

Table 5. Summary of classificatory discriminant Analysis (CDA): importance of characters in the identification of specimens. Abbreviations: ns – non-significant. Wilks' Lambda: 0.00419; approx. F (79.41)=5.9548; p<0.0000

Character	Wilks'	F-remove	p-level
ASCD	0.004861	0.86283	ns
ASLEN	0.005209	1.43631	ns
ASWI1	0.005105	1.26467	ns
ASWI2	0.005114	1.27892	ns
ASRA	0.005343	1.65681	ns
HYMCO	0.035894	51.96915	0.0000
LUG	0.007515	5.23378	0.0001
CONID	0.004545	0.34186	ns
ASCP	0.007607	5.38508	0.0001
HYPCOL	0.006948	4.29921	0.0008
ASCS	0.007263	4.81757	0.003

Table 6. The pairwise comparison of mean values (ascospore length/ascospore width/diameter of ascomata) by Student's t-test. The significance levels of different characters are separated with oblique line.
Significance levels: * = p < 0.05, ** = p < 0.01, *** = p < 0.001, ns = non-significant.

	Xan	*Vul*	*Usn*	*Sti*	*Pla*	*Par*	*Hyp*
Mel	***/***/ns	***/ns/ns	***/ns/ns	***/***/***	***/***/**	***/***/***	ns/***/ns
Xan		***/***/ns	***/***/ns	***/***/***	ns/**/**	ns/ns/***	ns/ns/ns
Vul			ns/ns/ns	***/***/***	***/***/***	***/***/***	**/***/ns
Usn				***/***/***	***/***/ns	***/***/ns	***/***/ns
Sti					***/***/***	*/***/***	***/***/***
Pla						***/**/ns	ns/ns/**
Par							**/ns/**

Table 7. Comparison of conidia in two groups.

		mean	min	max	SD
Vul (n=53)	Length	6.17	4.8	8	0.84
	Width	4.2	2.4	5.6	0.54
	Ratio	1.49	1.17	2.5	0.25
Xan (n=58)	Length	10.51	4.8	15.2	2.78
	Width	3.78	2.4	5.6	0.79
	Ratio	2.87	1.2	4.5	0.88

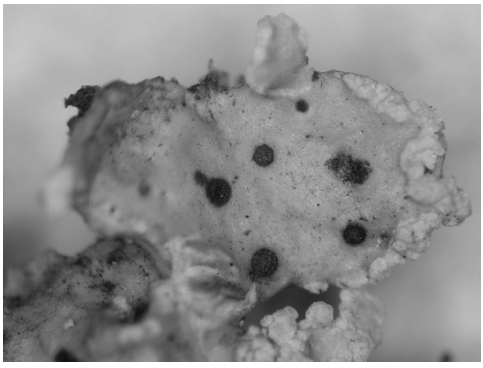

Fig. 1. Ascomata of *Abrothallus* specimen on thallus of *Vulpicida pinastri.* (Photo: A. Saag).

Fig. 2. Cross-section of *Abrothallus* specimen on *Parmelia* spp. (Photo: A. Suija).

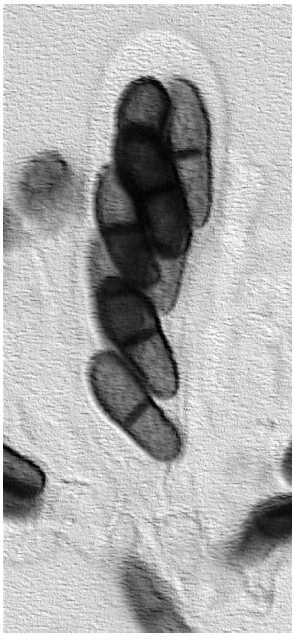

Fig. 3. A single ascus with eight brown 2-celled asymmetric ascospores. (Photo: A. Suija).

CURRICULUM VITAE

Ave Suija

Date and place of birth:	16 April 1969, Pärnu
Citizenship:	Estonian
Marital status:	married, two children
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Position:	University of Tartu, Institute of Botany and Ecology, researcher

Education

1976–1987	Pärnu 4. Secondary School
1987–1989	Tallinn Pedagogical Institute
1990–1995	University of Tartu, Botany and Ecology, B. Sc.
1995–1997	University of Tartu, Botany and Mycology, M. Sc.
1998–2005	University of Tartu, Ph. D. studies

Professional employment

1995–1997	University of Tartu, Institute of Botany and Ecology, lab. assistant.
1998–2001	University of Tartu, Institute of Botany and Ecology, senior lab. assistant.
2004–	University of Tartu, Institute of Botany and Ecology, researcher

Special courses

7 November–9 November 2003 *The application of molecular markers in studies of Cryptogam evolutionary ecology and conservation biology* (BRYOPLANET & Sect. Pl. Ecol. Syst., Dept. Ecology, Lund University, Sweden).

10 May–19 May 2004 *Lichen Taxonomy* (Dep. Syst. Bot., Evol. Biol. Centre, Uppsala University, Sweden)

February–May 2004 *Higher School Pedagogy* (Tallinn Pedagogical University).

Conferences

11 August–17 August 2002 *The 7th International Mycological Congress (IMC7)*, Oslo, Norway
16 August–21 August 2004 *The 5th Symposium of International Association for Lichenology (IAL5)*, Tartu, Estonia.

Publications

1. Jüriado, I., Lõhmus, P., Martin, J., Martin, L., Nilson, E., Piin, T., Randlane, T., Saag, A., Saag, L., Sarv, M., Suija, A., Temina, M. & Trass, H. 1999. Second checklist of lichenized, lichenicolous and allied fungi of Estonia. *Folia Cryptog. Estonica* 35: 1–132.
2. Jüriado, I., Lõhmus, P., Nilson, E., Randlane, T., Saag, A., Saag, L. & Suija, A. 2004. *Estonian Microlichens* (in Estonian). Tartu University Press, 583 pp.
3. Kalamees, K., Hanso, M., Järva, L., Jürisson, I., Karis, H., Kask, K., Kastanje, V., Kullman, B., Pärtel, K., Liiv, V., Noor, H., Normet, T., Parmasto, E., Põldmaa, K., Raitviir, A., Ramst, U., Ruubas, I., Sarv, J., Soobik, P., Suija, A., Sõmermaa, A., Vaasma, M., Vahter, H., Veldre, S., Öpik, M. 2000: *Mycobiota of Estonia* (in Estonian).
4. Randlane, T., Saag, A. & Suija, A. 2002: Biodiversity of lichenized taxa in Estonia: distribution of rare species. *Biblioth. Lichenol.* 82: 99–109.
5. Suija, A. 2005. Lichenicolous fungi and lichens in Estonia I. Ascomycota. *Nova Hedwigia* 80(1–2): 247–267.
6. Suija, A. 2005. Lichenicolous fungi in Estonia II. Basidiomycota and conidial fungi. *Nova Hedwigia* 80(3): 349–366.
7. Suija, A. & Alstrup, V. 2004. *Buelliella lecanorae*, a new lichenicolous fungus. *Lichenologist* 36(3–4): 203–206.
8. Suija, A. & Jüriado, I. 2002. Lichens and lichenicolous fungi of the Hiiumaa Islets Landscape Reserve (Estonia). *Folia Cryptog. Estonica* 39: 37–50.

Teaching

1998–2004 Practical classes (field and laboratory) in lichenology at University of Tartu.

Membership in organizations, councils and boards

Estonian Naturalists' Society (1994)

CURRICULUM VITAE

Ave Suija

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Haridus

1976–1987	Pärnu 4. Keskkool
1987–1989	Tallinna Pedagoogiline Instituut (praegu Tallinna Ülikool)
1990–1995	Tartu Ülikool, botaanika ja ökoloogia eriala, B. Sc.
1995–1997	Tartu Ülikool, botaanika ja mükoloogia eriala, M. Sc.
1998–2005	Tartu Ülikool, mükoloogia eriala, doktoriõpingud

Teenistuskäik

1995–1997	Tartu Ülikool, Botaanika ja Ökoloogia Instituut, laborant.
1998–2001	Tartu Ülikool, Botaanika ja Ökoloogia Instituut, vanemlaborant.
2004 –	Tartu Ülikool, Botaanika ja Ökoloogia Instituut, erakorraline teadur

Erialane täiendus

7–9 november 2003 *The application of molecular markers in studies of Cryptogam evolutionary ecology and conservation biology* (BRYOPLANET & Sect. Pl. Ecol. Syst., Dept. Ecology, Lund University, Sweden).

10–19 mai 2004 *Lichen Taxonomy* (Dep. Syst. Bot., Evol. Biol. Centre, Uppsala University, Sweden)

veebruar–mai 2004 Kõrgkoolipedagoogika (Tallinna Pedagoogika Ülikool).

Osalemine konverentsidel

11–17 August 2002 *The 7th International Mycological Congress (IMC7)*, Oslo, Norra

16–21 August 2004 *The 5th Symposium of International Association for Lichenology (IAL5)*, Tartu, Eesti.

Publikatsioonid

1. Jüriado, I., Lõhmus, P., Nilson, E., Randlane, T., Saag, A., Saag, L. & Suija, A. 2004: *Eesti Pisisamblikud*. Tartu Ülikooli kirjastus, 583 lk.
2. Jüriado, I., Lõhmus, P., Martin, J., Martin, L., Nilson, E., Piin, T., Randlane, T., Saag, A., Saag, L., Sarv, M., Suija, A., Temina, M. & Trass, H. 1999: Second checklist of lichenized, lichenicolous and allied fungi of Estonia. *Folia Cryptog. Estonica* 35: 1–132.
3. Kalamees, K., Hanso, M., Järva, L., Jürisson, I., Karis, H., Kask, K., Kastanje, V., Kullman, B., Pärtel, K., Liiv, V., Noor, H., Normet, T., Parmasto, E., Põldmaa, K., Raitviir, A., Ramst, U., Ruubas, I., Sarv, J., Soobik, P., Suija, A., Sõmermaa, A., Vaasma, M., Vahter, H., Veldre, S., Öpik, M. 2000: Eesti seenestik.
4. Randlane, T., Saag, A. & Suija, A. 2002: Biodiversity of lichenized taxa in Estonia: distribution of rare species. *Biblioth. Lichenol.* 82: 99–109.
5. Suija, A. 2005: Lichenicolous fungi and lichens in Estonia I. Ascomycota. *Nova Hedwigia* 80 (1–2): 247–267.
6. Suija, A. 2005: Lichenicolous fungi in Estonia II. Basidiomycota and conidial fungi. *Nova Hedwigia* 80 (3), 349–366.
7. Suija, A. & Alstrup, V. 2004: *Buelliella lecanorae*, a new lichenicolous fungus. *Lichenologist* 36(3–4): 203–206.
8. Suija, A. & Jüriado, I. 2002: Lichens and lichenicolous fungi of the Hiiumaa Islets Landscape Reserve (Estonia). *Folia Cryptog. Estonica* 39: 37–50.

Õppetöö

1998–2004 Kursuste "Mükoloogia", "Uurimismeetodid taimeökoloogias ja ökofüsioloogias" ning "Elusloodu se mitmekesisuse välipraktika" raames lihhenoloogia sise- ja välipraktikumide juhendamine.

Osalemine organisatsioonides

1994 – Eesti Looduseuurijate Seltsi liige