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Sea shore plants of the SW archipelago of Finland — distribution patterns and long-term changes during the 20th century

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Historical and contemporary records of 81 vascular plant species of shores from 412 islands in the archipelago of SW Finland are compared to visualise changes in distribution patterns over time, and to identify environmental variables that exert influence on the distribution and on the colonisations and extinctions of species. The environmental variables were measured using GIS. A logistic regression analysis was used to find variables that exert influence on the probability of species occurrences. The total number of species occurrences has increased by 22.7%. On the surveyed islands, frequencies of 60 species have increased or remained unchanged, and those of 21 species have decreased. More species have spread towards less maritime than towards more maritime conditions. Syntheses, including distribution maps, are presented for the species. The decrease in grazing pressure and the eutrophication of the Baltic Sea are probable reasons for the observed changes. Some species have changed their distribution patterns in relation to the environment in unpredictable manners. It is thus concluded that it is worthwhile to analyse the species separately in long term studies when possible.

Introduction

The vascular plants of the geolittoral zone represent a characteristic group of species of the islands in the SW Finnish archipelago, adapted to cope with the harsh conditions near the sea shore line. The shores in the area are made up of a mixture of habitat types including mud, clay, silt, sand, gravel, boulder, till and bare rock. The sea water is a source of nutrients, and a medium for seed dispersal. Water level fluctuations and exposure of the shores to salt, wind, sun, waves and grinding ice during the winter, have an impact on the distribution patterns and the species composition.

Historically, the shores in SW Finland have been used as pastures, which have turned shores with natural vegetation into shore meadows, especially where the substrate is made up of finer material. The resident population of the archipelago was at its peak density at the beginning of the 20th century (Hustich 1964), but this influence declined after the first half of the century along with the depopulation of the archipelago. Today, this effect of grazing live stock is minimal. Changes in the environment caused by indirect human influence, such as increasing nutrient loads of the seashores and airborne deposits, have escalated in the last 50–60 years. The increasing eutrophication of the Baltic Sea impacts on the productivity of the seashores (Bonsdorff *et al*. 1997, Rönnberg & Bonsdorff 2004), and airborne deposition of nitrogen and sulphur oxides causes acidification and increasing levels of nitrogen (Schöpp *et al*. 2003) affecting the whole island flora.

Resurveys of plant communities over time provide information on changes in species composition, and clues about how species respond to environmental changes (Wiegmann & Waller 2006). Ecological change over time is often hard to verify because of lack of reliable baseline data (Rooney *et al*. 2004), or because historical species lists only include rare or otherwise interesting species (Whittaker *et al*. 2001). To locate and correctly delimit historical study areas for resurveys is another, probably common obstacle.

In this study, I use a historical base line data set on the distribution of vascular plants on 412 islands in the archipelago of SW Finland, to study long-term changes in the distribution patterns of individual shore plant species in relation to environmental factors. The historical data set was collected during the 1930s and 1940s by Eklund (1958) and Skult (1960), in an era when the Baltic Sea was not eutrophicated, most of the archipelago was inhabited, and grazing sheep and cattle affected the vegetation on many of the islands.

The aims of this study are (1) to visualise the historical and contemporary distribution of the individual shore species on the surveyed islands, (2) to identify environmental variables that exert influence on the distribution of the species, and (3) to examine how the distribution patterns and number of occurrences of species have changed over time in relation to environmental variables on the islands.

The study area

The archipelago of SW Finland, hereafter the Archipelago Sea, is a shallow non-tidal sea area located in the Baltic Sea between Finland and Sweden. Variations in the air pressure result in water level fluctuations reaching from ca. 30 cm below to 90 cm above the mean water level (Vuori *et al*. 2006). The area of the archipelago covers about 15 000 km^2 and includes at least 22 000 islands (Granö *et al*. 1999). It is made up of different types of islands, from small islets almost entirely consisting of bare rock, to large islands with forests and settlements. This mosaic structure results in a wide range of conditions and habitats on the islands throughout the archipelago. Most of the islands have emerged from the sea during the past few thousand years, because of isostatic land uplift (currently 4 mm yr^{-1}, Kakkuri 1987) after the last Glacial Age terminating ca. 12 000 years ago. The average duration of the growing season is 180 days and the mean annual precipitation and period of ice cover is 500 mm and 70 days, respectively (Atlas of Finland 1993). The salinity is 5‰–6‰ (Vuori *et al*. 2006). The characteristics of the archipelago change gradually from the mainland to the open sea, forming a gradient from the inner archipelago near the mainland to the outer archipelago bordering the open sea. Generally, wooded islands become rarer and the trees wind-trimmed towards the outer archipelago islands. The extreme offshore archipelago consists of barren islands with little vegetation and the conditions are maritime. The complexity of the area renders a straightforward zonation (Häyrén 1948) of the area, from the inner archipelago to the outer archipelago, difficult. Aggregates of large islands far from the mainland often form secondary inner archipelagos with low maritimity. On the other hand, open and island-poor straits or "fjärds" (von Haartman 1945) penetrate deep into the inner archipelago, forming maritime enclaves in areas with otherwise low maritimity. The papers of von Numers (1995), von Numers and van der Maarel (1998) and Korvenpää *et al*. (2003) provide more detailed discussions of the vegetation characteristics of the area.

The island data

Knowledge of the historical flora in the archipelago of SW Finland is largely based on research undertaken by Eklund (1958) from 1918 to 1946. He compiled vascular plant species lists for

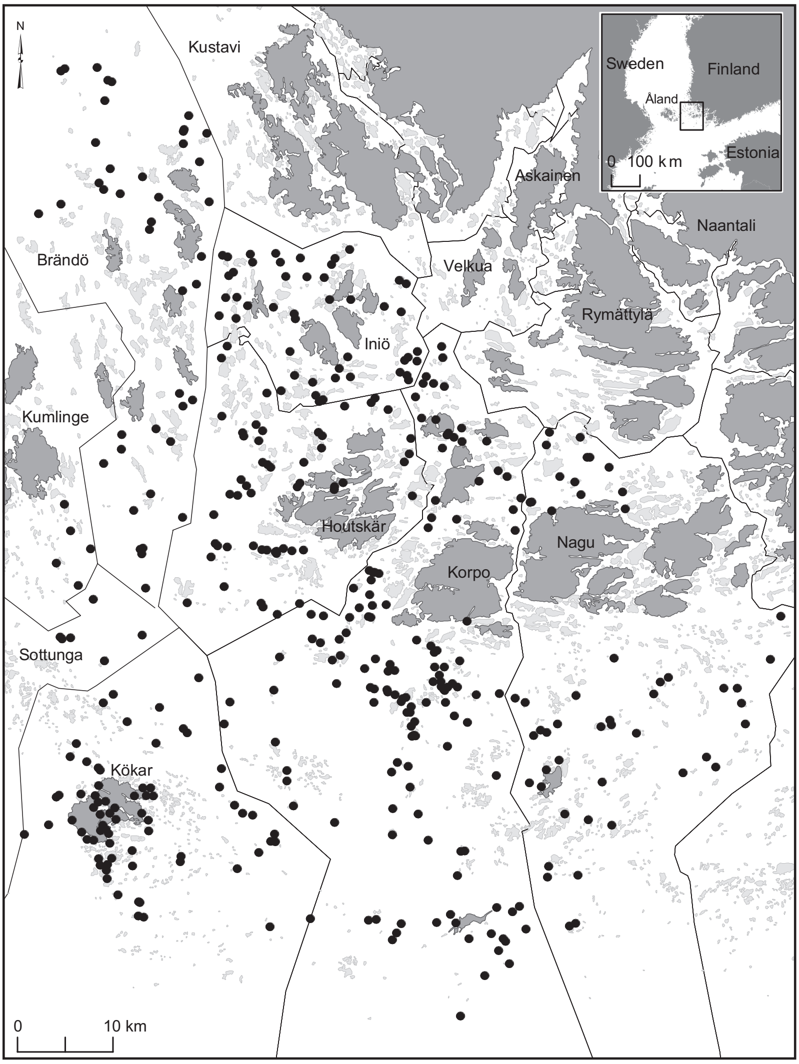

Fig. 1. The study area in the archipelago of SW Finland. The black dots indicate the 412 surveyed islands. Islands larger than 250 ha are dark. The historical municipality borders are marked with lines.

about 1600 localities in a large part of the archipelago of SW Finland (Eklund 1958). Most of these localities are individual islands, although some are parts of large islands. This historical data set has been entered into a database (von Numers 1996) and has been analyzed to classify the species and examine the floristic gradients and long term changes in the area (von Numers & van der Maarel 1998, Korvenpää *et al*. 2003). Historical and part of the now used contemporary data were used in von Numers and Korvenpää (2007) to study changes in the floristic gradients. The botanical notes of Skult (1960) from 116 islands in the Brunskär area (Korpo) provide additional base-line knowledge of the flora in the archipelago. Skult compiled his species lists in the 1940s, using the same methods as Eklund (Hannus & von Numers 2008). The data of Skult are included in the database used in this study. Vaahtoranta's (1964) study area, bordering Eklund's in the north, includes 171 islands surveyed in 1952–1955. One of these islands is included in this study.

Fieldwork for the contemporary data was conducted from 1996 to 2010. In total, 412 islands were re-surveyed within the study area of Eklund (Figs. 1 and 2). Of these islands, 388 were previously surveyed by Eklund, 23 by Skult and one by Vaahtoranta. The study area extends at most 100 km both in the S–N and W–E directions. The

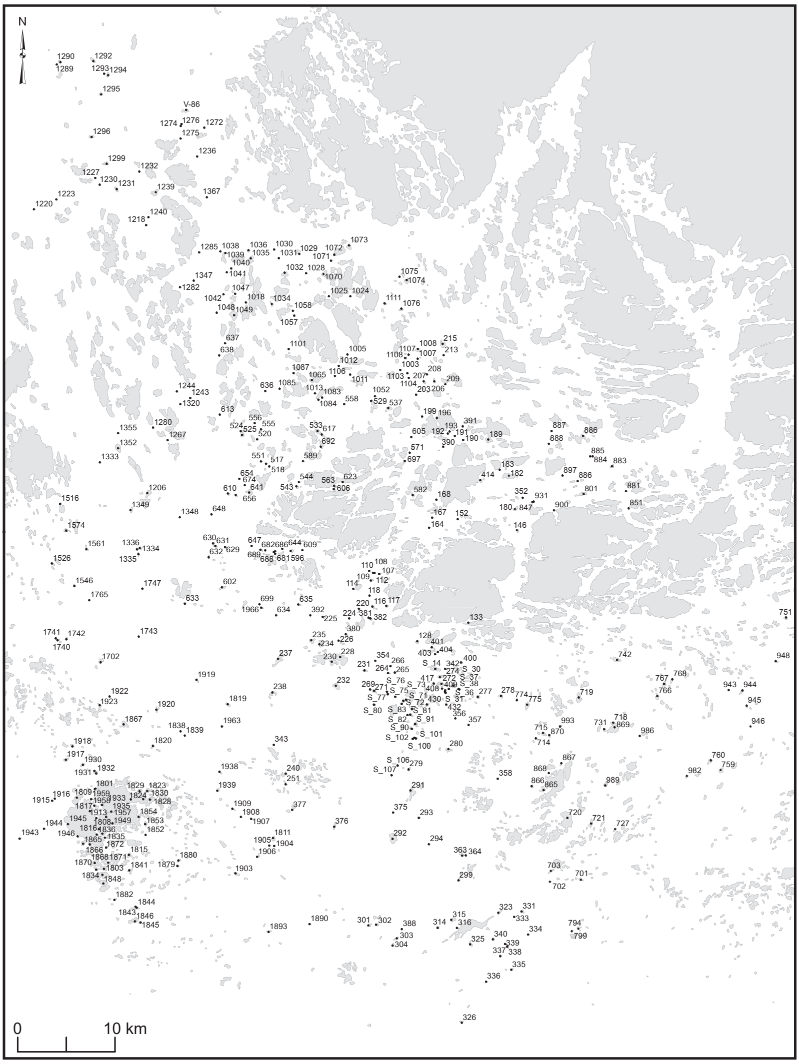

Fig. 2. The 412 surveyed islands numbered in accordance with Eklund (1958), Skult (1960, prefix S_*) and Vaahtoranta (1964, prefix V-86, one island).

islands vary in size, from small forestless islets to large forested islands, the mean island area being about 9.3 ha. The smallest island is 0.04 ha, the largest 173.5 ha and the total area surveyed was 3826 ha. The island perimeter (shore line length) is a more relevant measure than island area for the shore plants (*see* e.g. Nilsson & Nilsson 1982), and thus this measure is used in the analyses. The mean shore line length of the islands is 1437 m, minimum being 76 m, maximum 8933 m, and the total surveyed island shore line length 593.5 km, according to measurements made using the National Land Survey Topographic database map. Of the islands, 181 have a shore length shorter than 1 km, 148 between 1 km and 2 km, 51 between 2 km and 3 km and 32 a shore length longer than 3 km.

The fieldwork

The islands were surveyed during the same phase of the growing season as the one during which Eklund and Skult carried out their surveys. Usually the field season began around 15 June and continued to about 25 August. A small motorboat was used for the excursions. The islands were systematically surveyed and their entire area thoroughly searched. Some islands were surveyed twice, especially if the first surveys were made early in the season, or severe drought made it difficult to compile reliable species lists. Some of the largest islands demanded several days of work. The time taken for each island to survey was noted as a basis for future investigations. A species checklist derived from the database was used alongside the original island-specific species list of Eklund or Skult. The species lists of Eklund and Skult give information on species presence on the islands, with no indication of species abundance. The new species lists were compiled in a similar way.

Nomenclature and species included

This study is focused on the species of the geolittoral zone (shore between the mean water level and the high water level), the hydrolittoral (between mean water level and low water level) and the emergent species of the sublittoral (always under water). Du Rietz (1947) defined the shore as the area between the highest water limit and the lowest water limit. In practice, the geolittoral zone was specified as the zone between the lowest water limit and the last outposts of alder *Alnus glutinosa* or shrubs such as *Ribes nigrum*, *Calluna vulgaris* and *Vaccinium uliginosum* (Hannus & von Numers 2008). Although most shore species are bound to the shore, there are species for which there is no clear border, as one commonly finds also species belonging to other habitats on the shores. The shore species in Finland were defined by Palmgren (1960), and his guidelines were mainly followed. The selection of species is, in addition, based on experience gained during the field work. For instance, *Carex panicea*, *Linum catarctica* and *Stachys palustris* were included in the shore species, as these almost exclusively occur on shores on the surveyed islands. The nomenclature follows that of Hämet-Ahti *et al*. (1998) and Hæggström and Haeggström (2008).

Excluded taxa are: *Zostera marina*, *Zannichellia palustris*, *Najas marina*, genus *Potamogeton*, genus *Ruppia*, genus *Ranunculus*, subgenus *Batrachium*.

In the area, the genus *Atriplex* includes *A. littoralis*, *A. longipes* ssp. *praecox*, and *A. prostrata*. Occasionally other rare *Atriplex* species might have occurred. These are included in *A. prostrata*. *Carex viridula* var. *viridula* and *C. viridula* var. *pulchella* are treated collectively, as are *Myosotis laxa* ssp. *baltica* and *M. laxa* ssp. *caespitosa*, and *Valeriana officinalis* and *V. sambucifolia* ssp. *salina*. In all, 81 species were included in this study (Table 1).

Environmental variables

ArcView 9.2 GIS with extensions was used to measure the environmental variables and to create the distribution maps. Hawthorne's tools version 3.27 were used for the distance measurements. The environmental variables were measured from the National Land Survey Topographic database map (2002). A digital elevation model (DEM) with a pixel resolution of 10 m for the area was created with the ArcView Spatial Analyst tool "topo to raster", by interpolating elevation curves, including curves for both height (above sea level), depth (below sea level) and the shore line (0-level). The ArcView Spatial Analyst tool "Slope" was used to create a raster-layer depicting the slope (pixel resolution 10 m) from the DEM. The Isaeus (2004) raster describing exposure to wind and wave action (25 × 25 m resolution) was used to estimate the exposure of the shore line. For the variable "distance to mainland" a fix point on the mainland (*see* von Numers & van der Maarel 1998) was used. Large islands were defined as (inhabited) islands with an area larger than 250 ha (Fig. 1). The 13 measured environmental variables are listed in Table 2.

Statistical analyses

As there are data on species presences and absences, a generalized linear model (GLM) binary logistic regression analysis (SPSS 14.0) was used to determine the island variables that exert influence on the probability of species occurrence. The logistic regression analyses were performed on the species on the 331 islands (of totally 412) that were surveyed in the years 1996–2004. The interest was focused on the variables that significantly contributed to the models.

A stepwise selection method with entry testing based on score statistics, and removal testing based on the probability of likelihood-ratio statistics, based on the partial likelihood estimates was used. The obtained models were tested for significance using Hosmer & Lemeshow statistics and Nagelkerke R^2 in SPSS (Hosmer & Lemeshow 2000). In addition, the area under the receiver operating characteristics (AUC) to test for model discrimination was used. The area value varies between 0 and 1; an area of 0.5 means that the model performs no better than a random model, and an area of 1 indicates that presences and absences are perfectly discriminated.

The AUC value of about 0.7 was chosen as the lower limit for a model to be considered,

Table 1. The 81 shore species (in systematic order) of the 412 islands included in the study.

Ophioglossum vulgatum	*Lathyrus japonicus* ssp. *maritimus*	*Triglochin maritima*
Myrica gale	*Lathyrus palustris*	*Typha latifolia*
Montia fontana	*Lotus corniculatus*	*Typha angustifolia*
Honckenya peploides	*Lythrum salicaria*	*Juncus compressus*
Sagina maritima	*Linum catharticum*	*Juncus gerardii*
Spergularia salina	*Ligusticum scoticum*	*Juncus bufonius* ssp. *bufonius*
Silene viscosa	*Angelica archangelica* ssp. *litoralis*	*Juncus bufonius* ssp. *ranarius*
Silene vulgaris var. *littoralis*	*Hippophaë rhamnoides*	*Bolboschoenus maritimus*
Atriplex littoralis	*Centaurium littorale*	*Schoenoplectus tabernaemontani*
Atriplex prostrata	*Centaurium pulchellum*	*Blysmus rufus*
Atriplex longipes ssp. *praecox*	*Valeriana sambucifolia* ssp. *salina*	*Eleocharis uniglumis*
Salicornia europaea	*Myosotis laxa* ssp. *baltica*	*Carex glareosa*
Suaeda maritima	*Galeopsis bifida*	*Carex panicea*
Salsola kali	*Stachys palustris*	*Carex viridula* coll.
Polygonum aviculare ssp. *boreale*	*Solanum dulcamara*	*Festuca arundinacea*
Rumex crispus	*Veronica longifolia*	*Festuca rubra*
Isatis tinctoria	*Odontites litoralis*	*Festuca polesica*
Barbarea stricta	*Plantago major* ssp. *intermedia*	*Poa humilis*
Cochlearia danica	*Plantago maritima*	*Puccinellia capillaris*
Cakile maritima ssp. *baltica*	*Eupatorium cannabinum*	*Leymus arenarius*
Crambe maritima	*Aster tripolium*	*Elymus repens*
Lysimachia vulgaris	*Tripleurospermum maritimum*	*Deschampsia bottnica*
Glaux maritima	*Tanacetum vulgare*	*Hierochloe odorata* ssp. *baltica*
Rosa rugosa	*Artemisia vulgaris* var. *coarctata*	*Calamagrostis stricta*
Potentilla anserina ssp. *anserina*	*Cirsium arvense* var. *mite*	*Phalaris arundinacea*
Potentilla anserina ssp. *groenlandica*	*Sonchus arvensis* var. *maritimus*	*Alopecurus arundinaceus*
Vicia cracca	*Allium schoenoprasum*	*Phragmites australis*

Table 2. The environmental variables included in the logistic regression models.

Island geographical position (Finnish KKJ projected *x*- and *y*-coordinates of the island midpoint): (1) west–east, (2) south–north.
Length of the island shore line (island perimeter).
Height of the island (highest point of the island).
Total area of flat shores (shore areas with a slope less than 2 degrees within a buffer zone of 30 meter from the shore line).
Total area of non-rocky shore within a buffer zone of 30 meters from the shore line.
Total area of rocky shore within a buffer zone of 30 meters from the shore line.
Minimum island exposure (lowest exposure pixel value within a buffer zone of 30 meters from the island shore).
Maximum island exposure (highest exposure pixel value within a buffer zone of 30 meters from the island shore).
Island shelter (total land area divided by total area of water within a buffer zone of 2 km outwards from the island shore line).
Island shape (island area divided by island shore length)
Island distance from the mainland.
Island distance from large (inhabited) islands (*see* Fig. 1).

as this value is commonly considered the limit for a model with a reasonable accuracy (*see* e.g. Pearce & Ferrier 2000). The binary logistic regression models were made for the following three types of conditions:

Type I: to examine which variables exert influence on the present probability of occurrence: islands with no contemporary occurrences are compared with islands with contemporary occurrences.

Type II: to examine which variables exert influence on the colonisations: islands with both historical and contemporary occurrences (preserved) are compared with islands with only contemporary occurrences (colonisations).

Type III: to examine which variables exert influence on the turnover: islands from which the species has become extinct are compared with islands that have been colonised by the species.

Type I analysis was made for most of the species, except for the very common, that occur on almost every island, and the very rare, for which it was not possible to build reliable models. Type II analysis was made for species that have clearly increased, and type III for species that have decreased, or for species with a high turnover (many extinctions and colonisations). In the section dealing with individual species, the three types of analyses (I–III) are referred to. For the binary logistic regression model parameters and the AUC values, *see* Appendix.

Turnover was calculated using the formula TR = $(I + E)/(S_1 + S_2) \times 100$, where I is the number of immigrations and E is the number of species extinctions, S_1 and S_2 are the numbers of islands on which a particular species was present during the historical and the contemporary surveys, respectively (*see* e.g. Schoener 1988).

Results

General results

The total number of occurrences (presences of species for each island) was 12 147 in the historical data set and 14 906 in the contemporary data set, the increase thus being 2759 occurrences or 22.7%. The number of extinctions from the islands was 1339 and the number of colonisations 4098. The number of species whose frequencies have increased and decreased were 59 and 20, respectively (no change for *Festuca polesica* and *Potentilla anserina* ssp. *anserina*). The number of new species is 3, of which 2 (*Ligusticum scoticum* and *Rosa rugosa*) probably did not occur in the archipelago of SW Finland during the historical surveys. None of the species have become extinct, but five of the species (*Blysmus rufus*, *Carex glareosa*, *Suaeda maritima*, *Salsola kali*, *Salicornia europaea*) are very near extinction from the study islands. The number of species present on more than 50% of the islands has risen from 29 to 35. *Festuca rubra* is the most frequently occurring species in the historical data set, and is it still in the contemporary set. Species that stand out from the main pattern as having increased considerably in relation to other species are e.g. *Odontites litoralis*, *Artemisia vulgaris* var. *coarctata*, *Atriplex prostrata*, *Aster tripolium* and *Isatis tinctoria*. The decreasing species include e.g. *Montia fontana*, *Carex glareosa*, *Juncus ranarius* and *Poa humilis*. A summary graph of the frequencies of all species in both the historical and the contemporary data sets is presented in Fig. 3 and summary data on the species in Table 3.

The species: a synthesis of the results

Ophioglossum vulgatum (Fig. 4)

It has increased very markedly (from 97 to 221 island occurrences) in all parts of the study area, except in the southernmost area. According to Eklund (1958), it is a typical species of shore meadows. It was found on most types of shores. The probability of occurrence according to type I analysis increases with decreasing minimum island exposure. Type II analysis showed that the species has spread towards islands near the mainland and large islands. Type III analysis indicated that the probability of colonisations in relation to extinctions has increased towards the north.

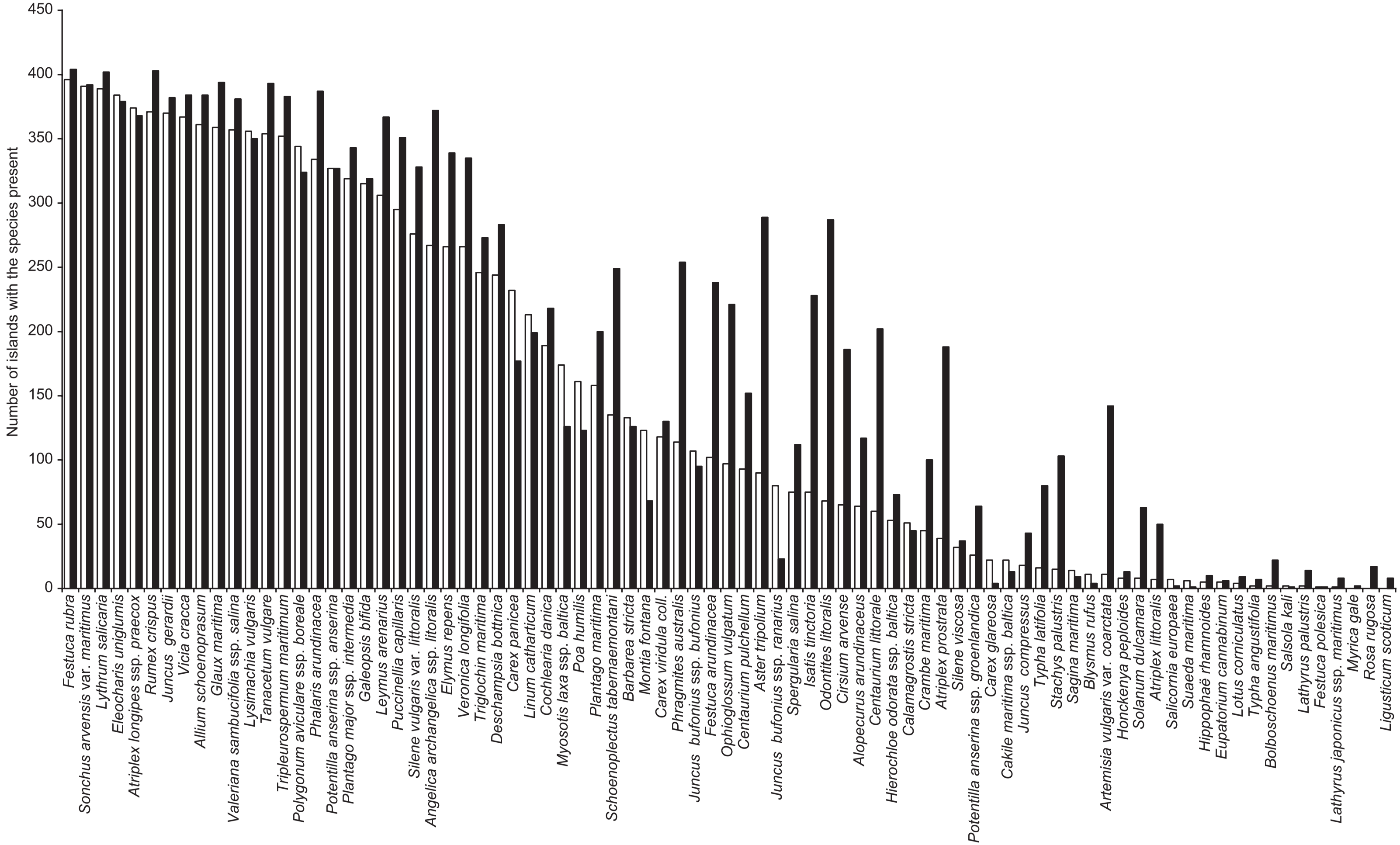

Fig. 3. The 81 species of the 412 islands in the archipelago of SW Finland ordered according to their historical frequency (historical: white bar, contemporary: black bar).

Table 3. Summary data on the 81 shore species on the 412 islands.

Species	Extinctions	Preserved	Colonizations	Historical total	Contemp. total	Change	Turnover	Hist. % of islands	Cont. % of islands	Change (%)
Ophioglossum vulgatum	18	79	142	97	221	124	50.3	23.5	53.6	127.8
Myrica gale	0	0	2	0	2	2	100	0	0.5	
Montia fontana	84	39	29	123	68	–55	59.2	29.9	16.5	–44.7
Honckenya peploides	0	8	5	8	13	5	23.8	1.9	3.2	62.5
Sagina maritima	8	6	3	14	9	–5	47.8	3.4	2.2	–35.7
Spergularia salina	30	45	67	75	112	37	51.9	18.2	27.2	49.3
Silene viscosa	7	25	12	32	37	5	27.5	7.8	9	15.6
Silene vulgaris var. *littoralis*	19	257	71	276	328	52	14.9	67	79.6	18.8
Atriplex littoralis	4	3	47	7	50	43	89.5	1.7	12.1	614.3
Atriplex prostrata	6	33	155	39	188	149	70.9	9.5	45.6	382.1
Atriplex longipes ssp. *praecox*	28	346	22	374	368	–6	6.7	90.8	89.3	–1.6
Salicornia europaea	6	1	1	7	2	–5	77.8	1.7	0.5	–71.4
Suaeda maritima	6	0	1	6	1	–5	100	1.5	0.2	–83.3
Salsola kali	1	1	0	2	1	–1	33.3	0.5	0.2	–50
Polygonum aviculare ssp. *boreale*	45	299	25	344	324	–20	10.5	83.5	78.6	–5.8
Rumex crispus	0	371	32	371	403	32	4.1	90	97.8	8.6
Isatis tinctoria	10	65	163	75	228	153	57.1	18.2	55.3	204
Barbarea stricta	60	73	53	133	126	–7	43.6	32.3	30.6	–5.3
Cochlearia danica	8	181	37	189	218	29	11.1	45.9	52.9	15.3
Cakile maritima ssp. *baltica*	16	6	7	22	13	–9	65.7	5.3	3.2	–40.9
Crambe maritima	7	38	62	45	100	55	47.6	10.9	24.3	122.2
Lysimachia vulgaris	23	333	17	356	350	–6	5.7	86.4	85	–1.7
Glaux maritima	3	356	38	359	394	35	5.4	87.1	95.6	9.7
Rosa rugosa	0	0	17	0	17	17	100	0	4.1	
Potentilla anserina ssp. *anserina*	32	295	32	327	327	0	9.8	79.4	79.4	0.0
Potentilla anserina ssp. *groenlandica*	6	20	44	26	64	38	55.6	6.3	15.5	146.2
Vicia cracca	9	358	26	367	384	17	4.7	89.1	93.2	4.6
Lathyrus japonicus ssp. *maritimus*	0	1	7	1	8	7	77.8	0.2	1.9	700
Lathyrus palustris	2	0	14	2	14	12	100	0.5	3.4	600
Lotus corniculatus	1	3	6	4	9	5	53.8	1	2.2	125
Lythrum salicaria	1	388	14	389	402	13	1.9	94.4	97.6	3.3
Linum catharticum	62	151	48	213	199	–14	26.7	51.7	48.3	–6.6
Ligusticum scoticum	0	0	8	0	8	8	100	0	1.9	
Angelica archangelica ssp. *litoralis*	9	258	114	267	372	105	19.2	64.8	90.3	39.3

continued

Table 3. Continued.

Species	Extinctions	Preserved	Colonizations	Historical total	Contemp. total	Change	Turnover	Hist. % of islands	Cont. % of islands	Change (%)
Hippophaë rhamnoides	0	5	5	5	10	5	33.3	1.2	2.4	100
Centaurium littorale	6	54	148	60	202	142	58.8	14.6	49	236.7
Centaurium pulchellum	23	70	82	93	152	59	42.9	22.6	36.9	63.4
Valeriana sambucifolia ssp. *salina*	8	349	32	357	381	24	5.4	86.7	92.5	6.7
Myosotis laxa ssp. *baltica*	95	79	47	174	126	–48	47.3	42.2	30.6	–27.6
Galeopsis bifida	41	274	45	315	319	4	13.6	76.5	77.4	1.3
Stachys palustris	1	14	89	15	103	88	76.3	3.6	25	586.7
Solanum dulcamara	0	8	55	8	63	55	77.5	1.9	15.3	687.5
Veronica longifolia	18	248	87	266	335	69	17.5	64.6	81.3	25.9
Odontites litoralis	2	66	221	68	287	219	62.8	16.5	69.7	322.1
Plantago major ssp. *intermedia*	22	297	46	319	343	24	10.3	77.4	83.3	7.5
Plantago maritima	20	138	62	158	200	42	22.9	38.3	48.5	26.6
Eupatorium cannabinum	1	4	2	5	6	1	27.3	1.2	1.5	20
Aster tripolium	2	88	201	90	289	199	53.6	21.8	70.1	221.1
Tripleurospermum maritimum	10	342	41	352	383	31	6.9	85.4	93	8.8
Tanacetum vulgare	6	348	45	354	393	39	6.8	85.9	95.4	11
Artemisia vulgaris var. *coarctata*	0	11	131	11	142	131	85.6	2.7	34.5	1190.9
Cirsium arvense	18	47	139	65	186	121	62.5	15.8	45.1	186.2
Sonchus arvensis var. *maritimus*	8	383	9	391	392	1	2.2	94.9	95.1	0.3
Allium schoenoprasum	8	353	31	361	384	23	5.2	87.6	93.2	6.4
Triglochin maritima	23	223	50	246	273	27	14.1	59.7	66.3	11
Typha latifolia	4	12	68	16	80	64	75	3.9	19.4	400
Typha angustifolia	0	2	5	2	7	5	55.6	0.5	1.7	250
Juncus compressus	6	12	31	18	43	25	60.7	4.4	10.4	138.9
Juncus gerardii	5	365	17	370	382	12	2.9	89.8	92.7	3.2
Juncus bufonius ssp. *bufonius*	57	50	45	107	95	–12	50.5	26	23.1	–11.2
Juncus bufonius ssp. *ranarius*	61	19	4	80	23	–57	63.1	19.4	5.6	–71.3
Bolboschoenus maritimus	1	1	21	2	22	20	91.7	0.5	5.3	1000
Schoenoplectus tabernaemontani	15	120	129	135	249	114	37.5	32.8	60.4	84.4
Blysmus rufus	8	3	1	11	4	–7	60	2.7	1	–63.6
Eleocharis uniglumis	16	368	11	384	379	–5	3.5	93.2	92	–1.3
Carex glareosa	19	3	1	22	4	–18	76.9	5.3	1	–81.8
Carex panicea	77	155	22	232	177	–55	24.2	56.3	43	–23.7
Carex viridula coll.	30	88	42	118	130	12	29	28.6	31.6	10.2
Festuca arundinacea	393	11	396	404	8	1.8	96.1	98.1	2	

Festuca polesica	0	1	0	1	1	0	0	0.3	0.3	0.0
Poa humilis	73	88	35	161	123	−38	38	39.1	29.9	−23.6
Puccinellia capillaris	8	287	64	295	351	56	11.1	71.6	85.2	19
Leymus arenarius	14	292	75	306	367	61	13.2	74.3	89.1	19.9
Elymus repens	19	247	92	266	339	73	18.3	64.6	82.3	27.4
Deschampsia bottnica	25	219	64	244	283	39	16.9	59.2	68.7	16
Hierochloe odorata ssp. *baltica*	21	32	41	53	73	20	49.2	12.9	17.7	37.7
Calamagrostis stricta	28	23	22	51	45	−6	52.1	12.4	10.9	−11.8
Phalaris arundinacea	6	328	59	334	387	53	9	81.1	93.9	15.9
Alopecurus arundinaceus	12	52	65	64	117	53	42.5	15.5	28.4	82.8
Phragmites australis	5	109	145	114	254	140	40.8	27.7	61.7	122.8

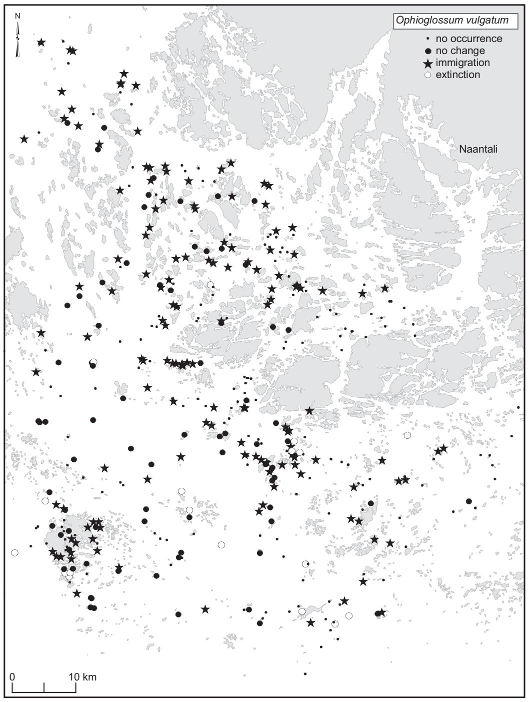

Fig. 4. Map of the species.

Myrica gale

The species is very rare in the area and was not noted during the historical surveys (Eklund 1958). Today it occurs on two of the surveyed islands (nos. 266, 278).

Montia fontana (Fig. 5)

It was typically found on moist shore meadows and the innermost parts of inlets. The species is hard to detect, especially later in the summer, and might have been overlooked on some islands. The species has decreased in frequency from 123 to 68. Most of the extinctions have taken place in the southern part of the area, while most of the colonisations have occurred in the north, a fact that is hard to explain. The turnover is high. According to type I analysis, the probability of occurrence of *Montia fontana* increases to the north, and with increasing island perimeter and area of flat shores. Type III analysis gave a good model, showing that islands with colonisations are situated closer to the mainland and on flatter shores as compared with islands with extinctions.

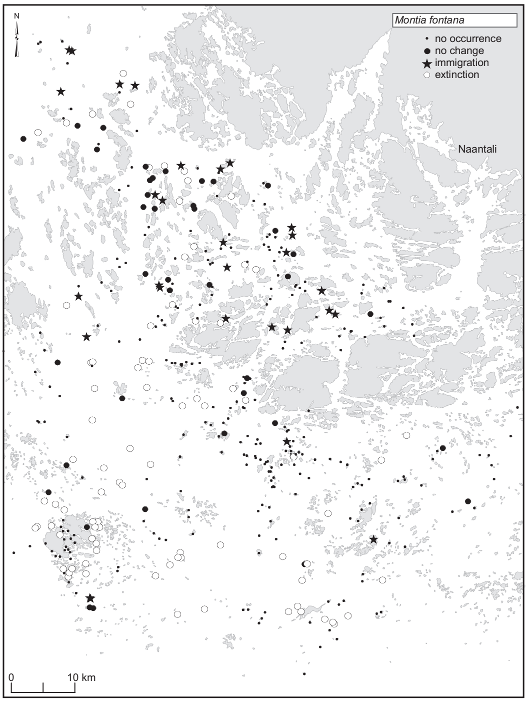

Fig. 5. Map of the species.

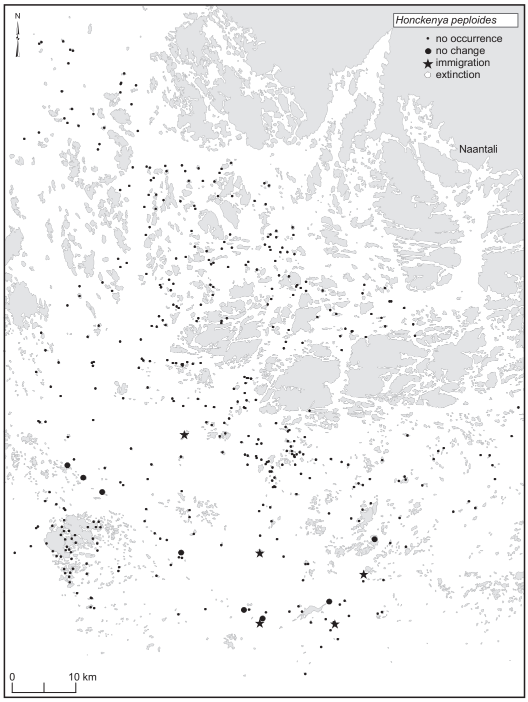

Fig. 6. Map of the species.

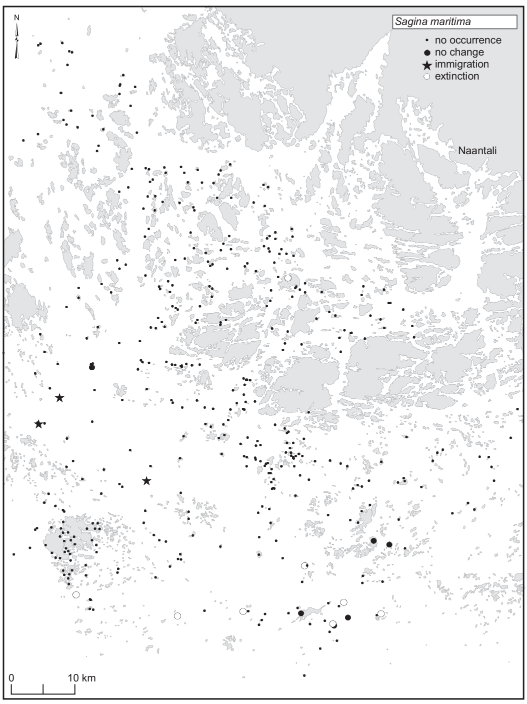

Fig. 7. Map of the species.

Honckenya peploides (Fig. 6)

It is unexpectedly rare, probably as a result of its dependency on the also rare, extensive sandy shores in the area. The number of occurrences has increased from 8 to 13, however.

Sagina maritima (Fig. 7)

Rare in the area. Because of its small size, it is very difficult to find, which might partly explain this rareness both in the historical and the contemporary data. It usually grew near the shoreline of islands in the southern part of the study area. The frequency has decreased from 14 to 9, but it remains uncertain how significant this decrease is.

Spergularia salina (Fig. 8)

It belongs to the increasing species in the area (from 75 to 112 island records). It was found in the entire study area on many types of flat shores, from sand to rock crevices. Type I analysis showed that the probability of occurrence

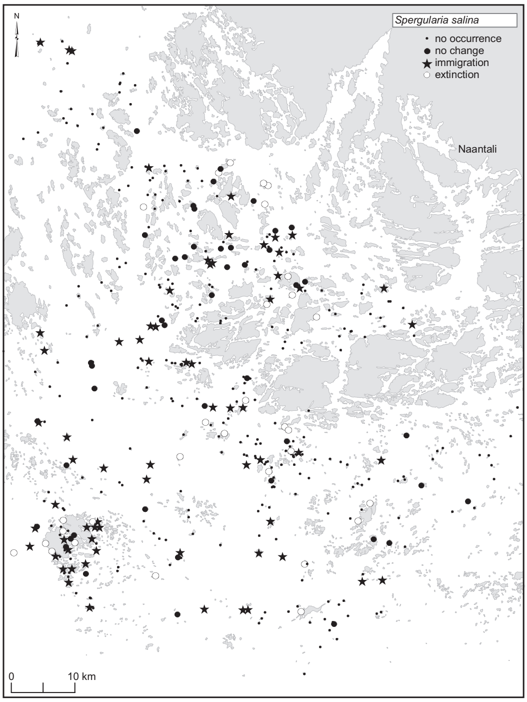

Fig. 8. Map of the species.

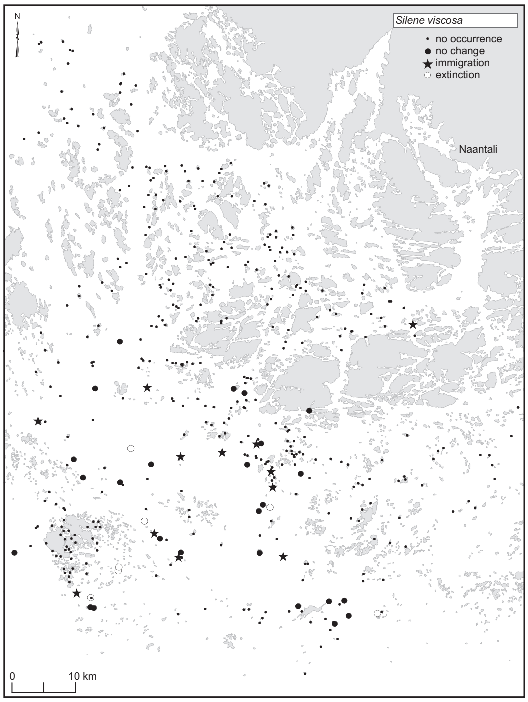

Fig. 9. Map of the species.

increases mainly with increasing flat shore area, but the model is weak. Type III analysis gave a weak non-interpretable model.

Silene viscosa (Fig. 9)

With 37 contemporary records as compared with 32 historical, *Silene viscosa* has increased somewhat in the area. It occurs only in the southern part of the study area and, with few exceptions, only on very exposed islands. It was usually found in cracks in the rock and on sandy heaths.

Silene vulgaris var. *littoralis* (Fig. 10)

Eklund (1958) included *S. vulgaris* var. *littoralis* among the *Schärenpflanzen*, which means that it should mostly grow on small islands in the outer archipelago. Today it belongs to the common shore species that occur on all types of shores on most of the islands. It has increased slightly (from 276 to 328 island records), and uncolonized islands in the northern part of the study area are now colonized. Type I model which shows that the probability of occurrence increases with

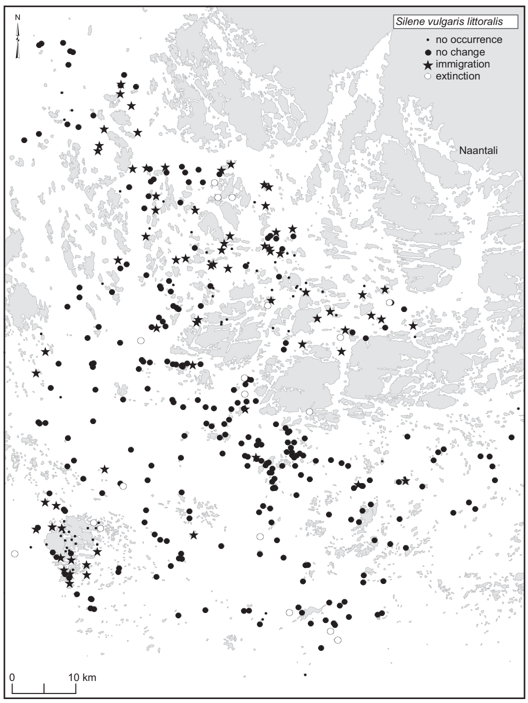

Fig. 10. Map of the species.

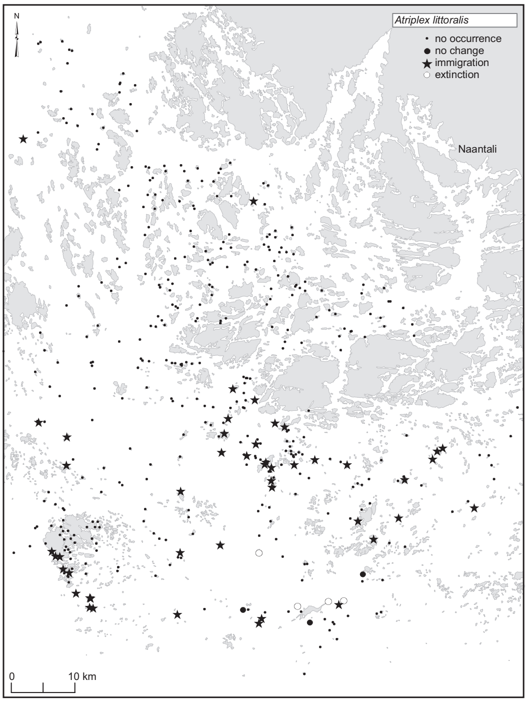

Fig. 11. Map of the species.

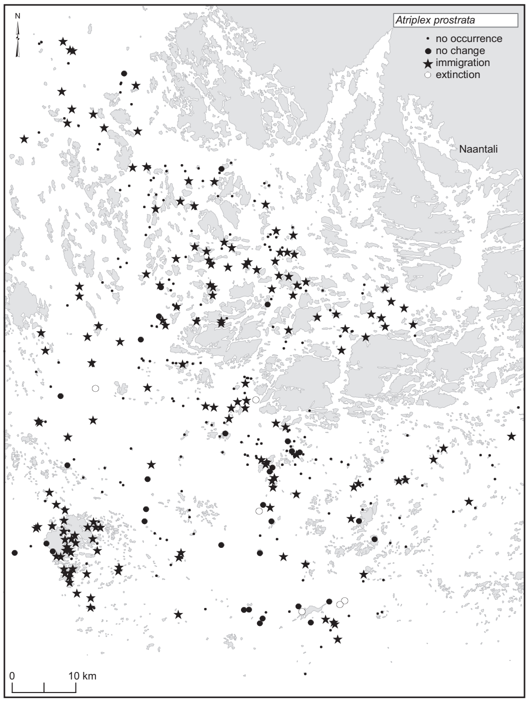

Fig. 12. Map of the species.

decreasing shelter, increasing minimum island exposure and distance from the mainland. Type II analysis gave a good model, showing that the islands with colonisations are situated closer to large, main islands and farther to the north, than the islands on which *S. vulgaris* var. *littoralis* was recorded during the historical and current surveys.

Atriplex littoralis (Fig. 11)

It is almost exclusively found in the southern part of the study area on exposed, sandy and rocky shores, but it occurs again in the northernmost part (pers. obs. outside the study area). There are only 7 historical records from the study islands, but the number of records has now increased to 50. Type I model reveals that the probability of occurrence increases towards the south and with an increasing area of rocky shores.

Atriplex prostrata (Fig. 12)

The species was fairly rare (39 records) during the historical surveys, but today it is common in the entire study area (188 records). It usually grows on wrack and other deposits on the shores. Type I analysis showed that the probability of occurrence increases with total area of non-rocky shores, distance from the mainland and increasing shelter. Type II analysis indicated that islands with colonization differ from islands with preserved occurrences by a smaller area of rocky shores and lower minimum island exposure. *Atriplex prostrata* has spread from islands in exposed environments to more sheltered islands, and that there is a marked increase in the whole study area.

Atriplex longipes* ssp. *praecox (Fig. 13)

It is very common in the area and grows next to the shore line among till or on wrack on almost all islands. The frequency has remained nearly unchanged (368 contemporary records). The distribution pattern is similar to that of *Polygonum aviculare* ssp. *boreale*.

Salicornia europaea (Fig. 14)

It is very rare in the area and was now found on

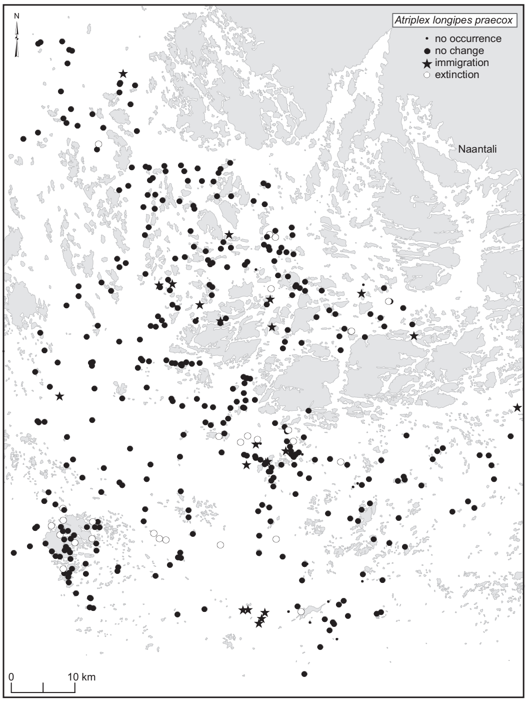

Fig. 13. Map of the species.

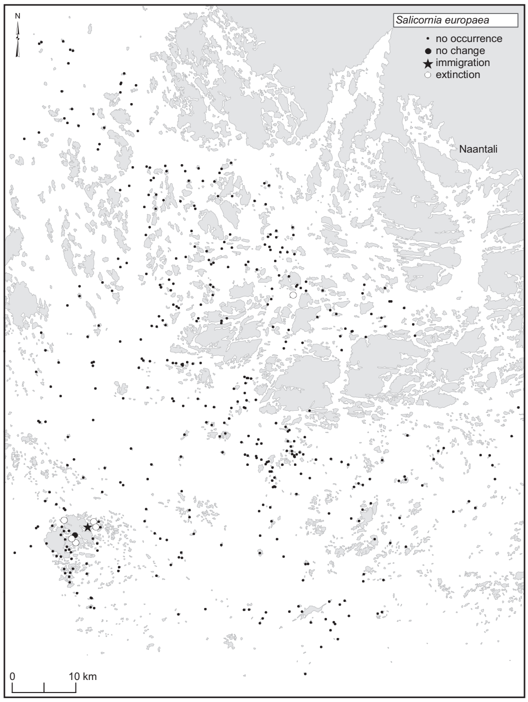

Fig. 14. Map of the species.

only two islands in Kökar. The probable reason for the extinctions (5 islands) is the increasing amount of reeds and other large herbs on the formerly open and muddy shores where it used to grow.

Suaeda maritima (Fig. 15)

It is very rare in the area. Eklund (1958) noted 12 localities in his whole study area. In the present study area, all 6 historical occurrences were from Kökar. Eklund (1958) found *S. maritima* on saline muddy shores. Only one occurrence (Kökar) was noted in the present study.

Salsola kali

It is extremely rare in the area, found only on Jurmo Sand (no. 323), where Eklund also found it. It was not noted on Fårö (Nagu, no. 720), Eklund's second locality.

Polygonum aviculare* ssp. *boreale

Very common species near the shore line, often

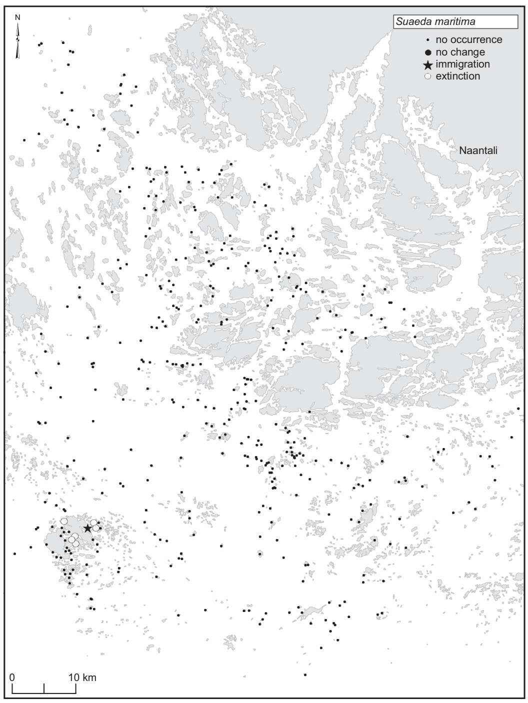

Fig. 15. Map of the species.

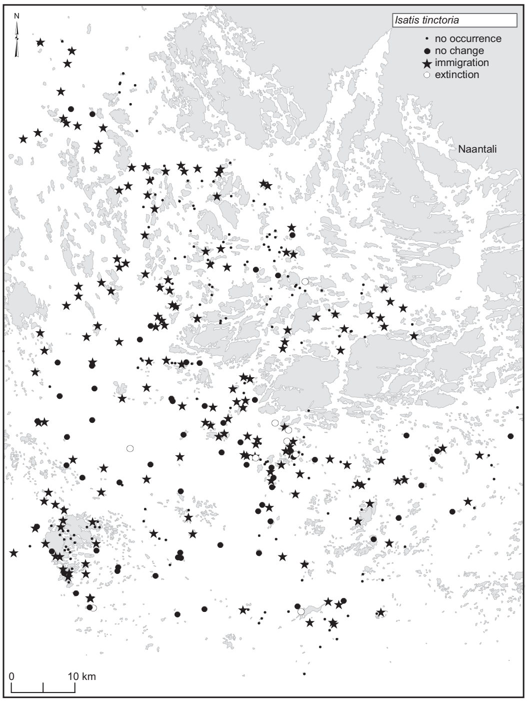

Fig. 16. Map of the species.

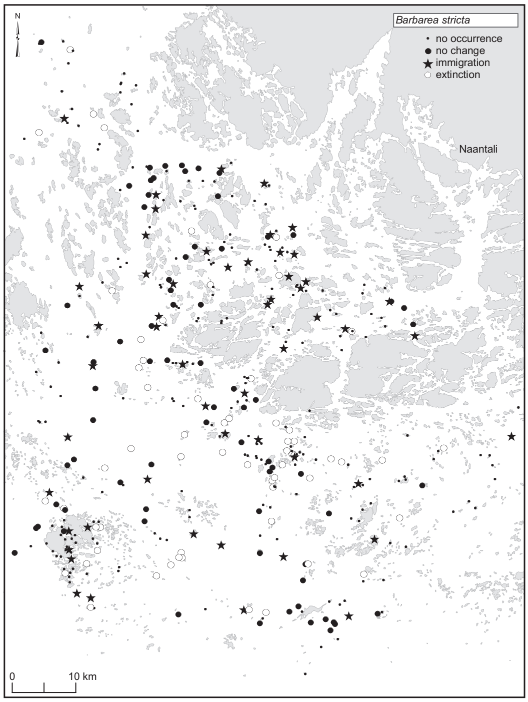

Fig. 17. Map of the species.

growing in debris on drift lines and other deposits on all types of shores in the entire area. Its frequency has slightly decreased (from 344 to 324).

Rumex crispus

It is very common in the area and occurs on almost every island on all types of shores. It has colonized the few remaining uncolonized islands and has increased from 371 to 403 island records.

Isatis tinctoria (Fig. 16)

The species is common in the area today, with 228 contemporary records, but was much rarer during the historical inventories (75 records). It was usually found on exposed till and sandy shores. The historical records are mostly from the southern outer archipelago area, and most of the colonisations are in the north. Type I analysis showed that the probability of occurrence increases with decreasing shelter, which is the variable which contributed most to the model. Type II analysis showed that the islands with colonisations differ from the islands with both old and contemporary occurrences by a more northern position and a shorter distance from large main islands.

Barbarea stricta (Fig. 17)

It is usually found on dry sand and gravel. The frequency has remained fairly constant (126 contemporary records). The map shows a peculiar distribution pattern, which was obvious also during the field-work. Most of the extinctions (60) took place on islands in the southern part of the study-area, while the colonisations (53) occurred mainly in the central and northern parts, but not in the northernmost part. Type I analysis did not result in a significant model. Type III analysis gave a good model showing that colonized islands differ from islands with extinctions by a northern position and a shorter distance to the large islands.

Cochlearia danica (Fig. 18)

According to Eklund (1958) *C. danica* is a

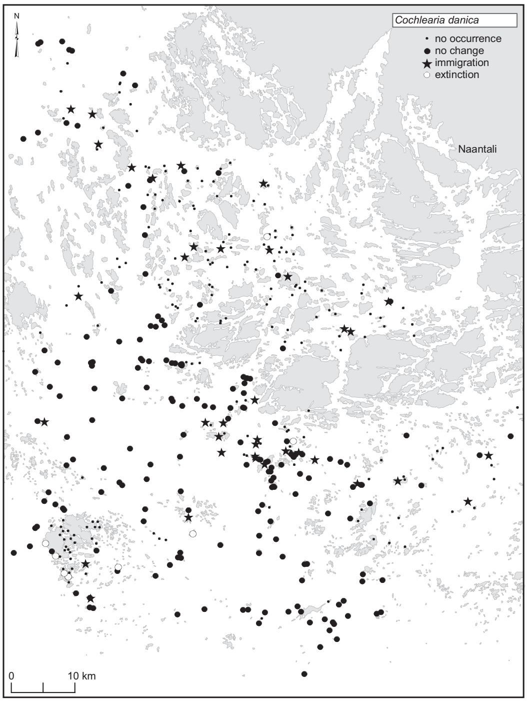

Fig. 18. Map of the species.

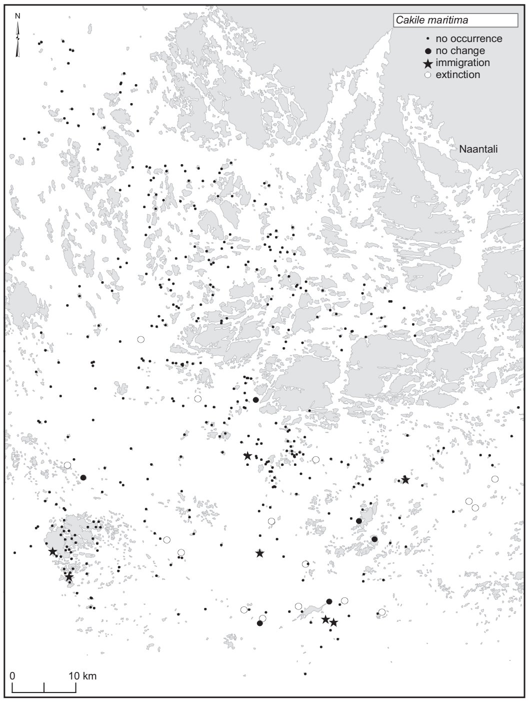

Fig. 19. Map of the species.

Schärenpflanze (island plant). It was almost exclusively found in rock crevices in the whole area, but with the highest frequency in the southern part. *Cochlearia danica* has increased somewhat in frequency (from 189 to 218). Type I analysis gave a good model (AUC 0.88) showing that the probability of occurrence increases with decreasing area of non-rocky shores, increasing maximum island exposure, decreasing shelter and increasing distance from the mainland and large main islands. This result is in agreement with *C. danica*'s character as an island plant. Type II analysis showed that islands with colonisations are located closer to the mainland than islands with both old and contemporary occurrences.

Cakile maritima* ssp. *baltica

The species is rare in the area and has decreased in frequency from 22 to 13 (Fig. 19). It usually grew on sandy shores in the southern part of the study area. None of the variables significantly contributed to the model in type III analysis.

Crambe maritima (Fig. 20)

It occurs only in the southern half of the study area, on exposed sandy and gravelly shores. It has increased markedly in frequency (from 45 to 100 island occurrences), but there is no clear expansion to the north. Type I analysis showed that the probability of occurrence increases towards the south, and with decreasing shelter and distance from large main islands. Type II analysis resulted in a weak non-interpretable model.

Lysimachia vulgaris (Fig. 21)

The species was very common in the entire area on all types of shores in both the historical and contemporary (350 contemporary records) data.

Glaux maritima (Fig. 22)

It is very common in the area (394 contemporary records). It colonised the few remaining uncolonized islands during the time between the historical and contemporary surveys, mainly in the

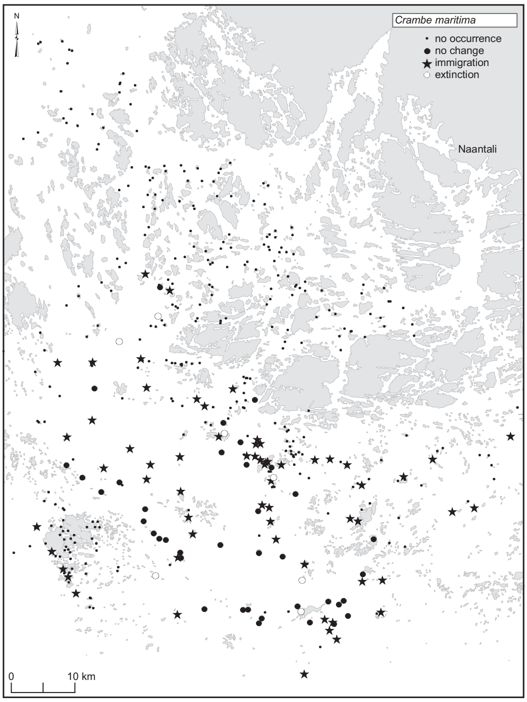

Fig. 20. Map of the species.

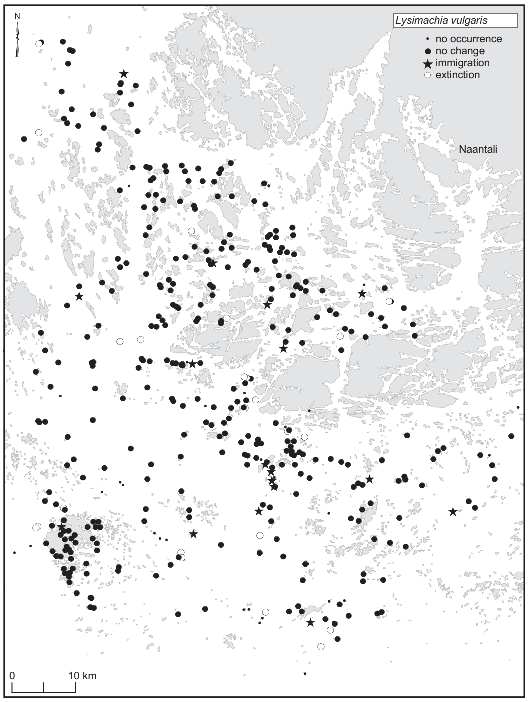

Fig. 21. Map of the species.

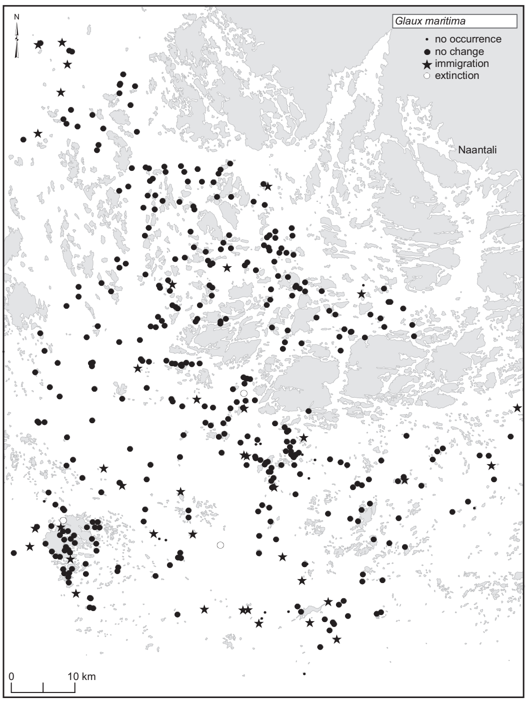

Fig. 22. Map of the species.

outer northernmost and the southernmost parts of the study area.

Rosa rugosa (Fig. 23)

The species is new in the area, and did probably not occur in the Archipelago Sea during the historical inventories. It is most likely rapidly spreading in the area. *Rosa rugosa* was found on 17 islands in the southern part of the study area.

Potentilla anserina* ssp. *anserina (Fig. 24)

It belongs to the common shore species in the area, occurring today on 327 of the islands on all types of shores all over the area. The frequency has remained unchanged.

Potentilla anserina* ssp. *groenlandica (Fig. 25)

In contrast to *P. anserina* ssp. *anserina*, *P. anserina* ssp. *groenlandica* has increased in frequency (from 26 to 64). Most of the old records are from southern maritime areas, but the species seems to have spread to the north and to less maritime

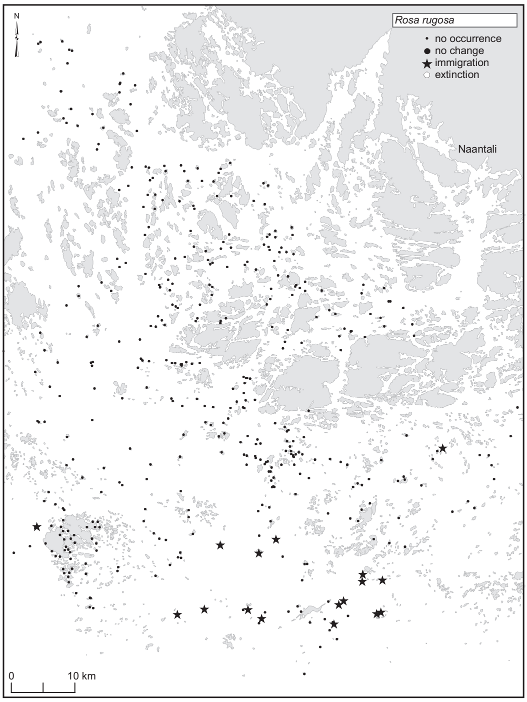

Fig. 23. Map of the species.

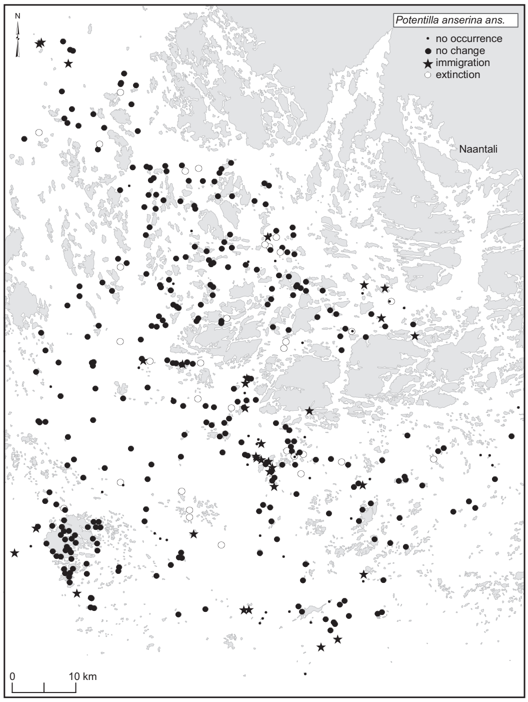

Fig. 24. Map of the species.

areas. According to type I analysis, its probability of occurrence increases with increasing distance from large islands. Type II analysis showed that the islands with colonisations differ from the islands with both old and contemporary records by a shorter distance to large main islands.

Vicia cracca

It is one of the commonest species of the surveyed islands, occurring on almost every island on all types of shores in both the historical and the contemporary data sets.

Lathyrus japonicus ssp. *maritimus* (Fig. 26)

The species is rare and unevenly distributed in the area, occurring now on 8 (previously on one) of the surveyed islands, on exposed sandy or gravelly shores.

Lathyrus palustris (Fig. 27)

Formerly a very rare species (2 occurrences) on the surveyed islands. It is still rare, but has

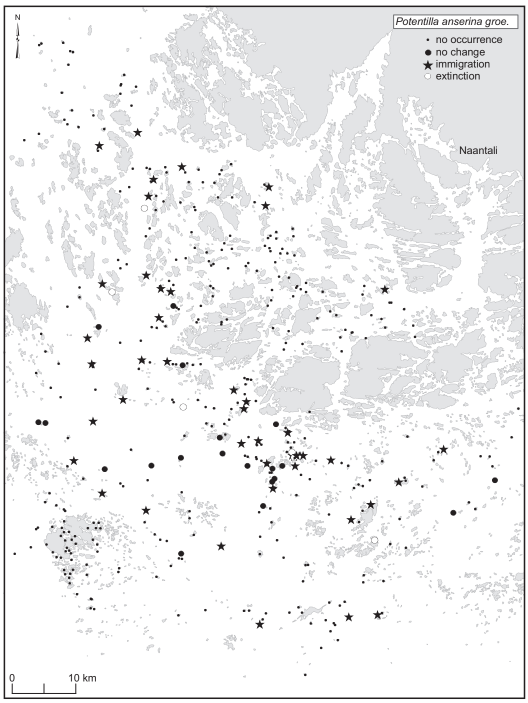

Fig. 25. Map of the species.

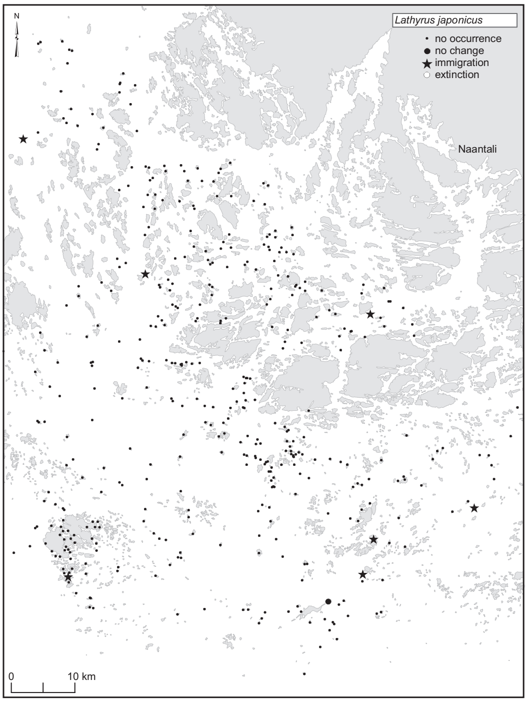

Fig. 26. Map of the species.

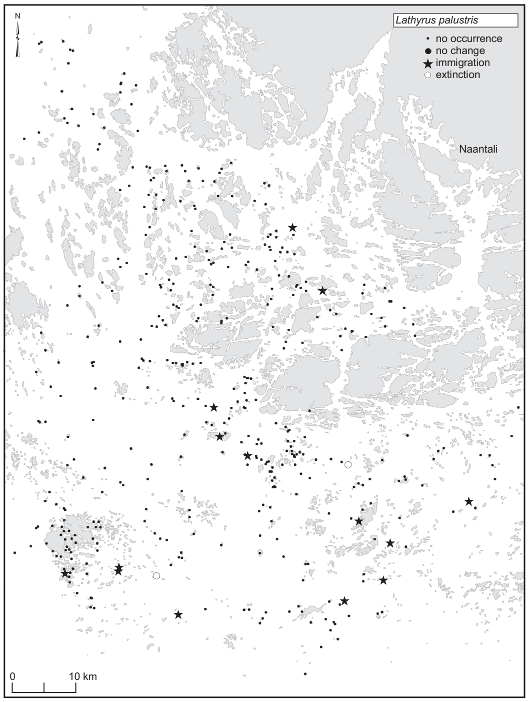

Fig. 27. Map of the species.

increased in frequency to 14 island records. It usually grew on flat, damp and sheltered shores. The impression gained during the field work and from the map is that the colonisations have taken place randomly. Type I analysis resulted in a weak non-interpretable model.

Lotus corniculatus

It is rare on the surveyed islands, but has increased (from 4 to 9 locals). The species was usually found on shore meadows. It primarily belongs to the flora of the larger main islands, and not to the small islands surveyed in this study.

Lythrum salicaria

It is very common on all types of shores on almost all of the surveyed islands. Most of the few previously uncolonized islands in the southern part of the study area are now colonised.

Linum catharticum (Fig. 28)

It is common in the whole study area, occurring mainly on low and flat shores near the shore line. The number of occurrences has slightly decreased from 213 to 199. The great number of extinctions and colonisations may partly be explained by the fact that the species is hard to detect because of its small size. Type I analysis showed that the probability of occurrence increases with an increasing shore length and a westerly position of the island. Type III analysis resulted in a weak non-interpretable model.

Ligusticum scoticum (Fig. 29)

It is new in the area, not found by Eklund or Skult. The species was found on 8 of the study islands, growing among stones, on wrack or till in the northernmost part of the study area. *See* also von Numers *et al*. (2009).

Angelica archangelica ssp. *litoralis* (Fig. 30)

According to Eklund (1958), the species is a typical "island plant", common in the outer archipelago, but getting scarcer towards the inner, more sheltered areas. Today, the species

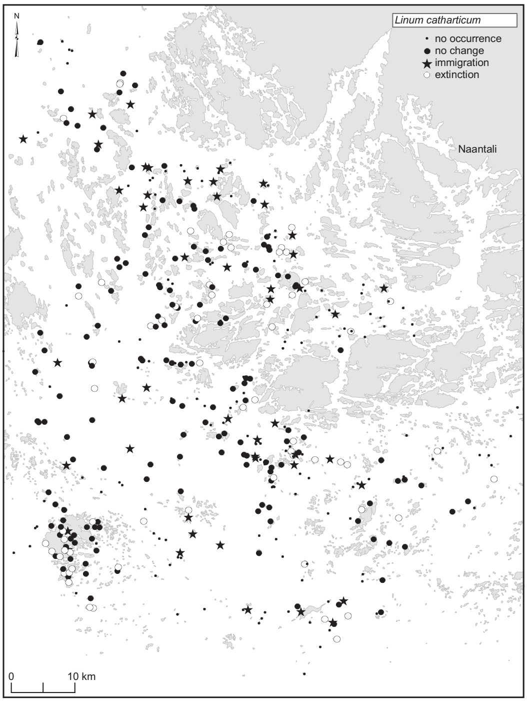

Fig. 28. Map of the species.

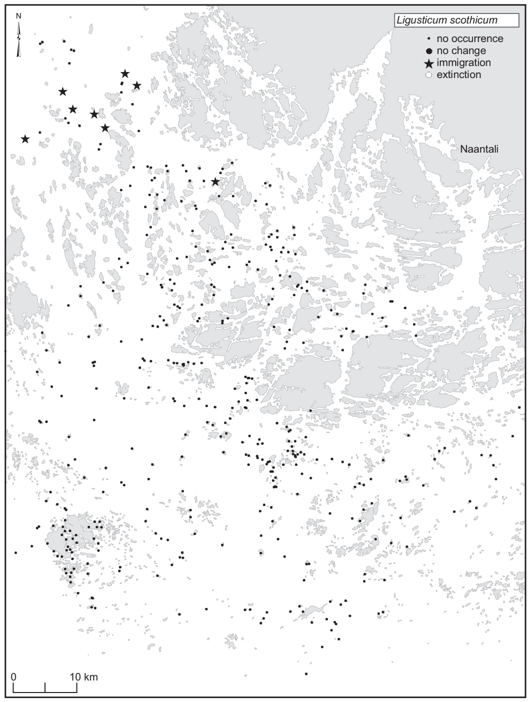

Fig. 29. Map of the species.

is common in the whole area. Most of the colonisations have taken place in the northern part of the area, where non-colonized islands were still available. It has thus markedly increased (from 267 to 372 island records). Type II analysis gave a good model, indicating that the islands with colonisations differ from the islands with both old and contemporary occurrences, by a higher degree of shelter and a shorter distance to the mainland, confirming spreading towards the inner archipelago.

Hippophaë rhamnoides (Fig. 31)

The species occurs, with one exception, only on the northernmost islands in the study area. The number of islands with the species has increased from 5 to 10.

Centaurium littorale (Fig. 32)

It is mainly found on gravelly shores or shore meadows. It is frequent in the central part of the area, but gets rarer towards the maritime southern and northern parts. The number of records

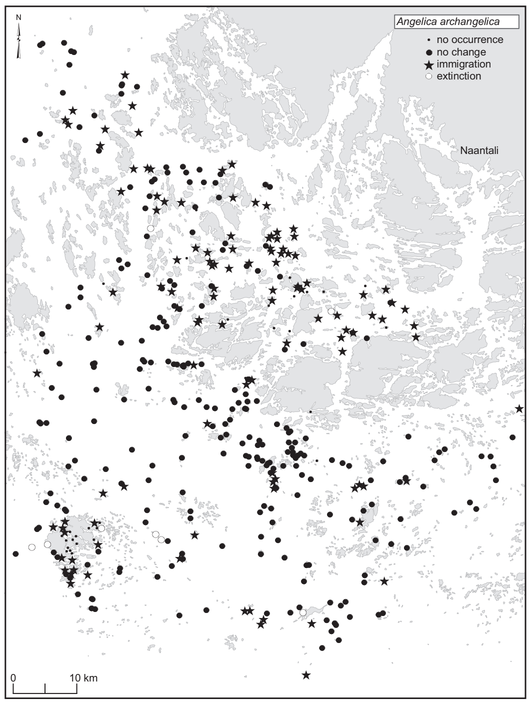

Fig. 30. Map of the species.

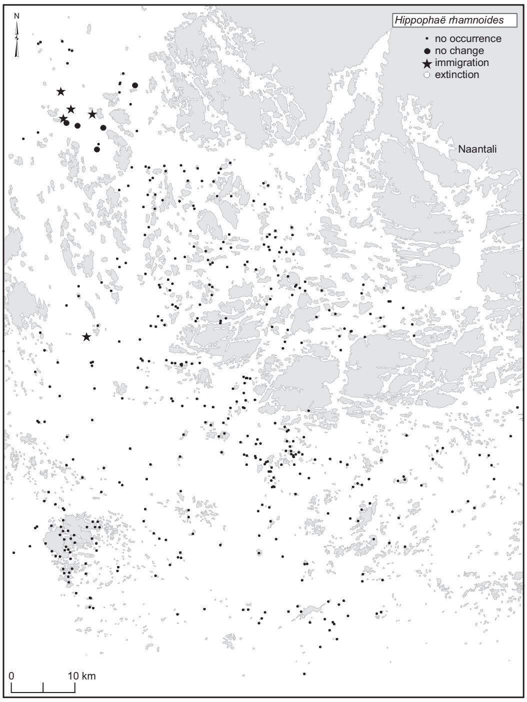

Fig. 31. Map of the species.

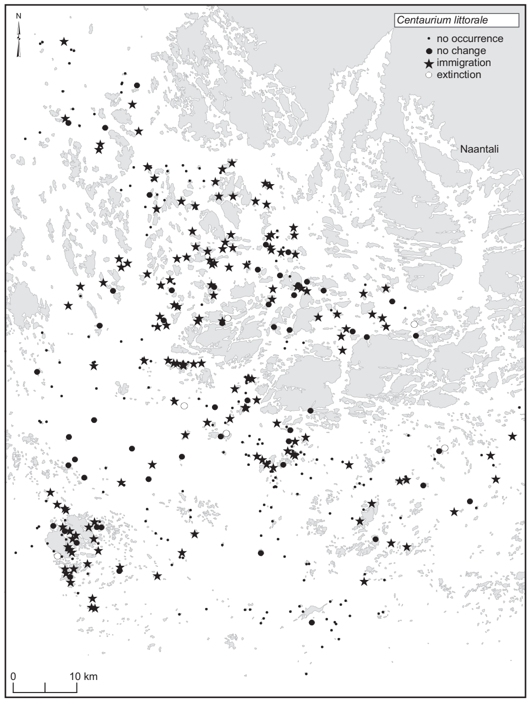

Fig. 32. Map of the species.

has more than tripled (from 60 to 202) during the time between the historical and contemporary surveys. Type I analysis showed that the probability of occurrence increases northwards and with an increasing area of flat shore, increasing shelter and decreasing minimum island exposure. Type II analysis gave a weak model, indicating that the islands with colonisations differ from the islands with both old and contemporary occurrences by a shorter shore line, indicating spreading to smaller islands.

Centaurium pulchellum (Fig. 33)

It usually grew on shores with silt-humus or shore meadows. The distribution resembles that of *C. littorale*, but the species is not as common. The number of records has increased from 93 to 152, and it is now distributed across the entire study area. Type I analysis gave a weak model, indicating that the probability of occurrence increases with increasing shelter and increasing non-rocky shore area. Type III analysis, on the other hand, gave — according to AUC — a good model, showing that islands with colonisations are less sheltered than those with extinctions. This result indicates spreading to more maritime islands.

Valeriana sambucifolia* ssp. *salina

Valeriana sambucifolia ssp. *salina* and *V. officinalis* are not separated, but the former is probably by far the commoner of these two. It belongs to the commonest of the shore species in the area. Its frequency has increased slightly (from 357 to 381), and today most of the islands are colonized by this species.

Myosotis laxa* ssp. *baltica* and *M. laxa* ssp. *caespitosa (Fig. 34)

The two subspecies are not separated in this study. *Myosotis laxa* ssp. *baltica* is undoubtedly the commonest of these. *Myosotis laxa* belongs to the decreasing species (from 174 to 126 occurrences). The turnover is high due to the great number of extinctions (95) and colonisations (47). Type I analysis showed that the probability of occurrence increases northwards,

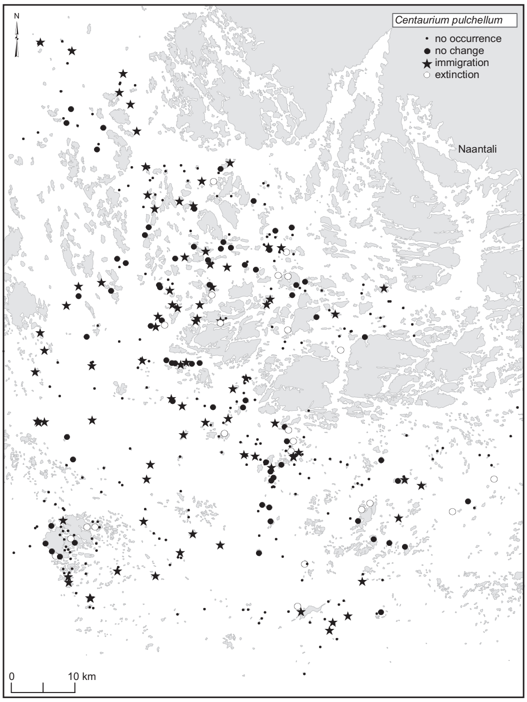

Fig. 33. Map of the species.

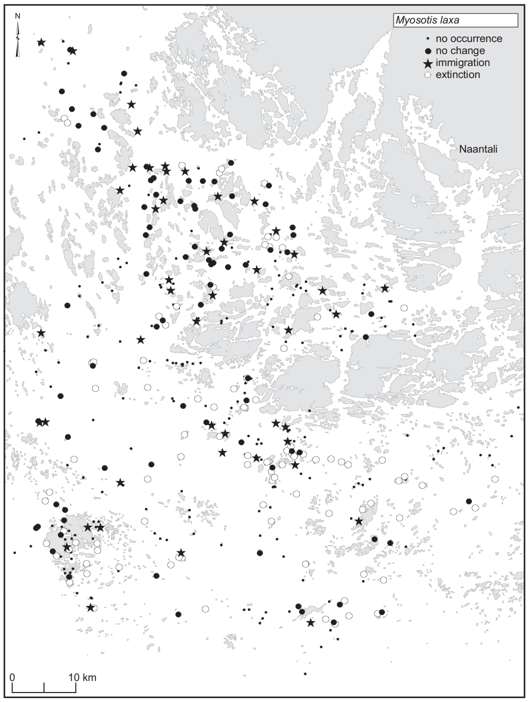

Fig. 34. Map of the species.

and with increasing shore length and increasing maximum island exposure. A northward position and area of flat shores separates islands with colonisations from islands with extinctions (type III analysis). The number of colonisations is proportionately greater in the northern part of the study area.

Galeopsis bifida (Fig. 35)

It is very common on all types of shores in the entire area, and especially frequent on beds of wrack and other deposits. The number of records has remained stable (319 contemporary records) during the time between the historical and contemporary surveys.

Stachys palustris (Fig. 36)

The species was usually found in the upper part of the shore, among dense vegetation in small inlets and on wrack on nutrient rich ground. Its frequency has increased very markedly (from 15 to 103). Type I analysis gave a good model, showing that the probability of occur-

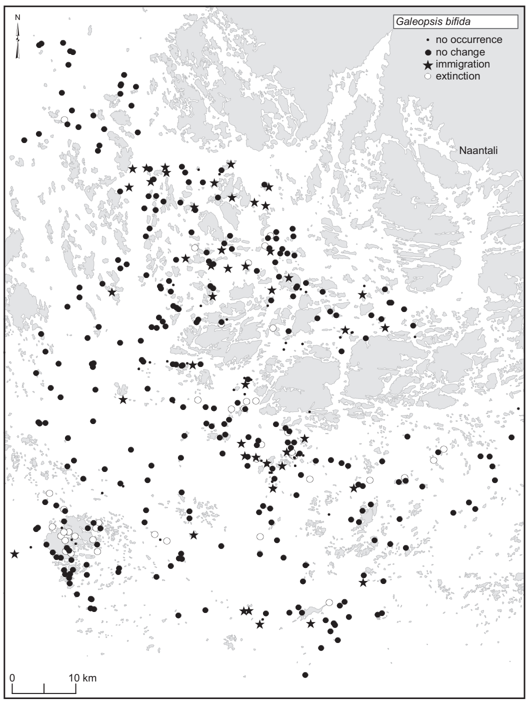

Fig. 35. Map of the species.

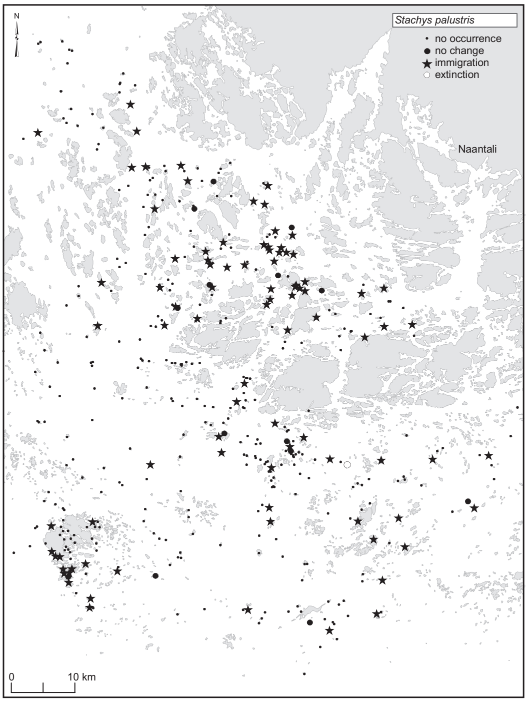

Fig. 36. Map of the species.

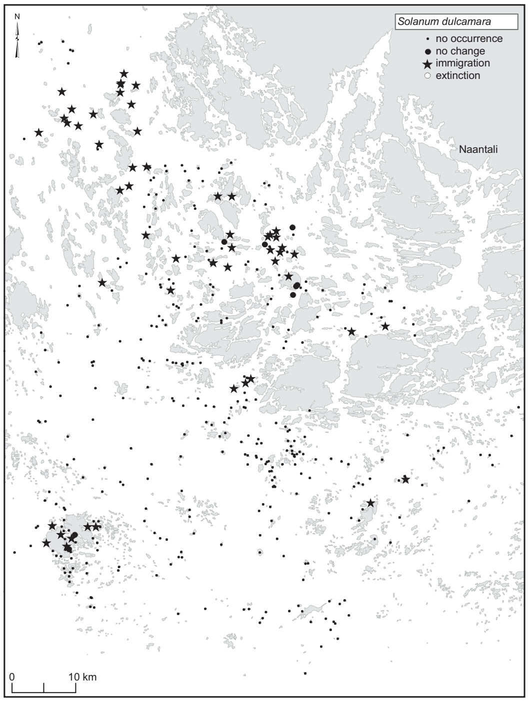

Fig. 37. Map of the species.

rence increases with area of non-rocky shores, distance from the mainland, increasing island maximum exposure and decreasing minimum island exposure. This seemingly contradictory result is explained by the fact that *S. palustris* often occurred in sheltered inlets of otherwise exposed islands. Type II analysis revealed that a shorter shore line separates the islands with contemporary records from islands with both old and contemporary records.

Solanum dulcamara (Fig. 37)

It grew in similar habitats as *Stachys palustris*, but also in rock cracks on small islands. Its frequency has clearly increased: now present on 63 as compared with just 8 in the historical data. No extinctions were noted. Its distribution is uneven, however, with clusters of localities situated near each other, and large areas, especially in the south, from where it is lacking. Type I analysis indicated that the probability of occurrence increases northwards and with increasing shelter and increasing area of non-rocky shores.

Veronica longifolia (Fig. 38)

It belongs to Eklund's (1958) "island plants". The species is very common in the entire area on all types of shores today. Its frequency has increased from 266 to 335. Type II analysis showed that islands with colonisations are situated closer to the mainland than islands with both old and contemporary records.

Odontites litoralis (Fig. 39)

It was found on most types of shores, but it is probably commonest on flat till shores. Its frequency has considerably increased (from 68 to 287) in the entire area, and the species can today be found on most of the islands. Type II analysis showed that islands that have been colonized by the species are situated closer to large main islands than islands with both old and contemporary records.

Plantago major* ssp. *intermedia (Fig. 40)

It grows on most of the islands in the entire area.

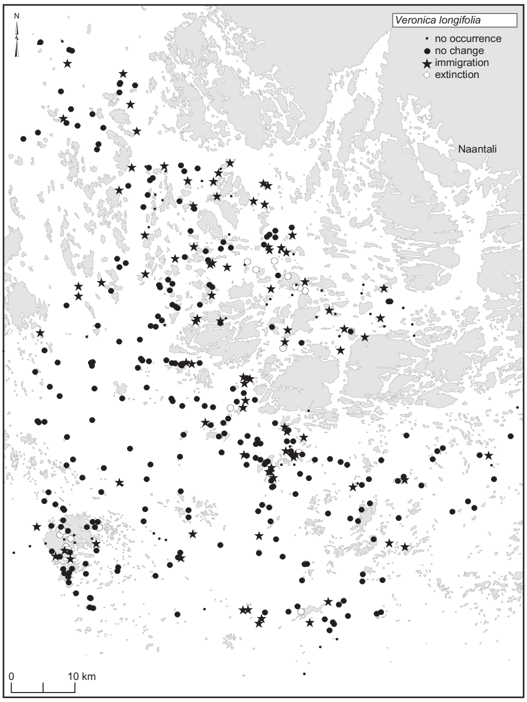

Fig. 38. Map of the species.

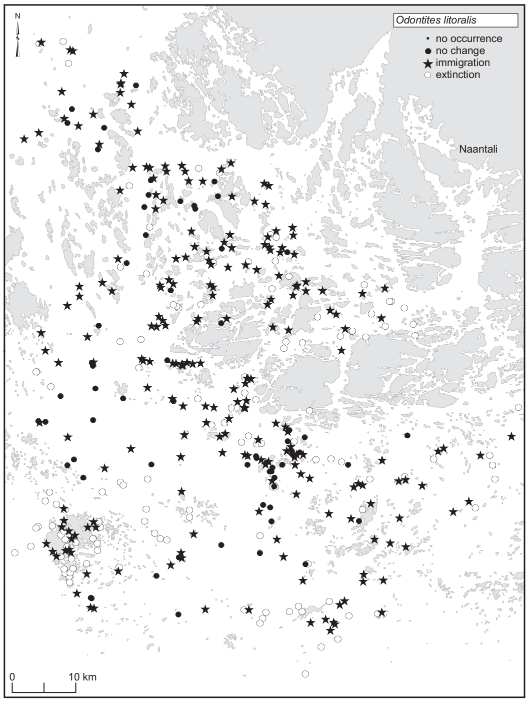

Fig. 39. Map of the species.

Its frequency has increased from 308 to 331. Colonisations, but also the extinctions, have taken place mainly in the southern part of the study area.

Plantago maritima (Fig. 41)

This species is not as common as *P. major* ssp. *intermedia*, and is rare in the maritime and highly exposed areas, especially in the south. It was usually found on gently sloping silt or gravelly shores and on shore meadows. Its frequency has increased (from 158 to 200). Type I analysis revealed that the probability of occurrence increases towards the mainland, with increasing area of non-rocky shore and shelter. Type II analysis gave a weak non-interpretable model.

Eupatorium cannabinum (Fig. 42)

All islands (6) with *E. cannabinum* are located in the southernmost part of the study area (Kökar, Fig. 42). It previously occurred on the limestone-rich island Kälklot, in the central part of the study area (Korpo), but it has disappeared from there.

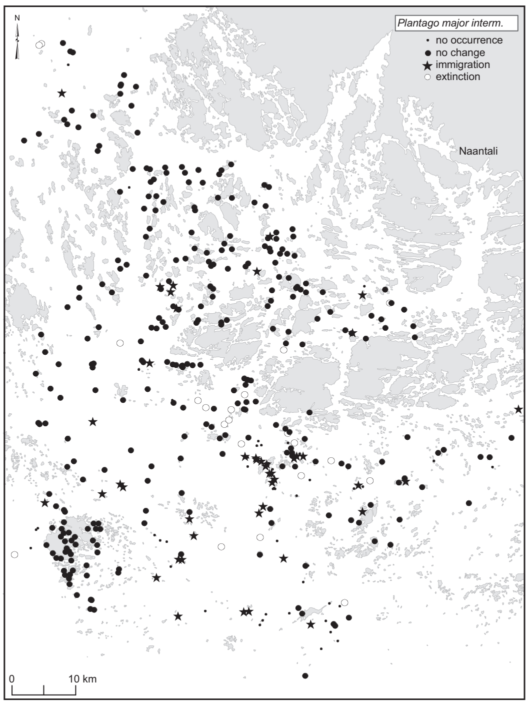

Fig. 40. Map of the species.

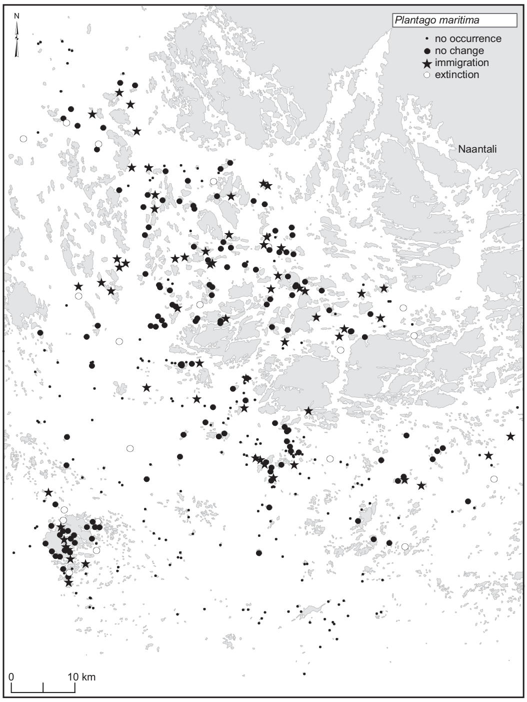

Fig. 41. Map of the species.

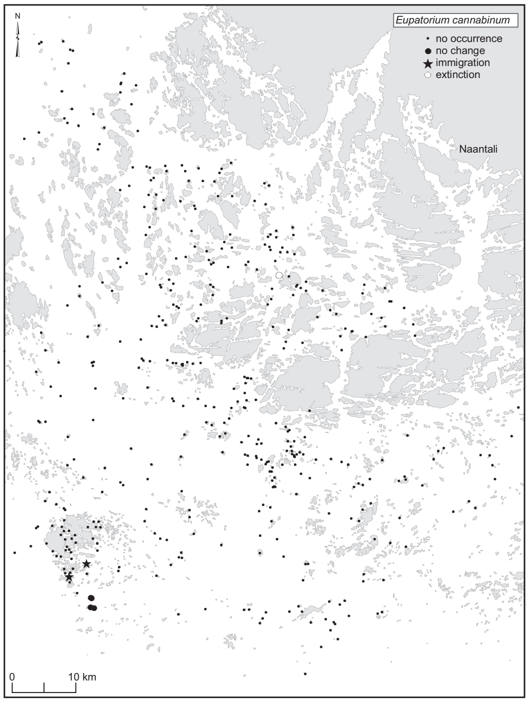

Fig. 42. Map of the species.

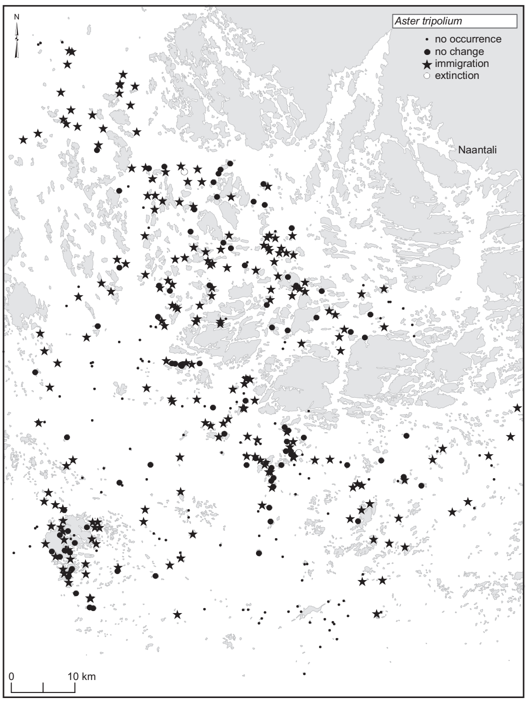

Fig. 43. Map of the species.

Aster tripolium (Fig. 43)

It is very common in the study area today. Its frequency has considerably increased (from 90 to 289 island records), with hardly any extinctions. It usually grows next to the mean water level similarly as *Deschampsia bottnica*. Type I analysis gave a good model, which includes only one significant variable; the probability of occurrence increases with decreasing minimum island exposure. The species is absent from the most exposed islands in the southernmost part of the study area. None of the variables contributed significantly to the model in type II analysis.

Tripleurospermum maritimum* ssp. *maritimum

It is one of the most common species of the shores, occurring on most of the islands (383) in the whole area on all types of shores.

Tanacetum vulgare

This species belongs to the commonest shore

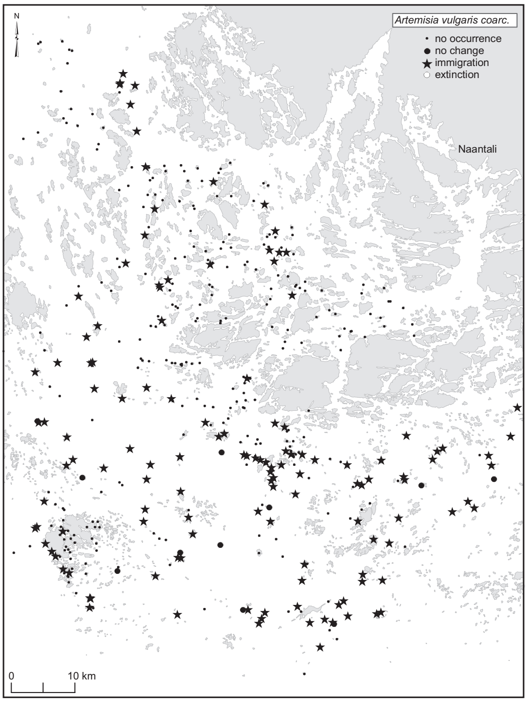

Fig. 44. Map of the species.

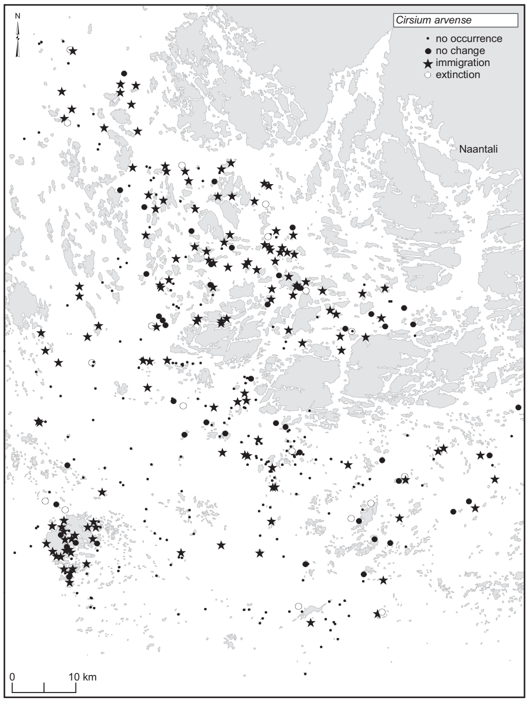

Fig. 45. Map of the species.

species in the area today, occurring on 393 of the surveyed islands.

Artemisia vulgaris* var. *coarctata (Fig. 44)

The frequency of *A. vulgaris* var. *coarctata* has increased from just 11 recordings during the historical inventories to 142 today. It was found throughout the entire area, but especially often in maritime areas on exposed shores. Most of the findings are from the maritime southern half of the study area. Type I analysis indicated that the probability of occurrence increases with increasing distance from large main islands and with decreasing shelter.

Cirsium arvense (Fig. 45)

Its frequency has increased from 65 to 186. This species is common, especially on gravelly shores, in the study area, except in the southernmost areas where it is rare. Type I analysis showed that the probability of occurrence increases as the area of non-rocky shores and the shelter of the islands increases. There is also an increased probability of occurrence to the north. Type II analysis gave a weak non-interpretable model.

Sonchus arvensis* var. *maritimus

It is one of the commonest species in the area, with 392 contemporary records. It occurs almost without exception on all islands both in the historical and the contemporary data sets.

Allium schoenoprasum

It is a very common shore plant in the area, occurring on most of the islands. The frequency has increased from 361 to 382 island records.

Triglochin maritima (Fig. 46)

A very common species on the surveyed islands, except on the exposed islands in the southernmost part of the study area. It mostly grew on flat gravelly shores and shore meadows. Its frequency has increased from 246 to 273. Type I analysis showed that the probability of occurrence

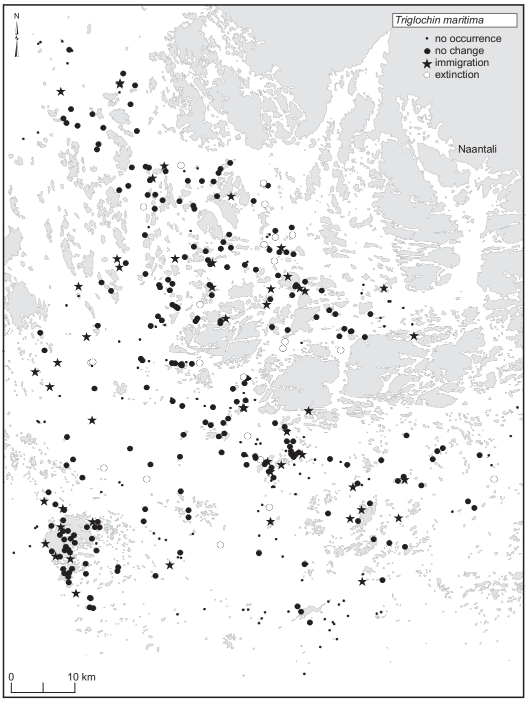

Fig. 46. Map of the species.

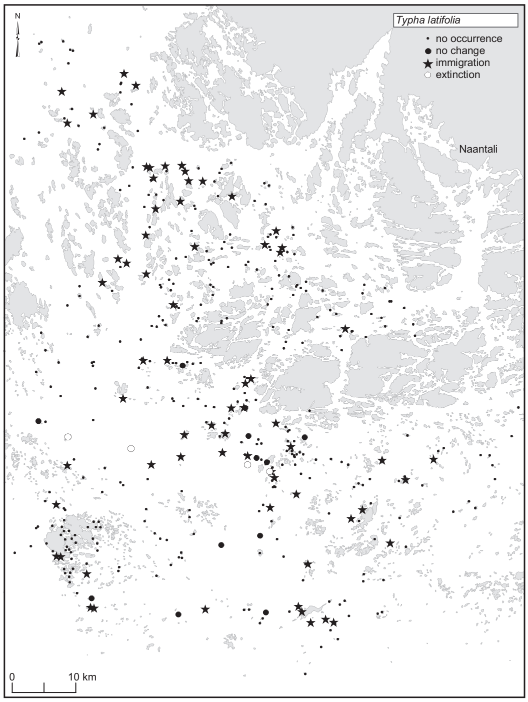

Fig. 47. Map of the species.

increases with decreasing minimum island exposure and increasing shore length and shelter. The comparison between the islands with extinctions and islands with colonisations (type III analysis) gave a good model, indicating that the probability of extinctions in relation to colonisations increases with decreasing shelter. The extinctions have mostly taken place in the open *fjärd*-areas.

Typha latifolia (Fig. 47)

It has increased very clearly in the area (from 16 to 80 records), with only few extinctions. According to Eklund (1958), the species is most abundant in the outer archipelago. Today it occurs in the whole study area, and was usually found in rock pools. The probability of occurrence increases with the area of rocky shore, probably mirroring the occurrences in rock pools. The model, however, is weak (AUC = 0.68).

Typha angustifolia

With just 7 new records, the species is rare on the study islands. All occurrences are from rock pools. The number of occurrences has increased from 2 to 7. Because of the small number of records, no statistical analyses were made.

Juncus compressus (Fig. 48)

It is one of the most typical species of rock crevices of very exposed islets in the outermost archipelago. Its frequency has increased from 18 to 43. Most of the records are from islands in the southern half of the study area. Type I analysis showed that the probability of occurrence increases with increasing exposure, but also with increasing distance from large islands. Type II analysis did not result in a significant model.

Juncus gerardii

This species was, and still is, one of the commonest shore plants in the area, occurring on most of the islands (382 contemporary records).

Juncus bufonius* ssp. *bufonius (Fig. 49)

Frequency of this species has decreased from

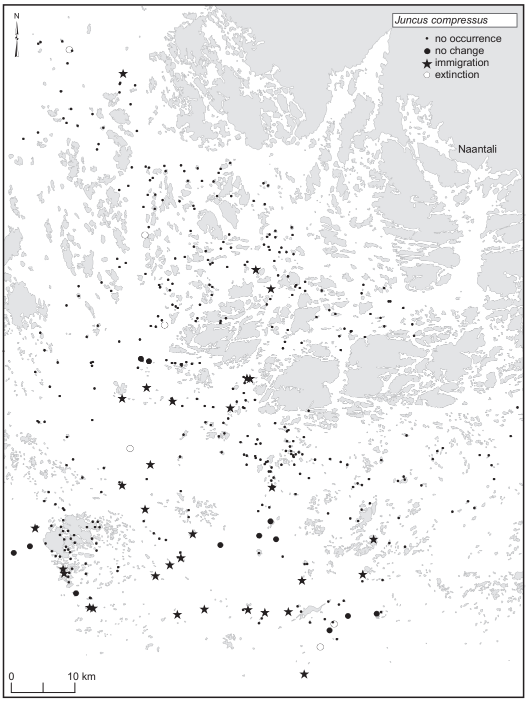

Fig. 48. Map of the species.

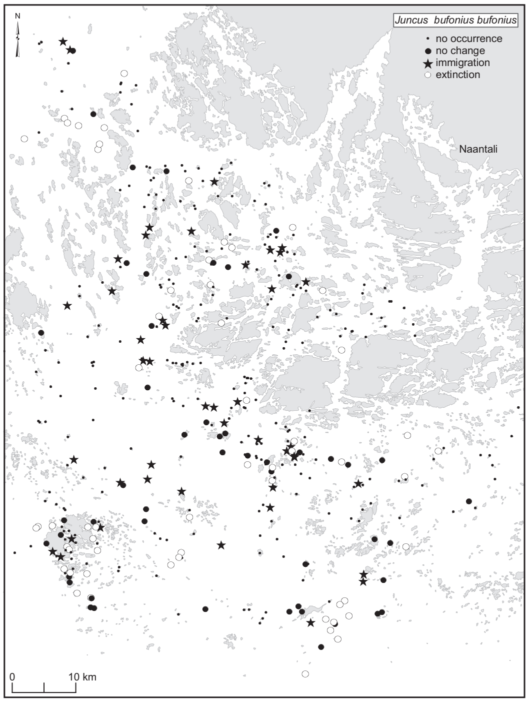

Fig. 49. Map of the species.

107 to 95. It was usually found on sandy or gravelly shores throughout the area. The turnover is high, with 57 extinctions and 50 colonisations, probably reflecting its character as a competition weak annual species. Type I and a type III analyses both resulted in weak non-interpretable models.

Juncus bufonius **ssp.** ***ranarius*** (Fig. 50)

According to Eklund (1958), this species is characteristic of wet and flat open shores with gravel or sand. It was also occasionally found in rock cracks. Its frequency has decreased from 80 to 23. Type I analysis showed that the probability of occurrence increases with increasing area of rocky shores and with decreasing island height. Type III analysis gave a weak non-interpretable model. As the number of extinctions is high (61); in addition, a comparison of islands with both historical and contemporary occurrences with islands with extinctions was made. None of the included variables, however, significantly contributed to the model.

Bolbochoenus maritimus (Fig. 51)

This species is rare on the studied islands. Eklund found it on only two of the now surveyed islands (Kökar); today its frequency has increased to 22. Eklund describes the species as irregularly distributed, mostly growing in sheltered inlets. The same description is valid today. Type I analysis indicated that the probability of occurrence increases with increasing area of non-rocky shores and a position in the western direction.

Schoenoplectus tabernaemontani (Fig. 52)

It was common already during the historical inventories, but the frequency has almost doubled since then: from 135 to 249 island records. New occurrences were noted in all parts of the study area. It usually grew in sheltered areas near the shore line or in rock pools. Type I analysis showed that the probability of occurrence increases to the west, with increasing island perimeter and decreasing minimum island exposure. Type II analysis gave a weak non-interpretable model.

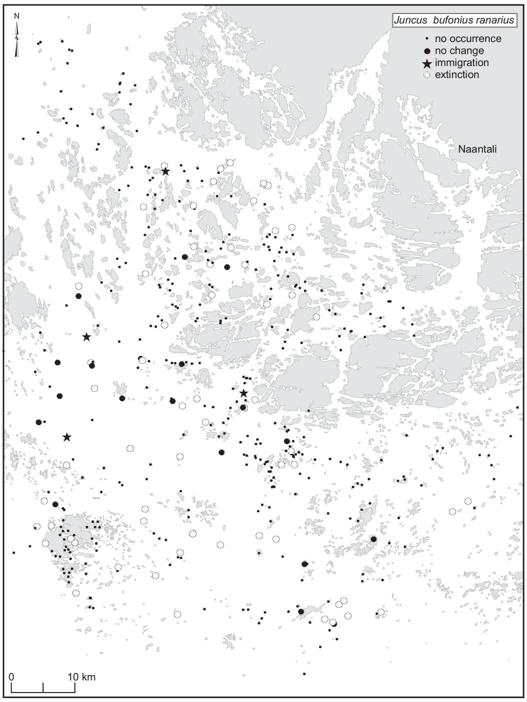

Fig. 50. Map of the species.

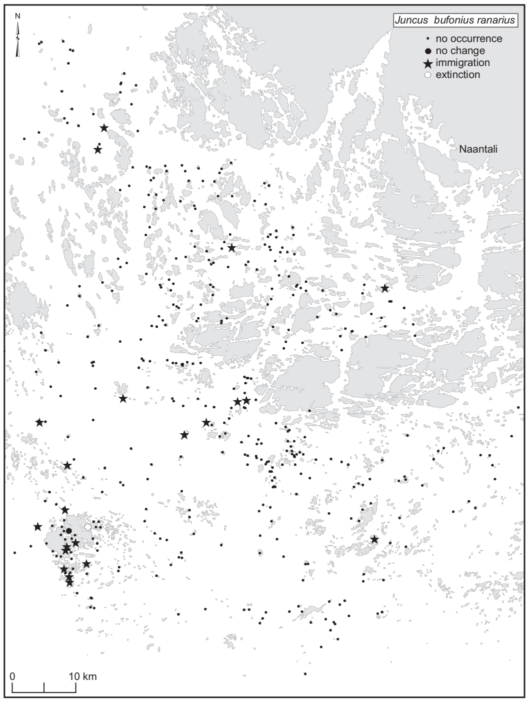

Fig. 51. Map of the species.

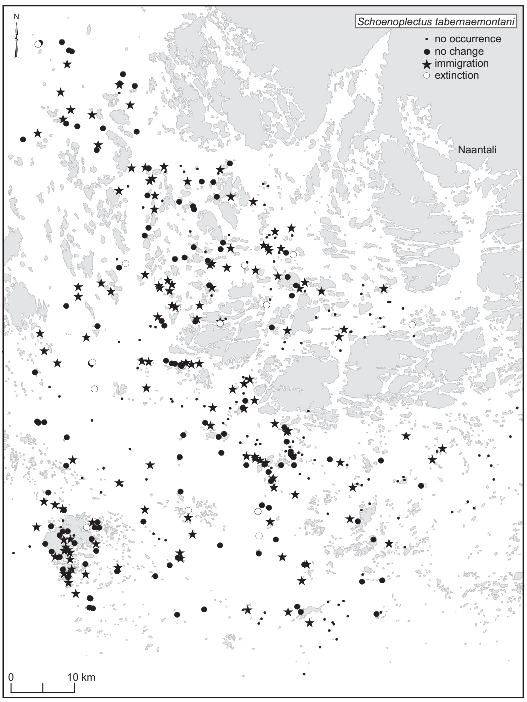

Fig. 52. Map of the species.

Blysmus rufus (Fig. 53)

One of the rarest shore plants in the area. Eklund (1958) reported 29 localities in his whole study area. On the islands studied now, the number of occurrences has decreased from 11 to 4, probably mirroring the decrease in the number and area of grazed shore meadows. The species was found on shore meadows in the southern part of the study area.

Eleocharis uniglumis

It is one of the most frequent species, with 379 island occurrences in the contemporary data set.

Carex glareosa (Fig. 54)

The species is very rare, and belongs to the clearly decreasing (from 22 to 4 records) species. It occurs according to Eklund (1958) on shore meadows and on shores with small stones and gravel.

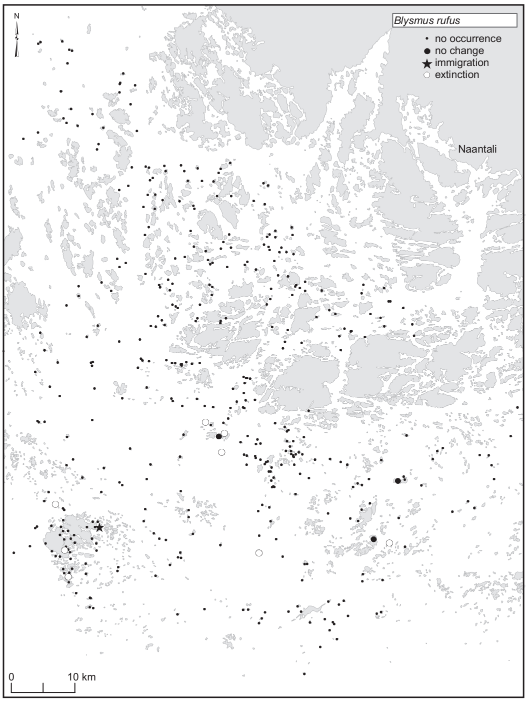

Fig. 53. Map of the species.

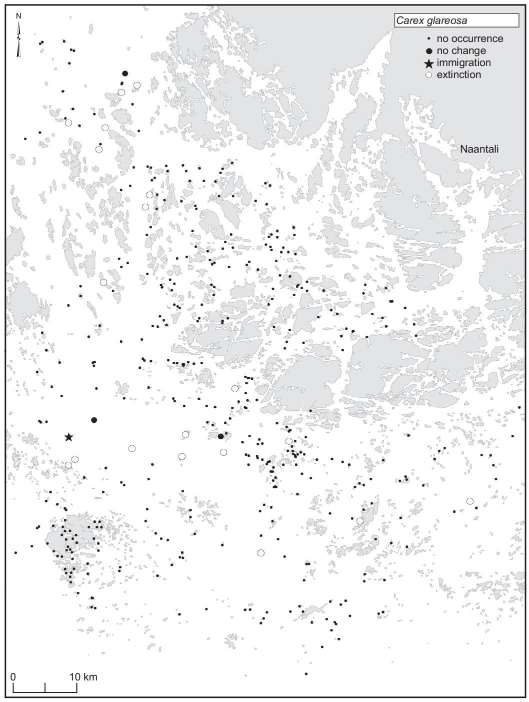

Fig. 54. Map of the species.

Carex panicea (Fig. 55)

It typically grows on shore meadows, in soil-filled rock depressions and in fen-like rock pools. The species is common, but the frequency has decreased, from 232 to 177 island records. Type I analysis gave an unusually good model (AUC = 0.87) which shows that the probability of occurrence increases with increasing shore curvature, decreasing minimum island exposure and shelter, and in the direction westwards. Type III analysis gave a weak non-interpretable model.

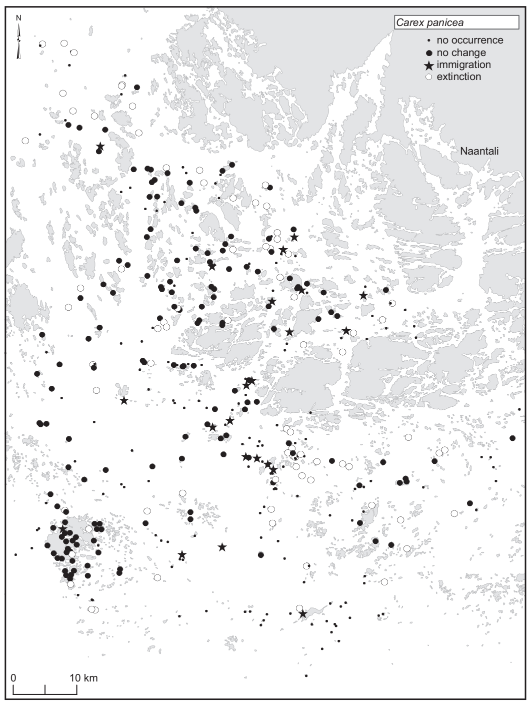

Fig. 55. Map of the species.

Carex viridula coll. (Fig. 56)

It is sually found in rock crevices on flat, vegetation-poor ground. Its frequency has increased from 118 to 130, but there is a considerable number of colonisations and extinctions. Type I analysis revealed that the probability of occurrence increases primarily with decreasing minimum island exposure. Type III analysis gave a hard to interpret result, showing that islands with extinctions are separated from islands with colo-

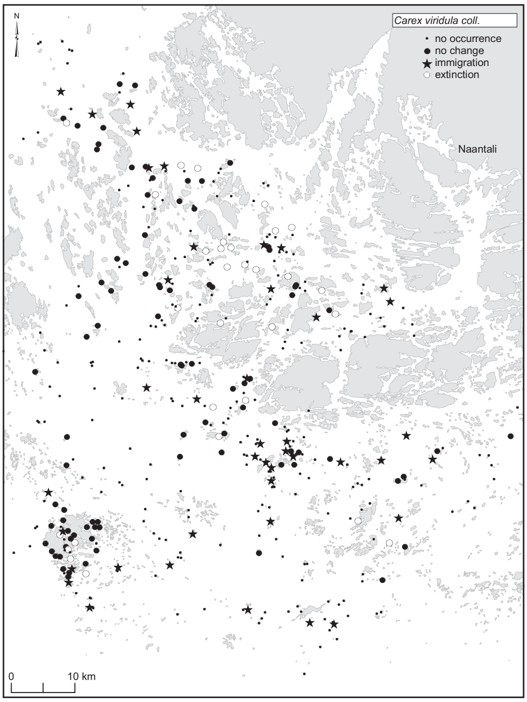

Fig. 56. Map of the species.

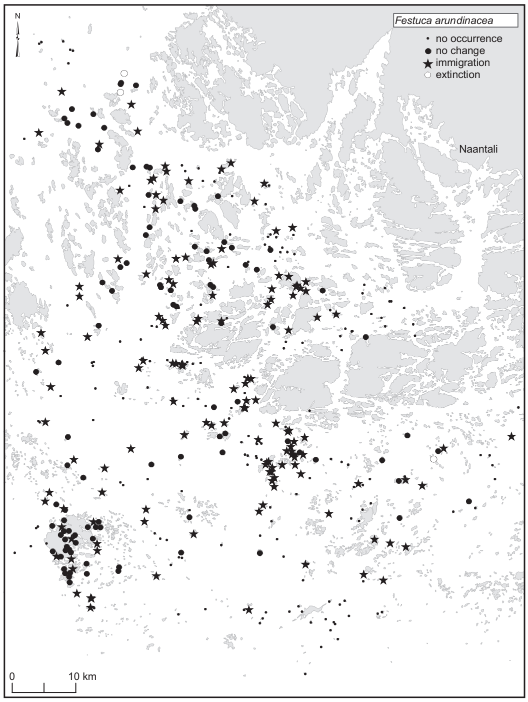

Fig. 57. Map of the species.

nisations by a shorter distance from large islands and a larger non-rocky shore area.

Festuca arundinacea (Fig. 57)

According to Eklund (1958), this species is irregularly distributed in the area, occurring mainly on till shores. Its frequency has more than doubled (from 102 to 238 island occurrences) since the historical inventories, and it is today common, except in the outermost parts of the area in the south and in the north. Type I analysis gave a good model, with the following variables increasing the probability of occurrence: increasing shore length, shelter, a position in the western direction and increasing distance from the mainland. Type II analysis revealed that islands with new occurrences are separated from islands with historical and contemporary occurrences by decreasing area of non-rocky shores and decreasing shelter.

Festuca rubra

The commonest shore species of all, occurring on almost every island in the whole area, in both the historical and the contemporary data sets.

Festuca polesica

The species was found on the sandy shores of one of the largest study islands (Nagu, Fårö) in the area. It was present here also during the historical inventories (Eklund 1958).

Poa humilis (Fig. 58)

It belongs to the decreasing (from 161 to 123 island records) shore species in the area. It grows mainly on shore meadows in the outer parts of the archipelago, and is benefitting from grazing. Type I analysis showed that the probability of occurrence increases with the area of non-rocky shores, increasing shelter and increasing distance from the mainland. Type III analysis gave a weak non-interpretable model.

Puccinellia capillaris

A typical species of the outer archipelago; it

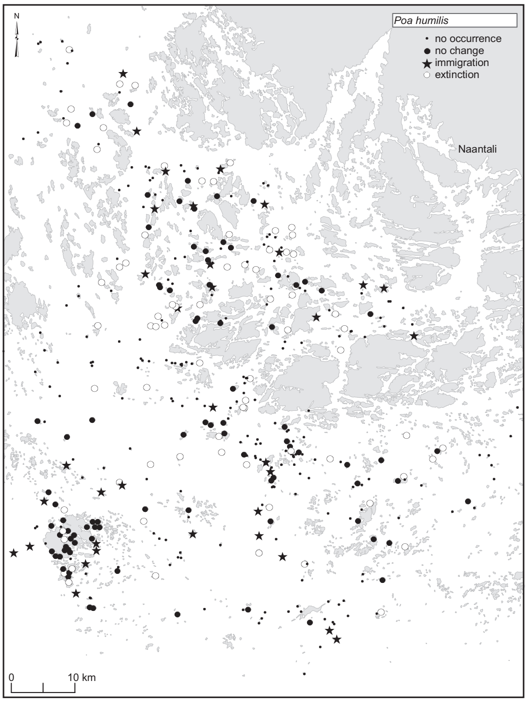

Fig. 58. Map of the species.

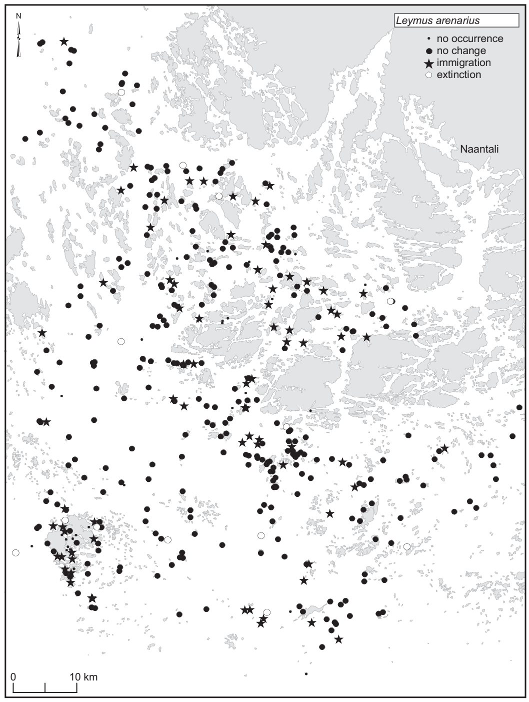

Fig. 59. Map of the species.

often grows in small cracks on rocky shores. It is, however, common everywhere in the study area (351 contemporary records), and has increased in frequency since the historical inventories. No logistic regression models were made for this wide-spread species.

Leymus arenarius (Fig. 59)

It is very common in the whole area today (367 contemporary records, somewhat more common than *Elymus repens*, and has increased as much. This species is most abundant on sandy and gravelly shores, but can be found on other shore types as well. Type II analysis revealed that the probability of colonization is associated with a shorter distance to large main islands and greater shelter as compared with islands with both historical and contemporary records.

Elymus repens (Fig. 60)

It is widespread in the entire study area, and grows on all types of stony and sandy shores. Its frequency has increased from 266 to 339. Because of its current commonness, only a type II analysis was made, which showed that the probability of new occurrences increases with an eastward position. In the historical data set almost all islands in the western part of the area were occupied, whereas there were still unoccupied islands in the east.

Deschampsia bottnica (Fig. 61)

It is common in the area and has increased since the historical inventories (from 244 to 283 island occurrences). It typically grows near the shore line on gravelly and stony shores. Eklund (1958) pointed out that the frequency of occurrence decreases towards north-east, and this statement is still valid. It does not occur in the former municipalities (today Naantali) of Velkua, Rymättylä and Merimasku (Fig. 1) to the north-east of the study area. Type I analysis showed that the probability of occurrence increases with increasing distance from the mainland, decreasing shelter and increasing area of rocky shores. Type II analysis showed that the probability of colonization increases eastwards.

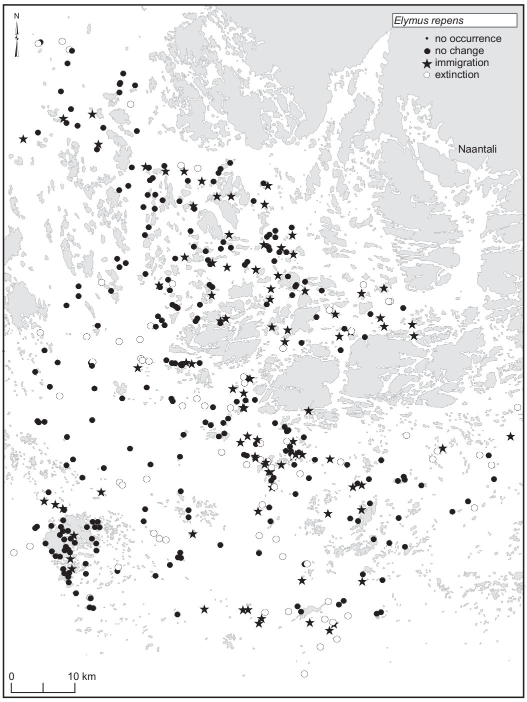

Fig. 60. Map of the species.

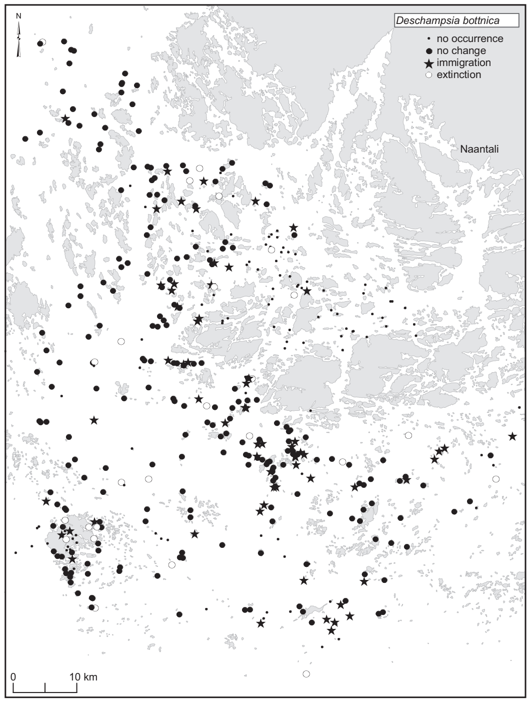

Fig. 61. Map of the species.

Hierochloë odorata* ssp. *baltica (Fig. 62)

This species has a markedly uneven distribution in the study area, a fact also pointed out by Eklund (1958). It was usually found on sheltered shores or on shore meadows. It has increased in frequency, from 53 to 73, but the turnover is high, with many extinctions (21) and colonisations (41), a fact also evident from the map. Type I analysis showed that the probability of occurrence increases primarily with an increasing distance from the mainland and with a decreasing minimum island exposure. Type III analysis indicated colonisations on small islands (with a short shore line) and extinctions from the large islands.

Calamagrostis stricta (Fig. 63)

It is quite rare in the area, and Eklund (1958) points out that it is irregularly distributed. Most records are from the northern part of the study area. It was usually found on damp shore meadows in similar types of habitats to those of *Hierochloë odorata* ssp. *baltica*. Frequency of *Calamagrostis stricta* has decreased somewhat (from 51 to 45 island records) and the turnover is high. Type I analysis showed that the probability of occurrence increases northwards and with increasing shore length and area of flat shores. Type III analysis was hard to interpret, as it indicated that decreasing island height contributes most to the model.

Phalaris arundinacea (Fig. 64)

The species grew on most of the surveyed islands (387) on all types of shores. The number of extinctions is very low (6) in relation colonisations (59). Type II analysis showed that the probability of colonisation increases with a decreased distance from the mainland and from large main islands, and the species has thus now colonised the few remaining islands that are situated in the vicinity of large inhabited islands.

Alopecurus arundinaceus (Fig. 65)

The number of records of *A. arundinaceus* has almost doubled (from 64 to 117). According to

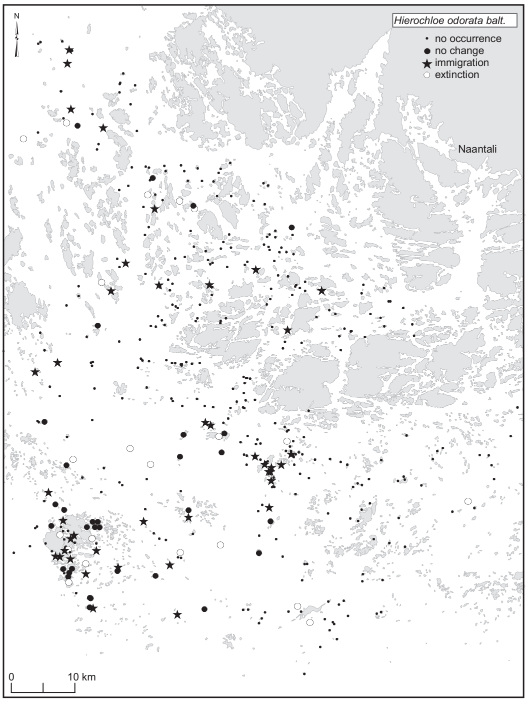

Fig. 62. Map of the species.

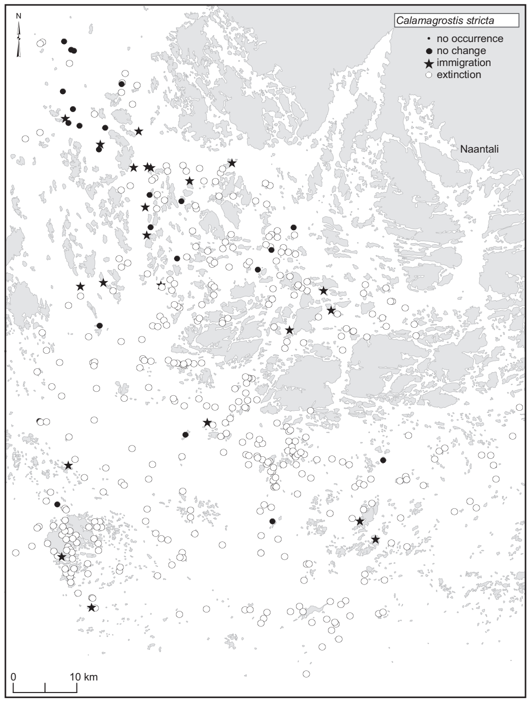

Fig. 63. Map of the species.

Eklund (1958) and also from the present observations, the species is irregularly distributed in the area. It typically grows on shore meadows or on till in the outer archipelago. It is noticeably rarer in the NE area. Type I analysis indicated that the probability of occurrence increases with increasing distance from the mainland, increasing shore-line length and decreasing exposure. According to the type II model the probability of colonisation increases with a shorter distance to the mainland and to large islands.

Phragmites australis (Fig. 66)

With 145 colonisations and just 5 extinctions *P. australis* belongs to the considerably increasing species. Formerly, it occurred mostly on large or sheltered islands or in inlets, but today it grows almost everywhere, except on the very exposed islands in the southernmost part of the area. Type I analysis showed that the probability of occurrence increases with a northern island position, decreasing minimum island exposure and increasing non-rocky shore area. Type II analysis revealed a higher minimum island expo-

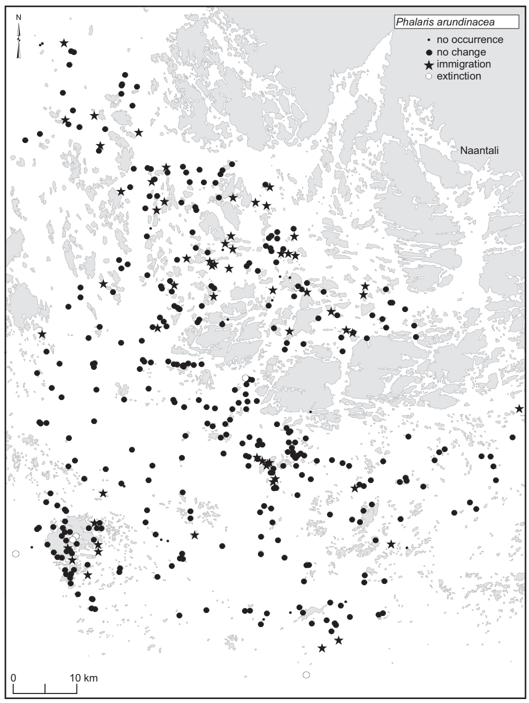

Fig. 64. Map of the species.

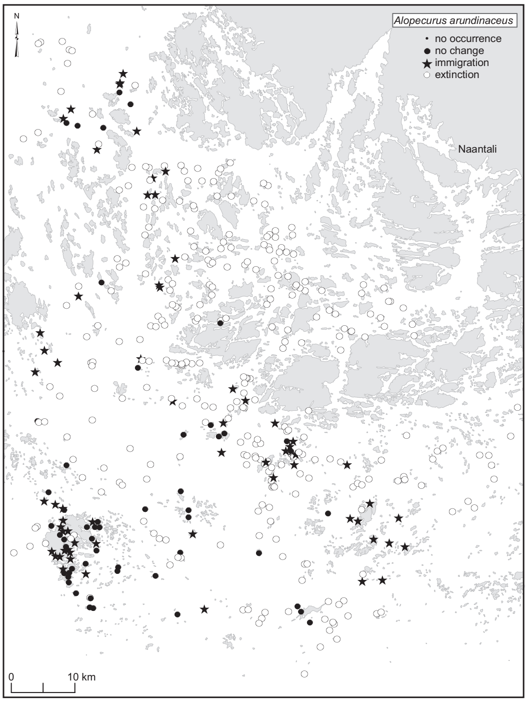

Fig. 65. Map of the species.

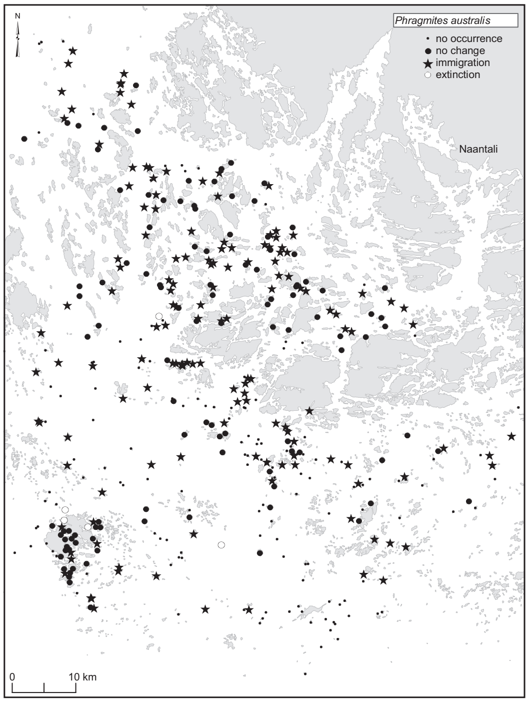

Fig. 66. Map of the species.

sure value and a lower degree of shelter of the colonized islands as compared with the island with both old and contemporary occurrences, signifying the dispersal towards maritime areas.

Discussion and synthesis

The general patterns found

To get a general picture of the species' changes in frequency, they were ordered according to their historical frequency (Fig. 3) and classified into five groups: historically very common (> 350 island presences), common (249–350), fairly common (150–250), rare (50–150) and very rare (< 50).

Most of the 14 species that are classified as historically very common based on the historical surveys (> 300 island presences) have increased in frequency or remained more or less stable. Some of the increasing species have colonised most of the few remaining uncolonized islands in the whole area. These species include: *Lythrum salicaria*, *Rumex crispus*, *Glaux maritima*, *Tanacetum vulgare* and *Tripleurospermum maritimum* ssp. *maritimum*.

Of the 11 historically common species (249–350 occurrences); *Phalaris arundinacea*, *Leymus arenarius*, *Plantago major* ssp. *intermedia*, *Puccinellia capillaris*, *Silene vulgaris* var. *littoralis*, *Veronica longifolia*, *Angelica archangelica* ssp. *littoralis* and *Leymus repens* have clearly increased in frequency. Of these, *Phalaris arundinacea*, *Leymus arenarius*, *Puccinellia capillaris* and *Angelica archangelica* ssp. *littoralis* are today very frequent (more than 350 island presences). A common characteristic for at least *Leymus arenarius*, *Silene vulgaris* var. *littoralis*, *Veronica longifolia*, *Angelica archangelica* ssp. *littoralis* is that they, according to the analyses (and the maps), have spread towards the inner archipelago to more sheltered islands.

The group consisting of historically fairly common species (150 to 250 island occurrences) include 15 species. In this group, we also have decreasing species (*Carex panicea*, *Linum catharticum*, *Myosotis laxa* ssp. *laxa*, *Poa humilis* and *Montia fontana*). *Schoenoplectus tabernaemontani*, *Phragmites australis* and *Festuca* *arundinacea* stand out as having increased considerably.

The group of historically rare species (50–150) consists of 12 species. Considerable changes in frequency have taken place among several of these. Especially noteworthy is the huge increase in frequency of *Ophioglossum vulgatum*, *Aster tripolium*, *Centaurium pulchellum*, *Isatis tinctoria*, *Odontites litoralis*, *Alopecurus arundinaceus*, *Centaurium litorale* and *Cirsium arvense*.

The group of historically very rare species (fewer than 50 island occurrences) includes 29 species. In this group, similarly as in the previous group, there are several species that have increased noticeably: *Crambe maritima*, *Atriplex prostrata*, *Potentilla anserina* ssp. *groenlandica*, *Juncus compressus*, *Typha latifolia*, *Stachys palustris*, *Artemisia vulgaris* var. *coarctata*, *Solanum dulcamara*, *Atriplex littoralis*, *Lathyrus palustris*, *Bolbochoenus maritimus*, *Rosa rugosa* (new), and *Ligusticum scoticum* (new). *Carex glareosa*, *Cacile maritima*, *Blysmus rufus*, *Salicornia europaea* and *Suaeda maritima* have decreased.

Changes in distribution patterns

The results of the logistic regression analyses and the distribution maps show that most of the species' distribution patterns have changed in the area. Species with similar changes in their distribution patterns can be grouped as follows.

Species that have spread inwards

Based on the analyses, these species have spread to less maritime conditions (closer to the mainland, closer to large main islands or to more sheltered islands) from maritime, outer archipelago areas. They include *Ophioglossum vulgatum*, *Phalaris arundinacea*, *Alopecurus arundinaceus*, *Leymus arenarius*, *Festuca arundinacea*, *Atriplex prostrata*, *Atriplex litoralis*, *Silene vulgaris* var. *littoralis*, *Cochlearia danica*, *Isatis tinctoria*, *Potentilla anserina* ssp. *groenlandica*, *Angelica archangelica* ssp. *litoralis* and *Odontites litoralis*.

Species that have spread outwards

An unexpectedly small number of species have spread towards more maritime areas (outwards). The most obvious species is *Phragmites australis*, which has spread from the sheltered shores and inlets to exposed areas. Also *Centaurium pulchellum* has increased in frequency and has spread outwards.

Species that have spread northwards

Ophioglossum vulgatum, *Atriplex litoralis* (according to map) *Silene vulgaris* var. *littoralis*, *Isatis tinctoria*, *Barbarea stricta*, *Myosotis laxa* and *Montia fontana* have spread northwards. Today very common *Silene vulgaris* var. *littoralis* seems to have colonized the remaining central and northern islands, as well as islands near the Kökar main islands.

Species that have spread eastwards

According to the analyses, two species (*Deschampsia bottnica* and *Elymus repens*) are spreading eastwards. For *Elymus repens* this pattern is hard to explain, as it is common in the areas to the east of the study area as well. *Deschampsia bottnica*, an endemic species with a distribution centred around the Gulf of Bothnia, is apparently widening its distribution to the east.

Species spreading to islands with shorter shore line

Type III analysis of *Hierochloë odorata* ssp. *baltica* indicated that islands with colonisations had a shorter shore line than islands with extinctions. This was also the impression gained during fieldwork. The average shore line of islands with colonizations (1470 m) is significantly shorter than the average shore line of the islands with extinctions (2170 m) (t-test: $t = 0.24$, d.f. = 47, $p = 0.010$). Disappearance of *H. odorata* ssp. *baltica* from large islands might be the result of shore meadow overgrowth. Simultaneously suitable habitats with low vegetation have appeared on the small islands. New occurrences of *Centaurium littorale* and *Stachys palustris* are — according to the logistic regression analyses of type II — situated on smaller islands than the stable occurrences. New occurrences of *Festuca arundinacea* are located on islands with a smaller area of non-rocky shores. The difference is clear (mean for stable islands 235 m^2 and for colonized islands 124 m^2; *t*-test: $t = 11.0$, d.f. 199, $p = 0.001$).

Likely reasons for observed changes

Grazing and mowing

The role of decreased grazing pressure is doubtlessly of importance for most of the species that have spread inwards or have generally increased. Grazing pressure during the historical inventories was periodically heavy on many of the islands, but the effect was diffuse, and is today hard to quantify, as cattle and sheep usually were transported from island to island during the summer to graze freely (*see* e.g. Eklund 1931, Hæggström 1990). Grazing pressure was, however, probably greatest on islands near large inhabited islands. Today cattle and sheep have, especially in maritime areas, been replaced by grazing geese and mute swans, which have significantly increased in numbers since the 1970s. The grazing effect of the birds is, however, probably marginal, but their role as vectors for seed dispersal might be significant (*see* e.g. Jerling *et al*. 2001).

Of the species spreading inwards, Eklund (1958) does, oddly enough, not classify any as suffering from antropogenic impact. According to Tyler (1969), *Centaurium littorale*, *Odontites litoralis* and *Ophioglossum vulgatum* are sensitive to grazing, which is in good agreement with the increase of these species in this study. Jutila (1999), however, claimed that *Odontites litoralis* benefits from grazing in a shore meadow area along the Gulf of Bothnian. In the present study, *O. litoralis* belongs to the species that have increased most dramatically. This is in agreement with results obtained from the Uppland archipelago in Sweden (Maad *et al*. 2009). For the rest of the species spreading inwards, the agreement is better (*see* also Jutila 1999). According to Jutila (1999), *Angelica sylvestris* (*A. archangelica* in the present study), *Festuca arundinacea*, *Lathyrus palustris*, *Lythrum salicaria*, *Ophioglossum vulgatum*, *Phragmites australis*, *Vicia cracca* and *Valeriana sambucifolia* are negatively influenced by grazing. All of these have increased in the present study. On the other hand, as indicated by Jutila (1999), *Carex glareosa*, *C. viridula* coll., *Eleocharis uniglumis*, *Elymus repens*, *Glaux maritima*, *Hippophaë rhamnoides*, *Juncus gerardii*, *Plantago maritima*, *Poa humilis* and *Potentilla anserina* ssp. *anserina* benefit from grazing. Of these *Carex glareosa*, *Eleocharis uniglumis* (marginally) and *Poa humilis* have decreased in the present study, whereas *Elymus repens*, *Juncus gerardii*, *Glaux maritima*, *Plantago maritima* and *Hippophaë rhamnoides* have increased.

Species that, in addition to the above mentioned, have most probably benefitted from reduced grazing pressure include: *Phalaris arundinacea*, *Alopecurus arundinaceus*, *Leymus arenarius*, *Atriplex prostrata*, *A. littoralis*, *Isatis tinctoria*, *Crambe maritima*, *Stachys palustris*, *Artemisia vulgaris* var. *coarctata*, *Veronica longifolia* and *Aster tripolium*. All of these have increased, and the decrease in grazing probably plays a role, but it is not possible to quantify this effect, or separate it from the effect of eutrophication. *Crambe maritima* is known to be eaten by sheep, and it was formerly also collected and eaten by man (Hæggström & Hæggström 2008).

Expansion of the species ranges northwards might partly be explained by the decreased grazing. *Ophioglossum vulgatum* and *Isatis tinctoria* has increased everywhere, but expansion northwards is very clear, as there are only a few historical records from the northern part of the area. Noteworthy is the fact that — according to Maad *et al*. (2009) — both *O. vulgatum* and *I. tinctoria* have not increased in the archipelago of Uppland. In the study area of Vaahtoranta (1964), located to the north of the present area, *I. tinctoria* is quite common up to the town of Rauma. This fact indicates that spreading northwards might partly be explained by decreasing grazing pressure, as *I. tinctoria* is a highly attractive food plant for cattle and sheep. This is true also for the northwards expanding *Atriplex litoralis* (Hæggström & Hæggström 2008), but as Vaahtoranta (1964) did not find *A. litoralis* to the north of the present study area, spreading might have other reasons as well. For *Barbarea stricta*, *Myosotis laxa* ssp. *baltica* and *Montia fontana*, no obvious explanations for the northward expansion can be found.

Eutrophication

Increasing eutrophication of the sea in the study area has taken place simultaneously with the decrease in grazing pressure (*see* e.g. Lundberg 2005). Both processes probably have a similar effect on the shore flora: large (perennial) species such as *Phalaris arundinacea*, *Phragmites australis*, *Atriplex littoralis*, *Angelica archangelica* ssp. *litoralis*, *Isatis tinctoria*, *Stachys palustris*, *Solanum dulcamara*, *Artemisia vulgaris* var. *coarctata* and *Aster tripolium* have increased. von Numers and Korvenpää (2007) show that the shore plants increasing in frequency have a higher demand for nutrients than the decreasing species. Accelerated accumulation of organic material on the shores during the last 2–3 decades, and its effect on species richness may be particularly pronounced on soil-poor outer archipelago islands. The ongoing land uplift reveals, and algae masses deposited on the shores add, a new, productive substrate. The result showing that only *Phragmites australis* and *Centaurium pulchellum* have actually spread outwards indicates, however, that the effect of decreased grazing might even be the more influential of the two factors.

During recent years dried-up, drifting algae formed a parchment-like layer along exposed shores, a phenomenon not occurring formerly (C.-A. Hæggström pers. comm.). This layer, which is hard to penetrate by plants, might be one reason for the decrease among the small species such as *Juncus bufonius* ssp. *bufonius*, *J. bufonius* ssp. *ranarius*, *Sagina maritima*, *Montia fontana* and *Myosotis laxa* ssp. *baltica*.

Comparability of the old and the new data sets

The difficulty of making valid comparisons between historical and contemporary data is an obstacle to documenting range changes in relation to environmental changes (Tingley & Bessinger 2009). In this study, a geographical precision problem is not present. Islands constitute well-defined study areas enabling reliable re-surveying. The land uplift in the area will cause a potential bias, however. The surface area of the islands has increased somewhat during the time between the two surveys and consequently a higher number of species is expected. It is, however, very difficult to assess the actual, and for most islands probably minor, increase in island over time. The increase in area is probably largest on flat islands with low exposure, whereas steep, exposed islands have most likely not been affected at all.

Eklund (1948, 1958) and Skult (1960) compiled the historical species lists for theoretical work, as well as for use as a basis for comparative studies in the future. Both authors compiled the species lists in a systematic way using forms. The same method was used during the present surveys. There is naturally no way to test the accuracy of the historical species lists, but they are most likely highly reliable. Of importance for the present study is the census efficiency of the individual species, which has to be the same in the historical and the contemporary surveys. Unfortunately, this is impossible to test. Most of the shore species are large and easy to detect, but there is, naturally, a larger risk to overlook the very small and inconspicuous species, such as *Centaurium pulchellum* and *Sagina maritima*.

Concluding remarks

The use of historical surveys for range change comparisons has grown rapidly (*see* e.g. Tingley & Beissinger 2009), but the number of botanical studies on range changes is low. This study is, as far as I know, unique by focussing on shore plants in an archipelago and also by relating the range changes to environmental variables. In this study, the distribution patterns and the long term changes of individual shore plant species in relation to the environment have been described and analysed. Studies on long term changes are usually presented with the species number per island (or area) as a basis. This generalisation gives the comprehensive picture of the changes, but might result in a loss of information. When focus is laid on the behaviour of the individual species, it is harder to get a broad picture, but as this study shows, such a picture might turn out too to be general. Individual species might change their distribution patterns in changing environment in unpredictable manners, which means that, ultimately, it is worthwhile to study the species individually whenever possible. This is relevant especially for the shore plants, as the island area is not the optimal basis for determining, for example, species–area relationships (*see* e.g. Nilsson & Nilsson 1978, Löfgren and Jerling 2002), but rather the shore length.

The period between these two surveys is about 60 to 80 years. The changes that have occurred are striking for several of the species. This study would not have been possible without foresight and great effort by Ole Eklund and Henrik Skult in collecting the historical data. Eklund (1948) finished one of his last articles with the words "it is the task of future plant biogeographers to compare these results with the results of new surveys, and to uncover the changes that have occurred."

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References

Atlas of Finland 1993: *Appendix 112*. — National Board of Survey and Geographical Society of Finland, Finland.

Bonsdorff, E., Blomqvist, M., Mattila, J. & Norkko, A. 1997: Long-term changes and coastal eutrophication. Examples from the Baltic Sea. — *Oceanologica Acta* 20: 319–329.

Du Rietz, G. E. 1947: Wellenrenzen als ökologische äquivalente der Wasserstandslinien . — *Zoologiska Bidrag från Uppsala* 25: 534–550.

Eklund, O. 1931: Über die ursachen der regionalen verteilung der Schärenflora Südwest-Finnlands. — *Acta Botanica Fennica* 8: 1–133.

Eklund, O. 1948: Skärgårdsväxterna och kalken. — In: Lindberg, H. (ed.), *Skärgårdsboken*: 315–339. Nordenskiöld-Samfundet i Finland, Helsingfors.

Eklund, O. 1958: Die Gefässpflanzenflora beiderseits Skiftet im Schärenarchipel Südwestfinnlands. — *Bidrag till Kännedom af Finlands Natur och Folk* 101: 1–342.

Granö, O., Roto, M. & Laurila, L. 1999: Environment and land use in the shore zone of the coast of Finland. — *Publicationes instituti geographici universitatis Turkuensis* 160: 1–76.

Hannus, J.-J. & von Numers, M. 2008: Vascular plant richness in relation to habitat diversity and island area in the Finnish archipelago. — *Journal of Biogeography* 35: 1077–1086.

Hæggström, C.-A. 1983: Vegetation and soil of the wooded meadows in Nåtö, Åland. — *Acta Botanica Fennica* 120: 1–66.

Hæggström, C.-A. 1990: The influence of sheep and cattle grazing on wooded meadows in Åland, SW Finland. — *Acta Botanica Fennica* 141: 1–28.

Hæggström, C.-A. & Hæggström, E. 2008: *Ålands flora*. — Ålandstryckeriet, Mariehamn.

Hämet-Ahti, L., Suominen, J., Ulvinen, T. & Uotila, P. (eds.) 1998: *Retkeilykasvio [Field flora of Finland]*. — Finnish Museum of Natural History, Botanical Museum. [In Finnish, with an English summary].

Hosmer, D. W. & Lemeshow, S. 2000: *Applied logistic regression*. — Wiley & Sons, New York.

Hustich, I. 1964: *Finlands skärgård, en ekonomisk-geografisk översikt*. — Ekonomi och samhälle, Skrifter utgivna vid Svenska handelshögskolan, Söderström & Co., Helsingfors.

Isæus, M. 2004: Factors structuring *Fucus* communities at open and complex coastlines in the Baltic Sea. — Ph.D. thesis, Dept. of Botany, Stockholm University.

Jerling, L., Löfgren, A. & Lannek, J. 2001: Växtlivet I Stockholms skärgård – mönster i tid och rum. — *Svensk Botanisk Tidskrift* 95: 212–226.

Jutila, H. 1999: Effect of grazing on the vegetation of shore meadows along the Bothnian Sea, Finland. — *Plant Ecology* 140: 77–88.

Kakkuri, J. 1987: Character of the Fennoscandian land uplift in the 20th century. — *Geological Survey of Finland*, Special Paper 2: 15–20.

Korvenpää, T., von Numers, M. & Hinneri, S. 2003: A mesoscale analysis of floristic patterns in the SW Finnish Archipelago. — *Journal of Biogeography* 30: 1019–1031.

Löfgren, A. & Jerling, L. 2002: Species richness, extinction and immigration rates of vascular plants on islands in the Stockholm archipelago, Sweden, during a century of ceasing management. — *Folia Geobotanica* 37: 297–308.

Lundberg, C. 2005: *Eutrophication in the Baltic Sea — from area-specific biological effects to interdisciplinary consequences*. — Ph.D. thesis, Åbo Akademi University.

Maad, J., Sundberg, S., Stolpe, P. & Jonsell, L. 2009: Floraförändringar i Uppland under 1900-talet — en analys från Projekt Upplands flora. — *Svensk Botanisk Tidskrift*

103: 67–104.

Nilsson, S. G. & Nilsson, I. N. 1978: Species richness and dispersal of vascular plants to islands in lake Möckeln, southern Sweden. — *Ecology* 59: 473–480.

Palmgren, A. 1961: Studier över havsstrandens vegetation och flora på Åland. I. Vegetationen. — *Acta Botanica Fennica* 61: 1–270.

Pearce, J. & Ferrier, S. 2000: Evaluating the predictive performance of habitat models developed using logistic regression. — *Ecological Modelling* 133: 225–245.

Rönnberg, C. & Bonsdorff, E. 2004: Baltic Sea eutrophication: area specific ecological consequences. — *Hydrobiologia* 514: 227–241.

Rooney, T. P., Wiegmann, S., Rogers, D. & Waller, D. M. 2004: Biotic impoverishment and homogenization in unfragmented forest understory communities. — *Conservation Biology* 18: 787–798.

Schoener, T. W. 1988: On testing the MacArthur-Wilson model with data on rates. — *American Naturalist* 131: 847–864.

Skult, H. 1960: Om kärlväxtfloran i Korpo, Brunskär, en utskärsarkipelag. — *Acta Societatis pro Fauna et Flora Fennica* 76: 1–101.

Schöpp, W., Posch, M., Mylona, S. & Johansson, M. 2003: Long-term development of acid deposition (1880-2030) for sensitive freshwater regions in Europe. — *Hydrology and Earth System Sciences* 7: 436–446.

Tingley, M. & Beissinger, S. R. 2009: Detecting range shifts from historical species occurrences: new perspectives on old data. — *Trends in Ecology and Evolution* 24: 625–633.

Tyler, G. 1969: Studies in the ecology of Baltic sea shore meadows. II. Flora and vegetation. — *Opera Botanica a Societate Botanica Lundensi* 25: 1–101.

Vaahtoranta, L. 1964: Die Gefässpflanzenflora im Schärenhof von Pyhämaa und Pyhäranta am Bottnischen Meerbusen, Südfinnland. — *Annales Botanici Fennici* 1: 292–363.

Whittaker, R. J., Willis, K. J. & Field, R. 2001: Scale and species richness: toward a general, hierarchical theory of species diversity. — *Journal of Biogeography* 28: 453–470.

von Haartman, L. 1945: Zur Biologie der Wasser- und Ufervögel im Schärenmeer Südwest-Finnlands. — *Acta Zoologica Fennica* 44: 1–120.

von Numers, M. 1995: Distribution, numbers and ecological gradients of birds breeding on small islands in the Archipelago Sea, SW Finland. — *Acta Zoologica Fennica* 197: 1–127.

von Numers, M. 1996: Ole Eklunds botaniska uppgifter från Skärgårdshavet sedda i dagens ljus. — *Nordenskiöld-Samfundets tidskrift* 55–56: 3–10.

von Numers, M. & Korvenpää, T. 2007: 20th century vegetation changes in an island archipelago, SW Finland. — *Ecography* 30: 789–800.

von Numers, M. & van der Maarel, E. 1998: Plant distribution patterns and ecological gradients in the Southwest-Finnish archipelago. — *Global Ecology and Biogeography Letters* 7: 421–440.

von Numers, M., Hæggström, C.-A., Hæggström, E., Franzén, H., Franzén, J. & Carlsson, R. 2009: Scots lovage *Ligusticum scoticum*, is spreading in the Åland islands, SW Finland. — *Memoranda Societas pro Fauna et Flora Fennica* 85: 1–5.

Vuori, K. M., Bäck, S., Hellsten, S., Karjalainen, S. M., Kauppila, P., Lax, H. G., Lepistö, L., Londesborough, S., Mitikka, S., Niemelä, P., Niemi, J., Perus, J., Pietiläinen, O. P., Pilke, A., Riihimäki, J., Rissanen, J., Tammi, J., Tolonen, K., Vehanen, T., Vuoristo, H. & Westberg, V. 2006: Suomen pintavesien tyypittelyn ja ekologisen luokittelujärjestelmän perusteet. — *Suomen ympäristö* 807: 1–151.

Wiegmann, S. M. & Waller, D. M. 2006: Fifty years of change in northern upland forest understories: Identity and traits of "winner" and "loser" plant species. — *Biological Conservation* 129: 109–123.

Appendix. Results of the logistic regression analyses (types I, II and III; *see* text for explanation) for the species; the final models. The AUC values of the models are given within parentheses.

	B	SE	Wald	d.f.	*p*	Exp(*B*)
Type I analyses						
Ophioglossum vulgatum (AUC = 0.73)						
Minimum exposure	–0.091	0.017	28.236	1	< 0.0001	0.913
West-east	–0.025	0.008	10.859	1	0.0010	0.975
Distance large island	0.099	0.038	6.806	1	0.0091	1.104
Montia fontana (AUC = 0.78)						
Flat shore area	0.033	0.013	6.784	1	0.0092	1.034
Shore line length	0.036	0.015	5.888	1	0.0152	1.037
South-north	0.052	0.010	29.237	1	< 0.0001	1.054
Spergularia salina (AUC = 0.69)						
Flat shore area	0.045	0.011	18.325	1	< 0.0001	1.046
South–north	0.016	0.007	5.673	1	0.0172	1.016
Silene uniflora (AUC = 0.87)						
Minimum exposure	–0.107	0.020	28.066	1	< 0.0001	0.899
Island shelter	–0.089	0.012	59.141	1	< 0.0001	0.915
Distance mainland	0.422	0.107	15.652	1	0.0001	1.525
Atriplex litoralis (AUC = 0.79)						
Area rocky shore	0.026	0.007	14.142	1	0.0002	1.026
South–north	–0.045	0.012	14.835	1	0.0001	0.956
Atriplex prostrata (AUC = 0.68)						
Area non-rocky shore	0.038	0.011	12.292	1	0.0005	1.039
Island shelter	0.012	0.006	4.282	1	0.0385	1.012
Distance mainland	0.163	0.064	6.558	1	0.0104	1.177
Isatis tinctoria (AUC = 0.78)						
Area rocky shore	0.022	0.008	7.620	1	0.0058	1.023
Minimum exposure	–0.036	0.014	6.864	1	0.0088	0.965
Island shelter	–0.041	0.007	31.298	1	< 0.0001	0.959
West–east	–0.016	0.009	3.405	1	0.0650	0.984
Distance mainland	0.182	0.083	4.783	1	0.0287	1.199
Cochlearia danica (AUC = 0.88)						
Area non-rocky shore	–0.066	0.015	20.925	1	< 0.0001	0.936
Maximum exposure	0.007	0.004	3.881	1	0.0488	1.007
Island shelter	–0.034	0.011	9.302	1	0.0023	0.966
Distance mainland	0.300	0.103	8.490	1	0.0036	1.350
Distance large island	0.184	0.062	8.733	1	0.0031	1.202
Crambe maritima (AUC = 0.86)						
Island shelter	–0.032	0.011	8.319	1	0.0039	0.969
Island shape	–0.037	0.014	6.993	1	0.0082	0.964
South–north	–0.063	0.011	33.795	1	< 0.0001	0.939
Distance large island	0.151	0.049	9.335	1	0.0022	1.163
Potentilla anserina ssp. *groenlandica* (AUC = 0.76)						
Minimum exposure	–0.064	0.031	4.237	1	0.0396	0.938
Distance large island	0.273	0.060	20.569	1	< 0.0001	1.314
Linum catharticum (AUC = 0.71)						
Maximum exposure	–0.005	0.002	6.481	1	0.0109	0.995
Shore line length	0.058	0.013	18.698	1	< 0.0001	1.060
West–east	–0.024	0.008	10.410	1	0.0013	0.976
Centaurium littorale (AUC = 0.79)						
Flat shore area	0.049	0.013	13.413	1	0.0002	1.050
Minimum exposure	–0.057	0.020	8.381	1	0.0038	0.945
Shelteredness	0.014	0.006	5.083	1	0.0242	1.014
South–north	0.032	0.007	19.540	1	< 0.0001	1.033
Centaurium pulchellum (AUC = 0.69)						
Area non-rocky shore	0.023	0.009	6.409	1	0.0114	1.023
Minimum exposure	–0.046	0.018	6.541	1	0.0105	0.955
Island shelter	–0.016	0.006	6.626	1	0.0101	0.984
South–north	0.014	0.006	4.888	1	0.0270	1.014

Continued

Appendix. Continued.

	B	SE	Wald	d.f.	*p*	Exp(*B*)
Myosotis laxa ssp. *baltica* (AUC = 0.76)						
Maximum exposure	0.004	0.002	4.520	1	0.0335	1.004
Shore line length	0.061	0.013	23.526	1	< 0.0001	1.063
South–north	0.047	0.008	35.047	1	< 0.0001	1.048
Stachys palustris (AUC = 0.84)						
Area non-rocky shore	0.052	0.012	18.575	1	< 0.0001	1.053
Minimum exposure	–0.132	0.035	14.286	1	0.0002	0.876
Maximum exposure	0.014	0.003	15.553	1	0.0001	1.014
South–north	–0.041	0.018	5.398	1	0.0202	0.960
Distance mainland	–0.888	0.206	18.612	1	< 0.0001	0.412
Solanum dulcamara (AUC = 0.87)						
Area non-rocky shore	0.086	0.026	10.866	1	0.0010	1.090
Island shelter	0.025	0.009	7.850	1	0.0051	1.026
Shore line length	–0.081	0.037	4.828	1	0.0280	0.922
South–north	0.062	0.012	27.801	1	< 0.0001	1.064
Plantago maritima (AUC = 0.90)						
Aea non-rocky Shore	0.093	0.021	20.253	1	< 0.0001	1.097
Island shelter	0.072	0.013	32.656	1	< 0.0001	1.075
Island shape	–0.016	0.009	3.516	1	0.0608	0.984
Distance mainland	–0.699	0.110	40.115	1	< 0.0001	0.497
Distance large island	0.115	0.055	4.324	1	0.0376	1.122
Aster tripolium (AUC = 0.83)						
Minimum exposure	–0.150	0.021	51.717	1	< 0.0001	0.861
Artemisia vulgare var. *coarctata* (AUC = 0.82)						
Minimum exposure	–0.053	0.018	8.881	1	0.0029	0.948
Maximum exposure	0.006	0.003	4.692	1	0.0303	1.006
Island shelter	–0.021	0.009	5.183	1	0.0228	0.979
Island shape	–0.052	0.014	13.432	1	0.0002	0.949
South–north	–0.024	0.009	7.349	1	0.0067	0.976
Distance large island	0.184	0.049	14.015	1	0.0002	1.202
Cirsium arvense var. *mite* (AUC = 0.84)						
Area non-rocky shore	0.065	0.016	16.338	1	0.0001	1.067
Island shelter	0.028	0.007	15.849	1	0.0001	1.029
Height	0.065	0.027	5.699	1	0.0170	1.067
South–north	0.037	0.007	24.661	1	< 0.0001	1.037
Triglochin maritima (AUC = 0.89)						
Minimum exposure	–0.055	0.018	9.850	1	0.0017	0.947
Island shelter	0.090	0.017	29.323	1	< 0.0001	1.094
Shore line length	0.115	0.028	16.370	1	0.0001	1.121
Typha latifolia (AUC = 0.68)						
Area non-rocky shore	–0.027	0.012	4.950	1	0.0261	0.973
Area rocky shore	0.036	0.008	18.507	1	< 0.0001	1.037
Juncus compressus (AUC = 0.82)						
Maximum exposure	0.011	0.002	25.526	1	< 0.0001	1.011
Distance large island	0.133	0.053	6.353	1	0.0117	1.142
Juncus bufonius ssp. *ranarius* (AUC = 0.754)						
Area rocky shore	0.034	0.009	13.204	1	< 0.0001	1.035
Height	–0.124	0.052	5.683	1	0.0170	0.884
Bolbochoenus maritimus (AUC = 0.86)						
Area non-rocky shore	0.052	0.011	22.590	1	< 0.0001	1.053
West–east	–0.066	0.021	9.997	1	0.0016	0.936
Schoenoplectus tabernaemontani (AUC = 0.79)						
Minimum exposure	–0.051	0.014	13.411	1	0.0003	0.950
Shore line length	0.070	0.019	13.463	1	0.0002	1.072
West–east	–0.039	0.008	21.544	1	< 0.0001	0.961

Continued

Appendix. Continued.

	B	SE	Wald	d.f.	*p*	Exp(*B*)
Carex panicea (AUC = 0.87)						
Minimum exposure	–0.090	0.022	17.670	1	< 0.0001	0.914
Island shelter	0.030	0.009	10.949	1	0.0009	1.030
Island shape	–0.088	0.015	35.397	1	< 0.0001	0.916
West–east	–0.037	0.009	15.519	1	0.0001	0.963
Carex viridula coll. (AUC = 0.79)						
Minimum exposure	–0.110	0.028	14.977	1	0.0001	0.896
Maximum exposure	0.007	0.003	4.408	1	0.0358	1.007
Shore line length	0.030	0.017	3.141	1	0.0763	1.031
Island shape	–0.033	0.015	4.953	1	0.0260	0.967
Festuca arundinacea (AUC = 0.84)						
Minimum exposure	–0.080	0.032	6.429	1	0.0112	0.923
Maximum exposure	–0.019	0.007	7.494	1	0.0062	0.981
Island shelter	0.038	0.014	7.636	1	0.0057	1.038
Shore line length	0.126	0.029	18.924	1	< 0.0001	1.134
West–east	–0.038	0.011	11.012	1	0.0009	0.963
Distance mainland	0.383	0.134	8.201	1	0.0042	1.467
Poa humilis (AUC = 0.78)						
Area non-rocky shore	0.058	0.012	22.485	1	< 0.0001	1.060
Island shelter	0.023	0.006	12.731	1	0.0004	1.023
Distance mainland	0.192	0.072	7.197	1	0.0073	1.212
Deschampsia bottnica (AUC = 0.86)						
Area rocky shore	0.025	0.012	4.104	1	0.0428	1.026
Minimum exposure	–0.160	0.024	43.520	1	< 0.0001	0.852
Island shelter	–0.060	0.009	43.822	1	< 0.0001	0.942
Distance mainland	0.611	0.110	30.986	1	< 0.0001	1.841
Hierochloë odorata ssp. *baltica*(AUC = 0.84)						
Minimum exposure	–0.131	0.037	12.590	1	0.0004	0.877
Shore line length	0.026	0.013	3.648	1	0.0561	1.026
Distance mainland	0.559	0.103	29.692	1	< 0.0001	1.748
Distance large island	0.111	0.046	5.724	1	0.0167	1.118
Calamagrostis stricta (AUC = 0.86)						
Flat shore area	0.031	0.015	4.410	1	0.0357	1.031
Shore line length	0.073	0.018	16.667	1	< 0.0001	1.076
South–north	0.069	0.014	25.922	1	< 0.0001	1.072
Alopecurus arundinaceus (AUC = 0.90)						
Minimum exposure	–0.070	0.029	5.854	1	0.0155	0.933
Maximum exposure	–0.010	0.004	5.602	1	0.0179	0.990
Shore line length	0.073	0.020	13.526	1	0.0002	1.076
Distance mainland	1.017	0.142	51.250	1	< 0.0001	2.765
Distance large island	–0.139	0.052	7.102	1	0.0077	0.870
Phragmites australis (AUC = 0.89)						
Flat shore area	0.060	0.019	10.262	1	0.0014	1.062
Minimum exposure	–0.152	0.030	25.678	1	< 0.0001	0.859
South–north	0.050	0.009	30.217	1	< 0.0001	1.051
Type II analyses						
Ophioglossum vulgatum (AUC = 0.714)						
South-north	–0.048	0.020	5.630	1	0.0177	0.953
Distance mainland	–0.736	0.222	11.041	1	0.0009	0.479
Distance large island	–0.141	0.045	9.705	1	0.0018	0.869
Silene uniflora (AUC = 0.84)						
Area non-rocky shore	0.029	0.010	7.727	1	0.0054	1.029
South–north	0.032	0.008	15.306	1	0.0001	1.033
Distance large island	–0.399	0.080	24.794	1	< 0.0001	0.671

Continued

Appendix. Continued.

	B	SE	Wald	d.f.	*p*	Exp(*B*)
Atriplex prostrata (AUC = 0.78)						
Area rocky shore	–0.035	0.009	15.735	1	0.0001	0.966
Minimum exposure	–0.066	0.019	11.783	1	0.0006	0.936
Isatis tinctoria (AUC = 0.71)						
South–north	0.027	0.011	6.099	1	0.0135	1.027
Distance large island	–0.156	0.046	11.782	1	0.0006	0.855
Cochlearia danica (AUC = 0.80)						
Island shape	–0.064	0.022	8.329	1	0.0039	0.938
Distance mainland	–0.723	0.167	18.699	1	< 0.0001	0.485
Potentilla anserina ssp. *groenlandica* (AUC = 0.88)						
Flat shore area	–0.094	0.045	4.260	1	0.0390	0.911
Minimum exposure	0.204	0.079	6.723	1	0.0095	1.226
Distance large island	–0.708	0.231	9.372	1	0.0022	0.493
Angelica archangelica ssp. *litoralis* (AUC = 0.82)						
Island shelter	0.062	0.010	41.407	1	< 0.0001	1.064
Distance mainland	–0.449	0.087	26.790	1	< 0.0001	0.638
Centaurium littorale (AUC = 0.67)						
Shore line length	–0.054	0.016	10.621	1	0.0011	0.948
Island shape	–0.027	0.015	3.511	1	0.0610	0.973
Stachys palustris (AUC = 0.74)						
Shore line length	–0.045	0.018	6.343	1	0.0118	0.956
Veronica longifolia (AUC = 0.75)						
Island shelter	0.027	0.008	11.081	1	0.0009	1.027
Distance mainland	–0.487	0.094	26.903	1	< 0.0001	0.615
Odontites litoralis (AUC = 0.75)						
Minimum exposure	0.059	0.025	5.430	1	0.0198	1.060
Distance large island	–0.252	0.051	24.605	1	< 0.0001	0.777
Festuca arundinacea (AUC = 0.69)						
Area non-rocky shore	–0.038	0.012	10.775	1	0.0010	0.963
Island shelter	–0.016	0.006	6.279	1	0.0122	0.984
Leymus arenarius (AUC = 0.70)						
Island shelter	0.023	0.009	6.153	1	0.0131	1.024
Distance large island	–0.134	0.065	4.266	1	0.0389	0.874
Elymus repens (AUC = 0.74)						
Shore line length	–0.054	0.025	4.495	1	0.0340	0.948
Island shape	0.022	0.013	2.875	1	0.0900	1.023
West–east	0.037	0.010	13.067	1	0.0003	1.037
Deschampsia bottnica (AUC = 0.75)						
Area rocky shore	–0.045	0.014	9.986	1	0.0016	0.956
West–east	0.039	0.011	12.245	1	0.0005	1.039
Height	0.063	0.031	3.960	1	0.0466	1.065
Phalaris arundinacea (AUC = 0.725)						
Area rocky shore	–0.045	0.017	6.851	1	0.0089	0.956
Island shape	–0.030	0.015	3.719	1	0.0538	0.971
Distance mainland	–0.169	0.089	3.625	1	0.0569	0.844
Distance large island	–0.120	0.058	4.305	1	0.0380	0.887
Alopecurus arundinaceus (AUC = 0.77)						
Area non-rocky shore	–0.025	0.012	4.551	1	0.0329	0.975
Distance mainland	–0.540	0.178	9.233	1	0.0024	0.583
Distance large island	–0.208	0.074	8.009	1	0.0047	0.812
Phragmites australis (AUC = 0.78)						
Minimum exposure	0.148	0.054	7.583	1	0.0059	1.160
Island shelter	–0.020	0.008	6.304	1	0.0120	0.980
Island shape	0.052	0.015	12.070	1	0.0005	1.053

Continued

Appendix. Continued.

	B	SE	Wald	d.f.	*p*	Exp(*B*)
Type III analyses						
Ophioglossum vulgatum (AUC = 0.80)						
Maximum exposure	–0.006	0.004	2.523	1	0.1122	0.994
South–north	0.051	0.021	6.121	1	0.0134	1.052
Montia fontana (AUC = 0.84)						
Flat shore area	0.050	0.019	6.723	1	0.0095	1.051
Distance mainland	–0.818	0.196	17.363	1	< 0.0001	0.441
Barbarea stricta (AUC = 0.74)						
South–north	0.030	0.014	4.715	1	0.0299	1.030
Distance large island	–0.186	0.074	6.397	1	0.0114	0.830
Centaurium pulchellum (AUC = 0.85)						
Island shelter	–0.066	0.018	13.946	1	0.0002	0.936
West–east	–0.071	0.027	7.174	1	0.0074	0.931
Myosotis laxa (AUC = 0.85)						
Flat shore area	0.120	0.029	16.445	1	0.0001	1.127
South–north	0.081	0.016	24.465	1	< 0.0001	1.084
Triglochin maritima (AUC = 0.93)						
Area rocky shore	0.118	0.049	5.712	1	0.0168	1.125
Island shelter	0.193	0.061	10.069	1	0.0015	1.213
Distance mainland	0.644	0.331	3.780	1	0.0519	1.905
Carex viridula coll. (AUC = 0.86)						
Area non-rocky shore	–0.064	0.028	5.306	1	0.0213	0.938
Maximum exposure	0.036	0.032	1.323	1	0.2501	1.037
Distance large island	0.287	0.154	3.467	1	0.0626	1.333
Hierochloë odorata ssp. *baltica* (AUC = 0.82)						
Area rocky shore	0.091	0.045	4.141	1	0.0419	1.096
Minimum exposure	–0.098	0.044	4.877	1	0.0272	0.907
Shore line length	–0.288	0.098	8.562	1	0.0034	0.750
Calamagrostis stricta (AUC = 0.83)						
West–east	–0.057	0.024	5.654	1	0.0174	0.944
Height	–0.148	0.053	7.770	1	0.0053	0.862