

Biogeographical determinants of lichen species diversity on islets in the West-Estonian Archipelago

Jüriado, Inga^{1,*}; Suija, Ave^{1,2} & Liira, Jaan^{1,3}

¹Institute of Botany and Ecology, University of Tartu, 40 Lai st., EE-51005 Tartu, Estonia;

²E-mail ave.suija@ut.ee; ³E-mail jaan.liira@ut.ee; *Corresponding author; E-mail inga.juriado@ut.ee

Abstract

Questions: Do islet area, number of biotopes and distance from the mainland shape lichen species richness on islets? Are there any species- or substrate group-specific trends associated with these factors?

Location: Islets of the west Estonian Archipelago, Estonia.

Methods: A species list was compiled for each of the 32 islets and the relative abundance of each species was estimated. The lichens were divided into seven groups according to their substrate preferences. Generalized linear model (GLIM) analysis was applied to test the effect of the islet traits on the number of lichen species on the islets and in the substrate groups. The probability of presence/absence and abundance of the most frequent species according to the islet traits were tested with GLIM and general linear mixed model.

Results: The lichen flora of the islets consisted of 326 taxa, the number of lichen species per islet varied from 2 to 197. Total number of species per islet and within the substrate groups was positively correlated with islet area and with number of biotopes, and negatively correlated with distance from the mainland; however, these relationships varied among the substrate groups. Although individual lichen species showed variation in responses, general trends in island biogeography were evident.

Conclusions: The distribution pattern of lichens on the studied islets follows the theory of island biogeography: the number of species per islet depends on isolation, area and biotope diversity. Species specific traits, such as dispersal strategy and growth form, as well as availability of a particular substrate are important for formation of the lichen flora on islets.

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

Nomenclature: Randle & Saag (1999, 2004) and Santesson et al. (2004) for lichens; Leht, M. (ed.) 1999 for vascular plants.

Abbreviations: AIC = Akaike's information criterion; GLIM = Generalized linear model; TLC = Thin layer chromatography.

Introduction

Biogeography and biodiversity of islands have 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 roles of island area and isolation on species richness – the number of species per island 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; 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; 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; 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). Besides the general patterns described, the influence of area, habitat diversity and distance largely depends on the group of studied organisms (e.g. Nilsson et al. 1988; Ricklefs & Lovette 1999).

Most island biogeography studies have focused on the species richness of vertebrates (e.g. Haila 1983; Heaney 1984; Nilsson 1986), vascular plants (e.g. Nilsson & Nilsson 1982; Deshayé & Morisset 1988; Kohn & Walsh 1994) and arthropods (e.g. Niemelä 1988; Kotze et al. 2000). However, there are some studies on the determinants underlying formation of the species richness of cryptogams such as bryophytes (Tangney et al. 1990) and

lichen fungi (Hayward & Hayward 1986; Seaward & Aptroot 2000) on islands. More often, cryptogamic studies focus on habitat area and connectivity effects of 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. Armesto & Contreras 1981; Slatter 1990; Lawrey 1991b, 1992; Kimmerer & Driscoll 2000).

Lichen fungi (lichens) can colonize a wide range of substrates even in harsh environmental conditions unsuitable for most organisms. Some lichens can establish in open habitats in the early stages of succession while others survive in late successional communities (Lawrey 1991a). Most lichens grow slowly, disperse passively and are adapted to particular substrates (tree bark, rock, soil, dead wood) (e.g. Armstrong 1988; Lawrey 1984, 1991a). Many species are thought to have poor dispersal ability (Dettki et al. 2000). Lichens on islands and on the seashore tolerate salinity, repeated drying and wetting and high light intensity (Lawrey 1984). This combination of properties makes lichen fungi an attractive group for studying in relation to island biogeography.

The lichen flora on the Baltic Sea islands along the western and northern coast of Estonia is relatively well known (e.g. Randlane 1986; Suija & Jüriado 2002). The aim of this paper is to clarify and quantify the limiting factors behind species richness of lichens on islets. We hypothesize that islet area, biotope diversity and islet isolation have a general impact on number of species per islet. We also assume that these effects vary among the lichen groups on different substrates and among the individual species.

Study area

Ca. 10% (4133 km²) of the territory of Estonia consists of the islands in the Baltic Sea (Raukas 1995). Most islands belong to the west Estonian Archipelago, with the largest 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 ca. 2000 years ago, during the Limnea stage of the Baltic sea (Kessel 1961). The formation and disappearance of the islets, amalgamation with each other or merging with the mainland continues nowadays due to the constant and relatively rapid uplift (2–3 mm per year) of the earth (Raukas 1995).

The investigated islets (32 islets with a combined land area of 4.15 km²) are located southeast and east of Hiiumaa island and around the island of Vormsi in the Väinameri sea (App. 1; Table 1). Most of the islets

consist of moraines, 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 gradually 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 of these islets (Leito & Leito 1991).

Estonia's temperate climate has warm summers and moderately cold winters (Raukas 1995). The climate of the archipelago is milder than that on the Estonian mainland because of the influence of the sea. On islands, the mean yearly air temperature is 6.1°C and the calculated mean relative humidity is 81.5%; south and southwest winds prevail (unpubl. data from the Estonian Meteorological and Hydrological Institute). The action of ice and waves is especially obvious for the smallest, periodically inundated, islets (area up to 0.1 ha) and also for some medium sized, more distant islets (e.g. Langekare, Anerahu). The islets closer to the mainland (e.g. Auklaid) are more sheltered from wind and waves by the other islets or large islands.

Table 1. Islet name, area, number of biotopes on islet, distance to the mainland and number of lichens on the studied islets.

No./ Islet	Area (ha)	No. of biotopes	Distance (km)	No. of lichen spp.
1 Kivirahu	0.1	1	0.7	2
2 Pähkrah	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 Uemererahu	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

The vascular plant communities on the studied islets belong to various stages of succession. The vegetation of the smallest islets is mostly early successional and frequently disturbed, consisting 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 in suprasaline grasslands. Large islets have more complex vegetation, including wooded meadows and different forest types. Granite and limestone are found in all habitats, from the seashore to the closed forest.

Direct anthropogenic impact is evident only on some large or medium sized islets due to permanent inhabitancy until the beginning of the 1970s (Saarnaki, Hanikatsi) and the activity of border guards until the 1990s (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

Lichen inventories were conducted from 2001 to 2004. Species lists of lichen, lichenicolous and allied fungi (below considered as 'lichens') were compiled for each islet (Nilson & Jüriado 2001; Suija & Jüriado 2002). Species observed only in previous expeditions have also been taken into account (Randlane 1986; Püttsepp unpubl.; Sander unpubl.). The lichen species were divided into groups according to their substrate preferences (hereafter 'substrate groups'). Seven substrate groups were defined:

1. Coniferous trees – *Pinus sylvestris*, *Juniperus communis*;
2. Deciduous trees – *Acer platanoides*, *Betula pendula*, *Fraxinus excelsior*, *Quercus robur*, *Sorbus aucuparia*, *Tilia cordata*, *Ulmus glabra*, and shrubs – *Lonicera xylosteum*, *Rhamnus catharticus*, *Ribes alpinum*, *Rosa* spp.;
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 – fungi and lichens growing on lichens (lichenicolous species).

The relative abundance of each 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.

All habitats suitable for lichen growth on the islets were sampled.

The collected specimens (ca. 1000) are kept in the lichenological herbarium at the University of Tartu (TU). For identification in the laboratory the stereomicroscope,

light microscope, 'spot tests', UV light and standardized thin layer chromatography (TLC) methods were used.

Islet traits

The environmental conditions on islets were characterized using the area of the islet, the number of biotopes per islet and islet distance from the mainland (Table 1). Islet areas were taken from the database of Estonian marine islands (Loopmann 1996) or were supplied by the administration of the Hiiumaa Islets Landscape Reserve. The number of biotopes was estimated using a modified biotope system of Leito & Leito (1991), produced for the islets of the Hiiumaa Islets Landscape Reserve:

1. without vegetation;
2. with coastal meadows and solitary shrubs;
3. with coastal meadows, solitary shrubs and solitary trees;
4. with coastal meadows, shrub lands and a few trees;
5. with coastal meadows, shrub lands, reedbeds, grasslands and some scattered trees;
6. with coastal meadows, shrub lands, reedbeds, grasslands and forest;
7. with coastal meadows, shrub lands, reedbeds, grasslands, wooded meadows and different types of forest.

Islet isolation was measured as the nearest distance to the mainland coastline (km) on a digital map from the Regio Estonian Road Atlas (Anon. 1999). The 'mainland' was defined as continental Estonia or large island of Hiiumaa or Vormsi, depending on which was the 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 group. In the models, all continuous islet traits 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 parameterization (Shao 1997). The factor effect profile method, using semi-residuals of the model, was used for graphical presentation of the factor effect on species richness (modified from the prediction profile method of Derringer & Suich 1980). Semi-residuals make it possible to illustrate the response of species richness to one factor at a time, while controlling for the effect of the other factors in the model.

Frequently recorded species, observed at least on six islets (20%, total 104 taxa), were used to examine species

specific patterns. The probability of presence/absence of each lichen species on an islet in relation to islet parameters (area, number of biotopes and distance from mainland) was modelled with logistic regression (i.e. Binomial error distribution, logit link-function; proc GENMOD, Anon. 1989). The presence of species specific response patterns in relation to islet traits was tested as the significance of the interaction term between the discrete factor 'species' and each islet parameter. Substrate group specific pattern was also tested but, as interaction terms were not significant, the results are not presented.

The factor design for analysis of the MIXED model (Littell et al. 1996) was similar to that of the previous model, but it evaluated abundance patterns rather than

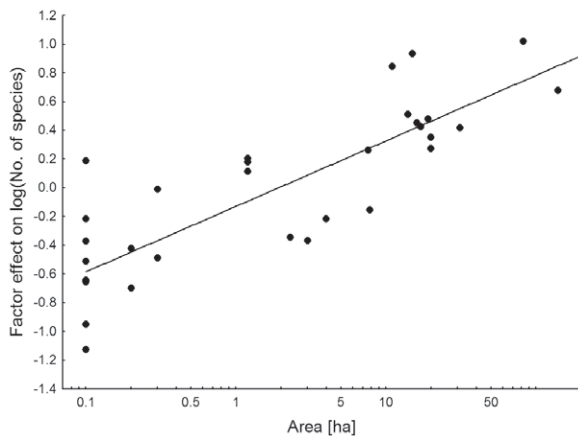


Fig. 1. The effect profile of islet area on log-number of species on islet, presented as model semi-residuals of species richness conditioning on the other two factors in the model (see Table 3).

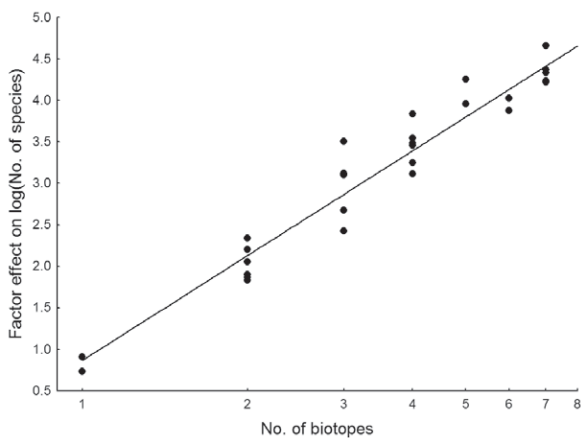


Fig. 2. The effect profile of number of biotopes on log-number of species on islet, presented as model semi-residuals of species richness conditioning on the other two factors in the model (see Table 3).

presence. The MIXED model contains islet traits, the fixed factor 'species' and the random factor 'islet'.

Results

Number of lichen species on islets

The total area of the 32 studied islets is 4.15 km², which constitutes ca. 0.01% of the Estonian land area. However, from this small and fragmented land 326 taxa i.e. 32% of the lichen species known in Estonia were found (App. 2). The most species-rich substrates on the islets were deciduous and coniferous trees, dead wood and granite (Table 2). The number of lichen species on islets varied from two 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 islet distance from the mainland (Figs. 1-3; Table 3).

The number of lichen species in substrate groups increased with islet area and number of biotopes, but decreased with distance from the mainland (Table 4). However, substrate group specific variations were observed (interaction terms significant, Table 4) i.e. the general trends could not be generalized to each substrate group.

Species richness on various substrates increased significantly with islet area for three substrates: coniferous trees, dead wood and soil (Fig. 4; Table 4). The number of species in all substrate groups, except species on dead wood, was correlated with the number of biotopes on the islet (Fig. 5). The negative relationship of distance from mainland and the number of lichen species on the selected substrates was significant for five out of seven

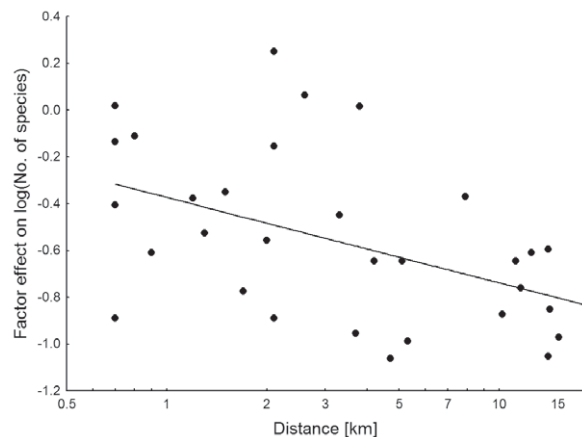


Fig. 3. The effect profile of distance on log-number of species on islet, presented as model semi-residuals of species richness conditioning on the other two factors in the model (see Table 3).

Table 2. Number of lichen species in seven groups according to their substrate preferences on the studied islets.

Substrate group	No. of species
Coniferous trees	75
Deciduous trees	114
Dead wood	86
Granite	93
Lichens	28
Limestone	47
Soil	35

substrate groups (coniferous trees, dead wood, granite, soil, lichens; Fig. 6).

We calculated a correlation coefficient of 0.57 ($p = 0.001$) between islet area and number of biotopes. In some cases species richness was related to one factor but not to the other. The number of lichens on coniferous trees and on soil was related to both area and the number of biotopes. Area was significant for the number of lichen species on dead wood, while on deciduous trees, granite, limestone and also for lichenicolous fungi, the number of biotopes was more important than the size of the islet (Table 4).

The probability of presence and the abundance of lichen species

All three biogeographic traits of islets were related to presence and abundance of lichen species on islets, but this varied by species (Table 5). According to the results of logistic regression and MIXED model analyses, 78 out of 104 fairly common lichen taxa had a significant relationship with one or two (in a few cases

Table 3. The results of GLIM analysis of the effect of islet area, number of biotopes and distance on the number of lichen species on the islet. The specifications of the GLIM model are: Poisson error distribution, log-link function and Pearson correction-coefficient for overdispersion. Islet traits are log-transformed. The estimated slope parameter with standard error is presented. Highly significant values in bold.

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

Table 4. The test results and the slope estimate of the GLIM analysis of the effect of islet area (Area), number of biotopes (Biot.) and distance (Dist.) on the number of lichen species in the substrate groups (Sub.). The specifications of the GLIM model are: Poisson error distribution, log-link function and Pearson correction-coefficient for overdispersion. Islet traits are log-transformed. Significance: * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.0001$; ns = not significant.

Main effect:	Area ***	Biot. ***	Dist. ***
Interaction term:	Sub.*Area ***	Sub.* Biot. ***	Sub.*Dist. ***
Slope estimates			
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 *

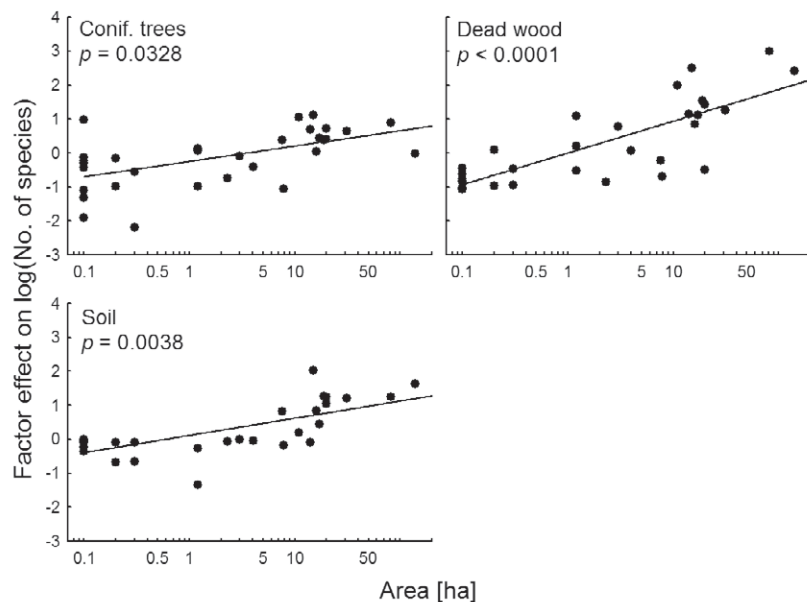


Fig. 4. The effect profile of islet area on log-number of species in substrate groups, presented as model semi-residuals of species richness conditioning on the other two factors in the GLIM analysis (see Table 4). Figures are presented only for substrate groups where the relationship was significant.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

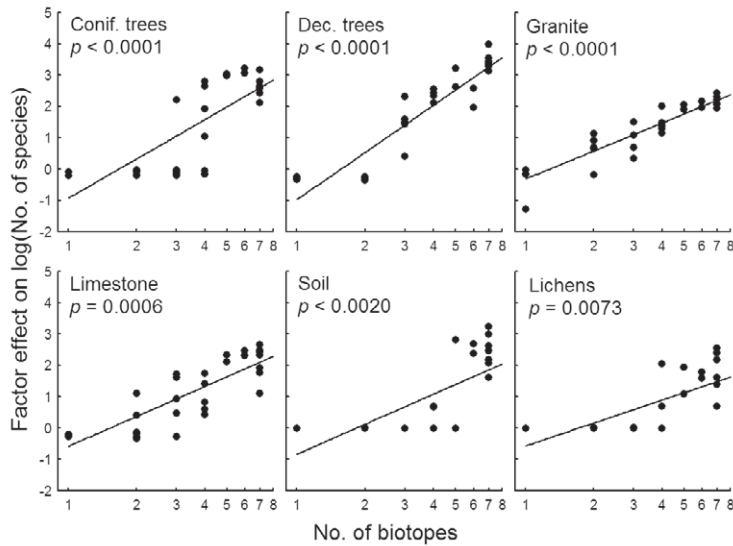


Fig. 5. The effect profile of the number of biotopes on log-number of species in substrate groups, presented as model semi-residuals of species richness conditioning on the other two factors in the GLIM analysis (see Table 4). Figures are presented only for substrate groups where the relationship was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

three) of the studied traits of the islets (App. 3). 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).

The results of the GLIM analysis of the presence/absence data revealed that the presence of 12, 32 and 15 species on the studied islets was related to islet area, number of biotopes and distance, respectively (Table 5; App. 3). Most of those species had higher odds of presence on large and more biotope-rich islets, or a decreasing probability of presence with distance. One exceptional species, *Rinodina gennarii*, had an increased probability of presence with distance from

the mainland.

In general, the abundance of lichen species showed logarithmic positive trends (or linear positive trends on the log-scale) with islet area and with number of biotopes on the islet (main effects significant; Table 5). Of these two factors, the species specific pattern was observed only for the number of biotopes (Table 5). The abundance of 31 taxa increased significantly with an increasing number of biotopes (App. 3). Within the general positive trend of species abundance to islet area, the most revealing patterns were observed for species from woody substrates and granite, and also from limestone and soil. The abundance of species was dependent on variable 'Distance' as revealed from MIXED model

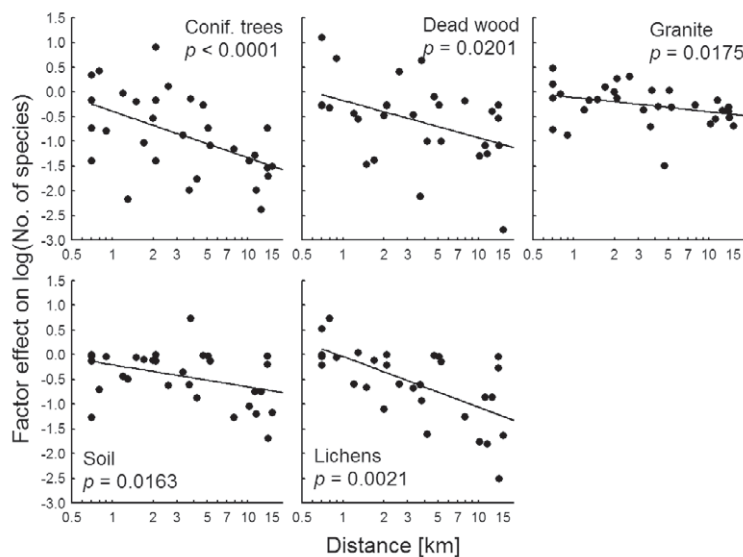


Fig. 6. The effect profile of the distance on log-number of species in substrate groups, presented as model semi-residuals of species richness conditioning on the other two factors in the GLIM analysis (see Table 4). Figures are presented only for substrate groups where the relationship was significant. Conif. trees = Coniferous trees.

Table 5. The results of logistic regression analysis (GLIM) on the dependence of species presence/absence on the islet traits and the test of MIXED model analysis on the species-specific relationships between species abundance and the islet traits. Islet traits are log-transformed. In MIXED model analysis, the factor 'Species' was treated as the fixed factor and 'Islet' as the random factor in the model. Highly significant values in bold.

Variable	Logistic regression of presence/absence			MIXED model of abundance		
	df	Wald statistic	<i>p</i>	df	<i>F</i>	<i>p</i>
Area	1	5.26	0.0218	1; 2715	39.07	0.0001
No. of biotopes	1	67.39	0.0001	1; 2715	46.15	0.0001
Distance	1	9.71	0.0018	1; 2715	0.31	0.5765
Species	74	179.06	0.0001	99; 2715	1.22	0.0708
Species*Area	74	102.16	0.0167	99; 2715	1.19	0.1023
Species*No. of biotopes	74	156.93	0.0001	99; 2715	2.37	0.0001
Species*Distance	74	137.70	0.0001	99; 2715	2.27	0.0001

analyses (Table 5). However, there was a large variation among species, as the abundance of eight species increased with distance and decreased for ten species.

Discussion

According to our results, the distribution pattern of lichen species on islets corresponds to the predictions of the theory of island biogeography (MacArthur & Wilson 1963, 1967): the number of lichen species on an islet increased logarithmically with islet area, and decreased with islet distance from the mainland. The positive correlation between the number of lichen species and area was earlier detected for islands (Hayward & Hayward 1986; Sipman & Raus 1999; Seaward & Aptroot 2000) and for island type saxicolous and old-growth forest lichen communities (Armesto & Contreras 1981; Slatter 1990; Lawrey 1991b, 1992; Kruys & Jonsson 1997; Berglund & Jonsson 2001). Habitat diversity, which increases with area, has been noted to be the major factor in species-area relationships (Hayward & Hayward 1986; Slatter 1990).

On the basis of our investigation, both area *per se* and biotope diversity influenced overall lichen species richness on islands, and these trends proved to be significant in most of the species groups according to their substrate preference. Taking into account the effects of biotope diversity and islet distance, a statistically significant effect of area on species richness was detected for lichens growing on soil, dead wood and conifers. Regarding the other factors, the relationship between biotope diversity and species richness was important for almost all substrate groups except for lichens on dead wood.

Larger islands have a more stable environment than small islands, as the probability and severity of destructive stochastic events (action of the wind, waves and ice) are lower. It has been shown that ground lichens establish in a community only after soil surface has been

stabilized (Belnap & Eldridge 2003), and the composition of the epigeic lichen flora of stable soils is dependent on soil characteristics, especially on soil texture, chemistry and water-holding capacity (Rosentrater & Belnap 2003). We noted that the species richness of epigeic lichens was correlated with islet area and habitat diversity, as both of these factors determine the extent of disturbance and the differentiation of soils. For instance, larger islets supported a higher abundance of the lichens typical of dry soils in light exposed habitats (*Cetraria islandica*, *Cladonia furcata*, *C. subrangiformis*, *Peltigera rufescens*).

Driftwood transported to islands by the sea is a natural habitat for epixylic species (Himmelbrant & Kuznetzova 2002). Colonization of driftwood assumes persistence of the substrate, while its stability is correlated with island area. In addition to driftwood, old wooden buildings (farmhouses, wooden quays, wooden windmills, fences), frequently present on larger islets, also serve as suitable substrates for the establishment of epixylic species. For example, we observed a strong positive relationship between islet area and the probability of presence and abundance of two common epixylic species, *Lecanora varia* and *Trapeliopsis flexuosa*, both able to grow on natural lignum and worked timber.

In the course of land uplift, which is correlated to islet area, deciduous trees and bushes dominate in the early stages of vegetation succession on smaller islets, while conifers appear in the later stages of succession on intermediate and large islets (Rebassoo 1972; Svensson & Jeglum 2003). It has been noted that species with dominating asexual dispersal strategy are late successional and more abundant in stable, less disturbed habitats (Kiss 1988; Dietrich & Scheidegger 1996). On the studied islets, the abundance of several foliose and fruticose lichen species was related only to islet area. The species *Parmeliopsis ambigua*, *Pseudevernia furfuracea*, *Tuckermannopsis chlorophylla* and *Vulpicida pinastri* predominantly disperse with asexual diaspores

and are restricted to conifers.

Most lichen species are highly specialized and have a narrow range of environmental niches (Barkman 1958; Ott et al. 1996). As an increasing number of biotopes provides a higher number of environmental niches (Williams 1943; Kelly et al. 1989), the positive correlation between biotope diversity and species richness of lichens is an expected outcome of our study. For instance, Lawrey & Diederich (2003) hypothesized that the diversity of lichen parasites (lichenicolous fungi) increases with the number of host lichen species. We observed that the species richness of lichenicolous fungi was correlated to the number of biotopes, and this relationship can be solely explained by the diversity of host species in the conditions of a high variability of habitats.

Several species found on the islets have a wide ecological amplitude. Analysis of the species distribution on the islets revealed that several epilithic and epiphytic lichens, whose abundance was positively correlated with the number of biotopes, are habitat generalists. Among these species, some of them (e.g. *Evernia prunastri*, *Hypogymnia physodes*, *Phlyctis argena*, *Ramalina farinacea*) are able to grow in different habitats on both deciduous and coniferous trees, while others (e.g. *Lecanora carpinea*, *Physcia stellaris*, *P. tenella*) grow on various deciduous trees and bushes with smooth bark. Many biotope diversity-dependent epilithic species (e.g. *Candelariella coralliza*, *Lecanora polytopa*, *Melanelia fuliginosa*, *Neofuscelia pulla*, *Parmelia saxatilis*, *Tephromela atra*, *Xanthoparmelia conspersa*) are typical of open, well lit environments (Wirth 1972) and they grow in the xeric supralittoral region and the terrestrial region (Fletcher 1973). We recorded these species most frequently in various open and semi-open grasslands, sheltered from seawater spray.

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). The impoverishing effect of isolation on species diversity has been noted in a few cryptogam studies carried out on islands (Tangney et al. 1990; Sipman et al. 2005), but it has proved insignificant for island-type communities (Armesto & Contreras 1981; Krøys & Jonsson 1997; Kimmerer & Driscoll 2000; Berglund & Jonsson 2001).

According to our results, it can be confirmed that isolation has a considerable negative impact on lichen species richness on islets, and 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 variation was observed.

The dispersal efficiency and viability of propagules depend on the reproduction mode as sexual diaspores (i.e. ascospores) are prevalent in long-distance dispersal and asexual diaspores are prevalent in short-distance dispersal (Bailey 1976; Hedenås & Ericson 2000). Most of the species whose abundance on the islet increased with distance from the mainland are typical early colonizers of rocky sites (e.g. *Caloplaca citrina*, *Lecanora helicopsis*, *Rinodina gennarii*) and woody substrates (e.g. *Physcia stellaris*, *Physconia distorta*) (Degelius 1964; Fletcher 1973). They disperse solely by ascospores, except for *Caloplaca citrina*, which also reproduces asexually. However, we found also two exclusively asexually reproducing (sorediate) lichens, *Lepraria incana* and *Phlyctis argena*, whose abundance was positively correlated with islet distance. Most of the species, whose distribution showed a negative correlation with distance, are characterized by the restricted production of soredia (e.g. *Hypogymnia physodes*, *H. tubulosa*, *Parmelia sulcata*, *Parmeliopsis ambigua*, *Physcia dubia*, *Tuckermannopsis chlorophylla*).

Disturbances on distant islets in open seas are more intense than on islets near mainland coasts. A loosely attached growth form is a disadvantage in the conditions of the destructive influence of the wind and waves (Fletcher 1973). On the studied islets, the species which had a positive relationship between abundance and distance have either a crustose or a tightly attached flattened foliose thallus (e.g. *Caloplaca citrina*, *Lecanora helicopsis*, *Physcia stellaris*, *Phlyctis argena*), while the species which had a negative relationship between abundance and distance have a loosely attached thallus (e.g. *Hypogymnia physodes*, *Physcia dubia*, *Tuckermannopsis chlorophylla*).

In conclusion, the species richness of lichens appears to respond, in a general way, to islet area, biotope diversity and isolation, according to the theory of island biogeography. Besides these general patterns, the influence of area, biotope diversity and distance varies among groups of lichens established according to their substrate preference. Additionally, presence and abundance of each lichen species on islets is the result of a combination of its dispersal strategy, growth form and ecological requirements. Large islets support species which require stable environmental conditions e.g. species with loosely attached foliose and fructicose thalli. Diversity of biotopes per islet supports presence both of habitat specialists and generalist species. The species richness of distant islets is supported by species which have flattened thalli, disperse mainly by sexual diaspores (ascospores) or have high production of asexual soredia.

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