

Changes in distributions of selected vascular plants in a Baltic archipelago

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The aim of the study was to find indications of climate change by studying changes in frequency and distribution patterns of 18 plant species occurring predominantly on islands. I compared climate-related predictors of islands with species extinctions to islands with colonizations. The study was conducted on 436 islands in the archipelago of SW Finland in the northern Baltic Sea. The data were collected between 1996 and 2012 and, the historical data mainly in the 1930s. I measured predictors, including area, exposure and topographical diversity, in a GIS and used binominal logistic regression to determine which predictors exert an influence on the probability of species occurrence. The number of observations of the selected plants increased by 8.4%, but not by as much as all plant species occurring on the studied islands (10.6%). Species with a generally northern distribution in Finland increased more than thermophilic species. An unambiguous effect of climate warming on the selected plants is not evident. One of the proposed reasons for this is the small-scale topography and the mosaic of different microclimates on the islands that buffer the effect of a large-scale climate warming.

Introduction

Eklund (1937) defined a group of vascular plant species occurring in the archipelago of SW Finland as island plants (*Schärenpflanze*) in a long-forgotten and hardly ever cited paper *Klimabedingte Artenareale* (“Climate-dependent species distribution”). These species occur only sparingly on the large islands or on the mainland, but usually grow on the small islands. This group includes several littoral species, but also species of the supralittoral. According to Eklund (1937, 1958) the distribution of these species is shaped by the climate of the small islands. A large proportion of Eklund’s island species are southern

thermophiles benefiting from the long growing season of the small islands and, in relation to the mainland, from the long frost-free autumn, which is due to the warming effect of the sea water that retains heat from the warm summer months. There are also species with a generally northern (boreal) distribution among the island plants. These, in turn, benefit from the maritime climate of the peripheral islands close to the open sea. In all, Eklund (1937, 1958) defined 32 species as island plants in the archipelago of SW Finland.

Climate warming is considered a major threat to the Earth’s biodiversity (Fischlin *et al.* 2007, Rosenzweig *et al.* 2007). The distribu-

tion of species is expected to shift towards the poles and higher altitudes (e.g. Parmesan *et al.* 2003). According to Tietäväinen *et al.* (2009), the annual mean temperature in Finland rose by 0.93 ± 0.72 °C during the last 100 years. The rise in mean temperature was strongest in spring, but during the last 50 years the warming was clearly strongest in winter, the rise in the winter mean temperature from 1958 to 2007 being 3.47 ± 2.78 °C. Linkosalo *et al.* (2009) used a systematically collected set of data on phenological events in Finland (leaf bud burst and flowering dates of six deciduous tree species) that has continued uninterrupted since the 1840s, to reveal trends in the timing of these events. This “biological thermometer” showed an increase in spring temperature of 1.8 °C per century, which is in agreement with the measurements carried out at the meteorological stations in Finland.

This change in climate could be reflected in changes in distribution and frequency of the island plants as defined by Eklund, and this idea was the inspiration for this study. Here, I used historical and current observations to relate the distribution of island plants, and the changes thereof, to environmental predictors that mirror the climate of the islands.

The aims of this study were (1) to find indications of climate change by studying the changes in the frequency and in the distribution patterns of the island plants, by comparing historical and current occurrences (2) to find island climate-related predictors that exert an influence on the probability of occurrence of the island plants, and (3) to find indications of climate change or environmental change by comparing the climate-related predictors of islands with extinctions (or of islands with the plant occurring during both times) to islands with colonization.

Material and methods

Eklund (1958) compiled vascular plant species lists for about 1600 localities in a large part of the archipelago of SW Finland. Most of these localities are individual islands, although some are parts of large islands. These historical data were entered into a database and 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, von Numers & Korvenpää 2007). 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 (1960) compiled his species lists in the 1940s, using the same methods as Eklund. Skult’s data were included in the database used in this study. Vaahtoranta’s (1964) study area, bordering Eklund’s in the north, included 171 islands surveyed in 1952–1955. One of those islands was included in this study.

The current data were collected between 1996 and 2012. In total, 436 islands were re-surveyed within Eklund’s study area (Fig. 1). Of these islands, 401 were previously surveyed by Eklund, 23 by Skult and one by Vaahtoranta. The study area extends about 100 km in the S–N direction and 80 km in the W–E direction (Fig. 1). The islands vary in size, the mean island area being about 9.9 ha. The smallest island is 0.04 ha, the largest 173.5 ha and the total area surveyed was 4335 ha. Island height varies between ca. 2.5 m a.s.l. and 43 m a.s.l., the mean height being ca. 11 m a.s.l.

Study area

The archipelago of SW Finland is a shallow, non-tidal and low-saline (Suominen *et al.* 2010) sea area in the northern Baltic Sea. The area of the archipelago covers about 15 000 km² 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 woods and settlements. This mosaic structure results in a wide range of conditions and habitats on the islands throughout the archipelago. Most of the islands emerged from the sea during the past few thousands of years, because of isostatic land uplift (currently 4 mm per year; Kakkuri 1987) after the last Glacial Age which ended 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 are 500 mm and 70 days, respectively (Atlas of Finland 1993). The characteristics of the archipelago change gradu-

ally 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. 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 (influenced by the sea). 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 penetrate deep into the inner archipelago, forming maritime enclaves in areas with otherwise low maritimity.

Fieldwork

The islands were surveyed during the same phase of the growing season as the one when Eklund and Skult conducted their surveys. Usually the field season began around 15 June and continued to about 5 August. 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 drought made it difficult to compile reliable species lists. A species checklist derived from the database was used alongside the original island-specific species list of Eklund or Skult. These lists gave information on species presence on the islands, with no indication of species abundance. The new species lists were compiled in a similar way.

Island plants

Eklund (1958) defined 31 plant species as island plants. I did not include typical littoral plants, for which clearly other factors than climate, such as eutrophication of the Baltic Sea and grazing, exert a dominating influence on the distribution patterns (von Numers 2011). Species whose distributions cover large parts of Finland (Lampinen & Lahti 2012), with no observable

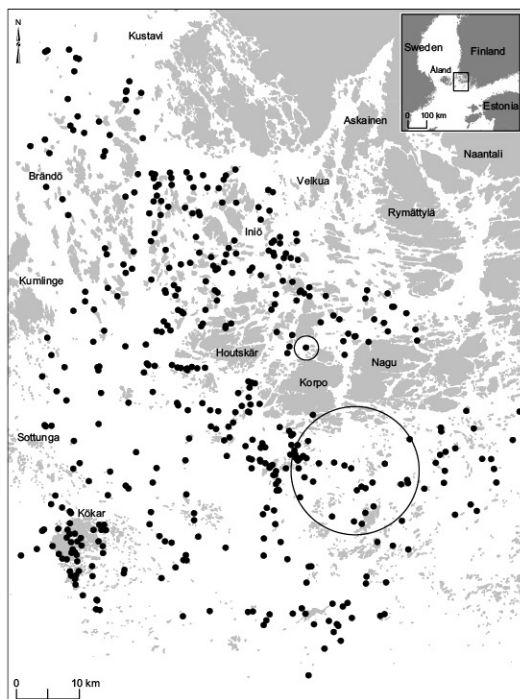


Fig. 1. The 436 islands included in the study. Circles show areas used to calculate local exposure (radius 2 km) and large-scale exposure (radius 10 km) for each island.

climate-linked distribution boundary, were also excluded. Included were thus the thermophile species that occur only in southern and southwestern Finland, and the boreal species with a northern general distribution in Finland. A total of 18 island plants fulfilled these requirements and were thus included in the present study (Table 1).

Predictors

I measured six predictors which mirror the climate of the islands (Table 2). All predictors were measured within GIS (ArcView 9.3.) using map data obtained from the Finnish land survey. I created a digital elevation model, DEM (resolution 10 m), using the Spatial Analyst tool TopoToRaster. This DEM was based on elevation curves (both below and above the sea surface) and the shoreline. I used the ArcView tool *Focal Statistics* to calculate standard deviations of the eleva-

Table 1. The species included in the study. "Thermophile" characterization is mainly based on Eklund (1958) and the general distribution in Finland follows Lampinen and Lahti (2012). * = distributed especially in the SW archipelago: ** = most common in the northern part of Finland. *** Pertain to the study area only, and are based on Eklund (1958) and own observations.

Species (distribution map)	Thermophile	General distribution in Finland	Habitat**	Remarks***
Increased frequency				
<i>Agrimonia eupatoria</i> (Fig. 2)	yes	SW	stony hillocks, slopes with junipers and occasionally in groves	–
<i>Arrhenatherum elatius</i> (Fig. 3)	yes	SW	stony slopes with e.g. junipers	rare on large islands
<i>Cochlearia danica</i> (Fig. 4)	no	S & SW*	among stones and in fissures in rocks near the littoral zone	occurs in the outer archipelago and on small islands in open waters
<i>Cornus suecica</i> (Fig. 5)	no	coast & N**	near rock-pools and wet fragments of maritime birch, <i>Betula pubescens</i> , groves	boreal species, distribution limited to maritime areas
<i>Erysimum strictum</i> (Fig. 6)	no	coast & N	supralittoral part of dry, gravelly shores	boreal species
<i>Geranium sanguineum</i> (Fig. 7)	yes	SW	stony slopes, heath-like areas, etc.	distribution did not change markedly
<i>Hypericum hirsutum</i> (Fig. 8)	yes	SW*	on sunny and stony slopes, e.g. among creeping junipers and sometimes in groves	
<i>Rhamnus cathartica</i> (Fig. 9)	yes	SW*	on stony slopes, in groves and in former wooded meadows	distributed evenly across the area decreases towards NE
<i>Scrophularia nodosa</i> (Fig. 10)	yes	S	upper parts of stony shores, among stands of alders, on herb rich slopes, etc.	common in the area
<i>Vaccinium uliginosum</i> (Fig. 11)	no	S to N**	bogs and wet depressions, especially in the outer part of the archipelago	twice as frequent as <i>C. suecica</i>
<i>Vincetoxicum hirundinaria</i> (Fig. 12)	yes	SW*	on rocky ledges, stony slopes and fissures in the rock	common in the area
Decreased frequency				
<i>Carex muricata</i> (Fig. 13)	yes	S	on stony meadows and sunny slopes with shrubs and dense undergrowth	unevenly distributed
<i>Dactylorhiza sambucina</i> (Fig. 14)	yes	SW*	man-made habitats, such as pastures, and in addition on limestone	found in the central, limestone-rich (Houtskär) area and in Kökar; decreasing probably because of the overgrowth of former pastures and meadows
<i>Melampyrum cristatum</i> (Fig. 15)	yes	SW	pastures and meadows	rarest, 14 current and 16 historical records most of which are from islands near Kökar
<i>Origanum vulgare</i> (Fig. 16)	yes	SW	maritime and stony, herb-rich slopes with junipers	common in the area

<i>Scutellaria hastifolia</i> (Fig. 17)	relatively rare in the area	herb-rich slopes and among creeping junipers	S & SW	yes
Negligible frequency change				
<i>Cardamine hirsuta</i> (Fig. 18)	most abundant of the studied species	forest-poor, flat islands, e.g. among creeping junipers on thin soil layers	SW	yes
<i>Draba incana</i> (Fig. 19)	boreal species	maritime heaths, gravel shores and often among creeping junipers in dry places	coast & N	no

tion values for the 10×10 m pixels of the DEM inside each island shoreline, and used this value as a measure of island topographical diversity.

Potential total solar radiation (Mj cm^{-2}) based on slope, aspect and angle of solar radiation for the period 1 May–31 September was calculated for each 10×10 m island pixel using the ArcView tool *Area Solar Radiation*. Areas of low and high solar radiations were determined as predictors per island. These predictors were eventually dropped from the analyses as they were highly correlated with the predictor “island topographical diversity” and with each other.

I tested the correlation between the above predictors, as strong correlation may cause problems in model fitting and interpretation (Graham 2003, Heikkinen *et al.* 2006). In this study, collinearity should be of minor concern as Pearson’s correlation coefficients between the predictors were smaller than 0.50 [at most 0.46: between total area of land within a buffer zone of 10 km and position (south–north)]. The correlation between the predictors’ “local exposure” and “large-scale exposure” to the sea was 0.33.

Statistical methods and maps

I used a binary logistic regression analysis (SPSS 19.0) to determine how the predictors exerted an influence on the probability of species occurrence. Logistic regression analyses were performed on the species of the 425 islands (of a total of 436) that were surveyed in the years 1996–2011. 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 models obtained were tested for significance using Hosmer and Lemeshow statistics and Nagelkerke R^2 in SPSS (Hosmer & Lemeshow 2000). The predictors were tested for significance using Wald statistics. Only the significantly contributing predictors are further dealt with. The analyses were designed to answer the following two questions:

1. How do the island predictors affect the probability of occurrence of the individual species? In this case, islands with no occurrences of the species were compared with islands with occurrences. This analysis was made for the current data for all species.

Table 2. Six predictors considered in the study that affect climate on the islands.

1. Island area: larger area results in a decreasing effect of the surrounding sea
2. Island topographical diversity: higher topographical diversity was considered to result in a more diverse set of available types of microclimates because of e.g., varying degrees of solar radiation and shelter from wind
3. Position (south–north)
4. Position (west–east)
5. Total area of water within a zone of 2 km from the shoreline of the island (local exposure to the sea)
6. Total area of water within a zone of 10 km from the shoreline of the island (large-scale exposure to the sea)

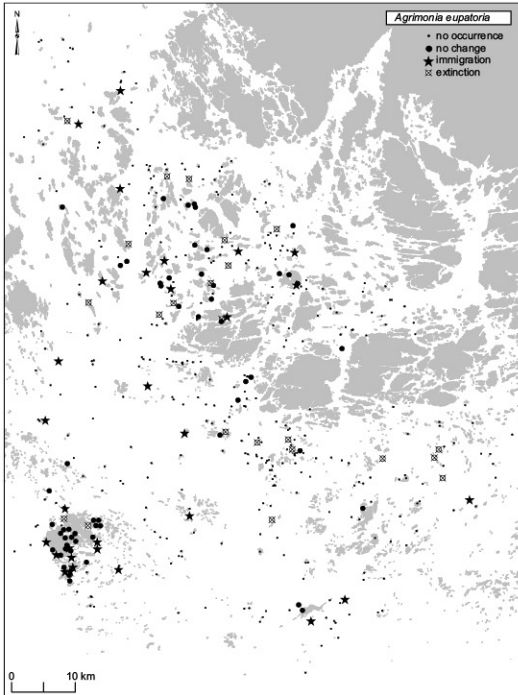


Fig. 2. Changes in the distribution of *Agrimonia eupatoria*.

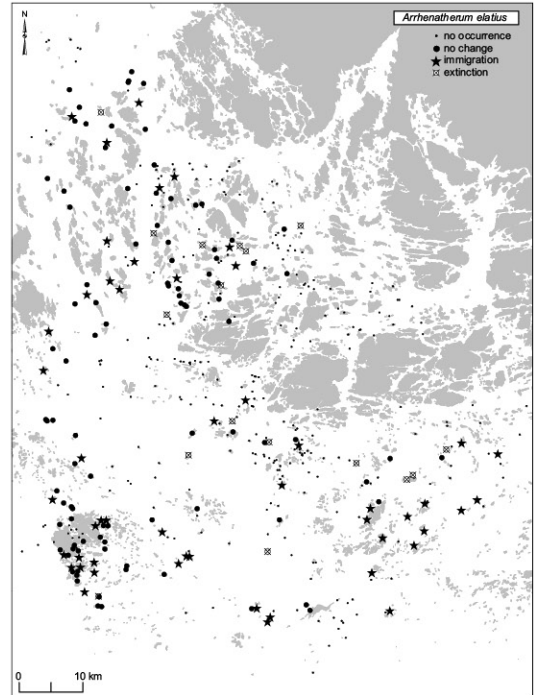


Fig. 3. Changes in the distribution of *Arrhenatherum elatius*.

2. How do the predictors of the islands with extinctions of a species differ from the islands with colonization? This analysis was made for the species whose numbers of extinctions and colonization were large enough for a reliable result. For some of the species the number of extinctions was very low in relation to colonizations. In such a case, islands with both a historical and a current record were compared with islands with only a current record.

A turnover rate was calculated for each species using the formula: $(\text{extinctions} + \text{colonizations}) / (\text{historical species number} + \text{current species number})$; see e.g. Schoener (1983).

A canonical correspondence analysis (CCA; CANOCO 4.5, CANODRAW 4.14; Microcomputer Power, Ithaca, NY, US) was carried out for the contemporarily surveyed islands, and was based on all species (493) with a frequency of three or more island occurrences. I included all species of the islands in the CCA, to visualize the position of the island plants in relation to the other species. The predictors in the CCA were

the same as those used in the binary logistic regression analyses. The distribution maps were created in Arc Map 10.0.

Results

The total number of historical island-plant records was 2210 and the number of current records 2396 (8.4% increase) on 436 islands. Accordingly, the number of extinctions (389) was smaller than the number of colonizations (575). The number of unchanged occurrences was 1821. Of the studied 18 species, 11 increased in frequency (Table 1, Figs. 2–12) and 5 decreased (Table 1, Figs. 13–17), while frequency changes of 2 species were negligible (Table 1, Figs. 18–19). The detailed results are summarised in Tables 3–5 and Appendices 1 and 2.

CCA analysis of the current data

The result of the CCA analysis (Fig. 20) gener-

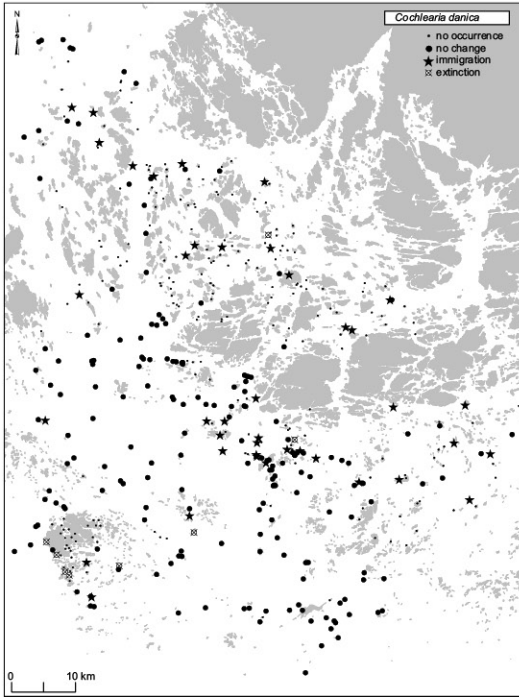


Fig. 4. Changes in the distribution of *Cochlearia danica*.

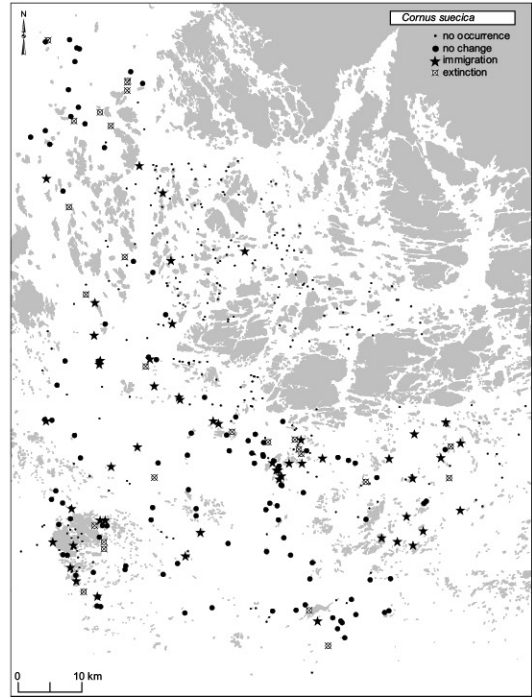


Fig. 5. Changes in the distribution of *Cornus suecica*.

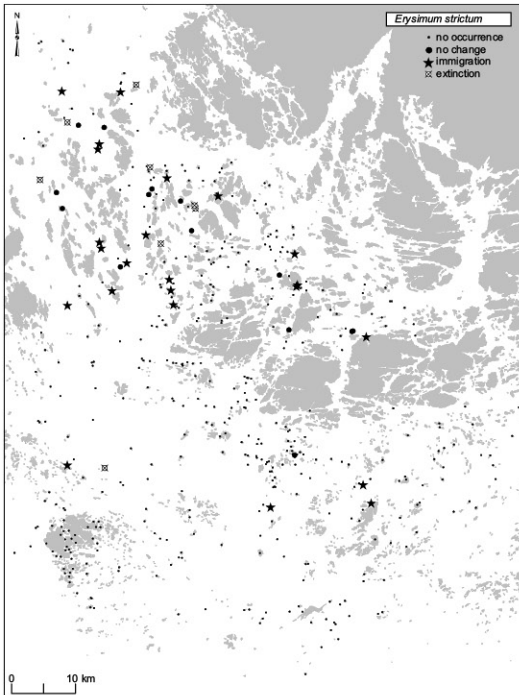


Fig. 6. Changes in the distribution of *Erysimum strictum*.

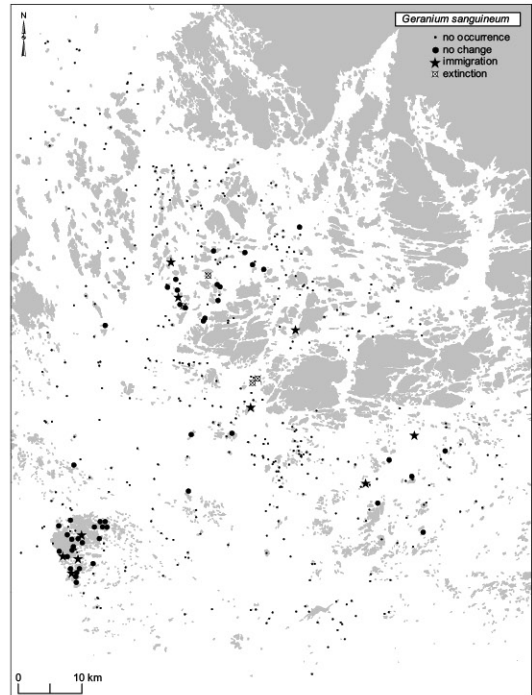


Fig. 7. Changes in the distribution of *Geranium sanguineum*.

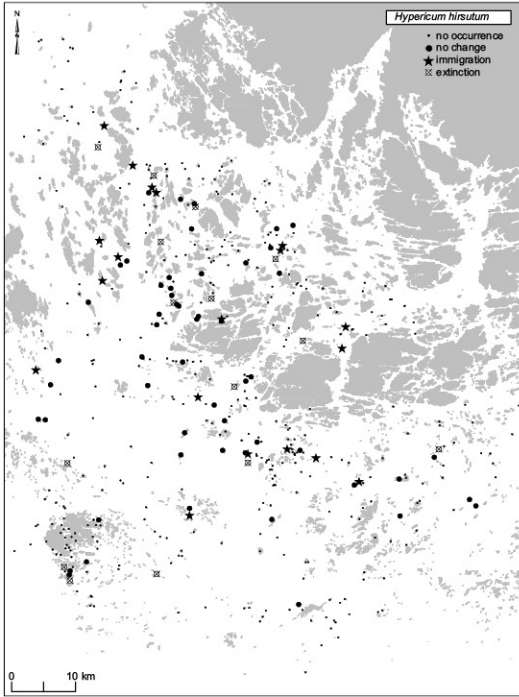


Fig. 8. Changes in the distribution of *Hypericum hirsutum*.

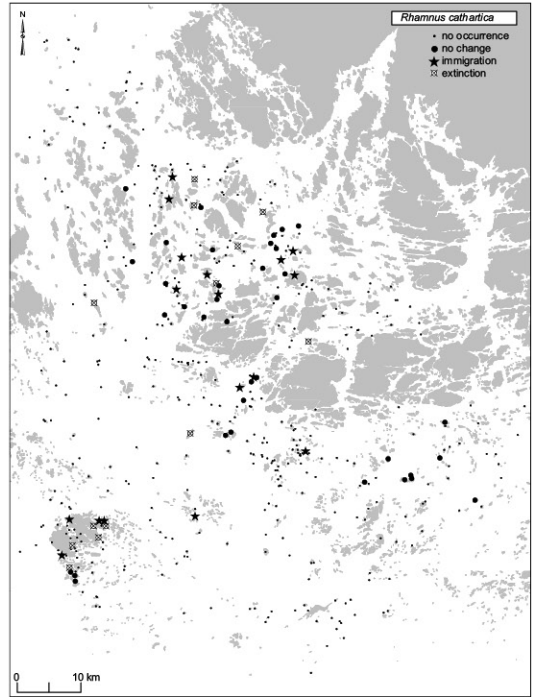


Fig. 9. Changes in the distribution of *Rhamnus cathartica*.

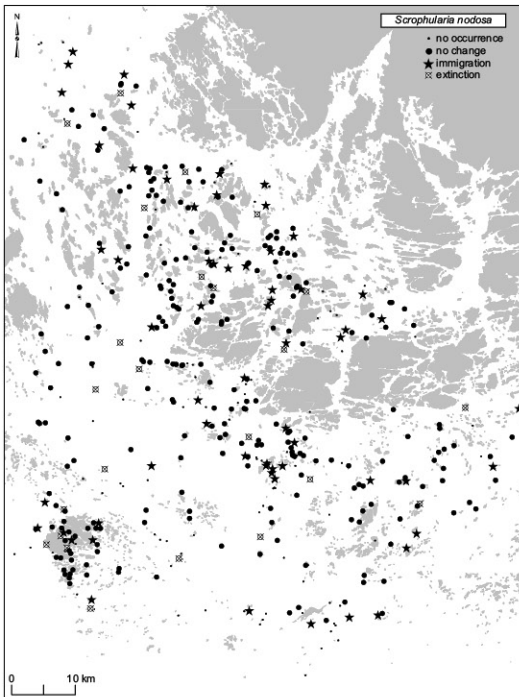


Fig. 10. Changes in the distribution of *Scrophularia nodosa*.

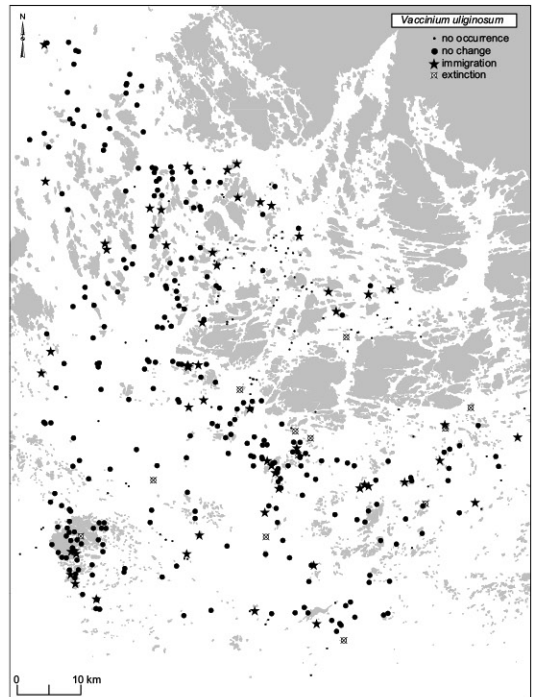


Fig. 11. Changes in the distribution of *Vaccinium uliginosum*.

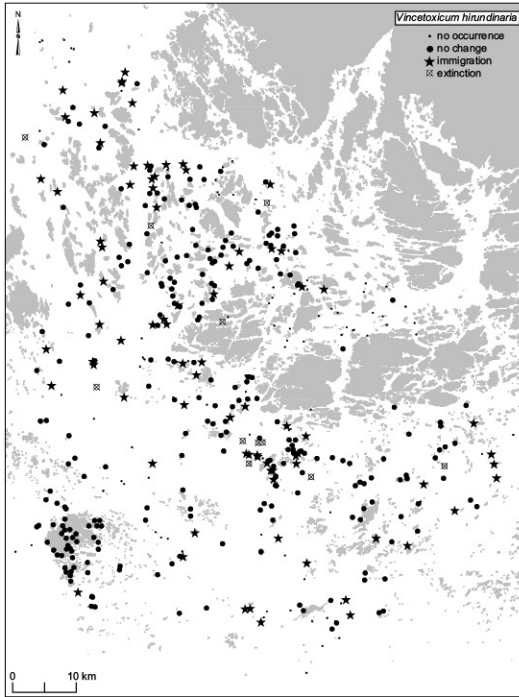


Fig. 12. Changes in the distribution of *Vincetoxicum hirundinaria*.

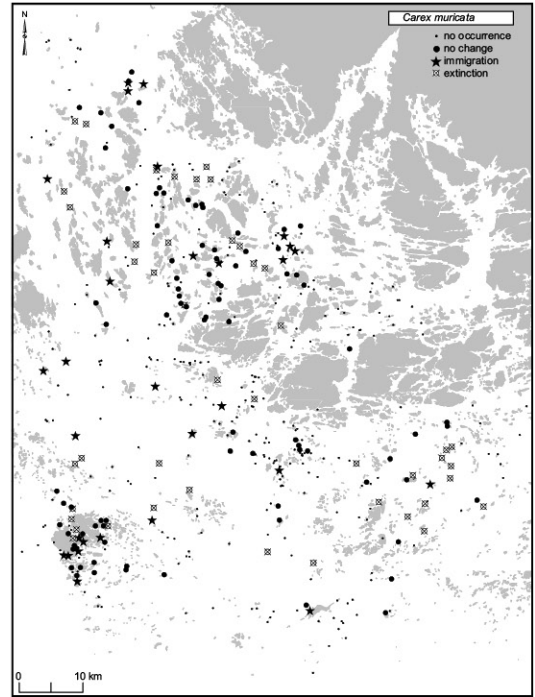


Fig. 13. Changes in the distribution of *Carex muricata*.

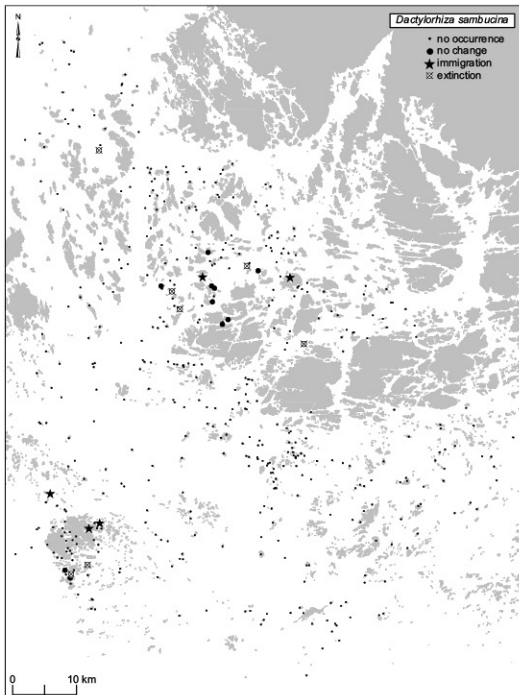


Fig. 14. Changes in the distribution of *Dactylorhiza sambucina*.

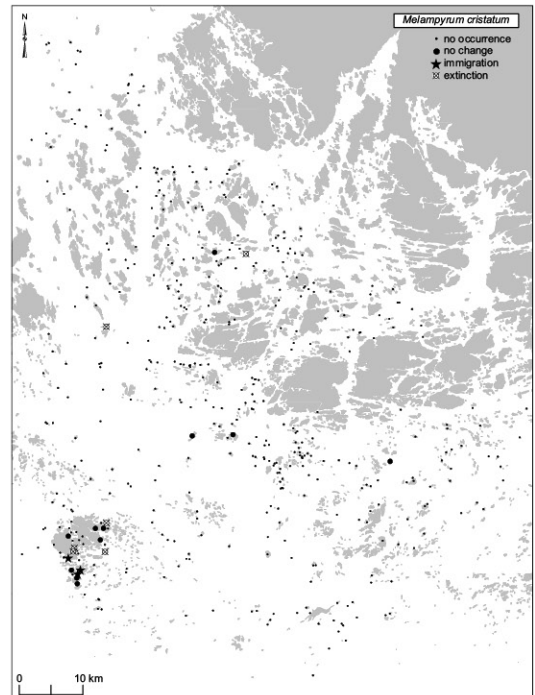


Fig. 15. Changes in the distribution of *Melampyrum cristatum*.

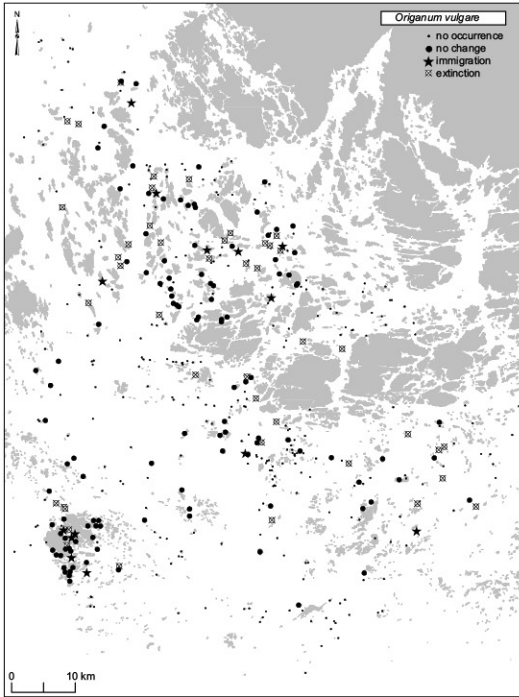


Fig. 16. Changes in the distribution of *Origanum vulgare*.

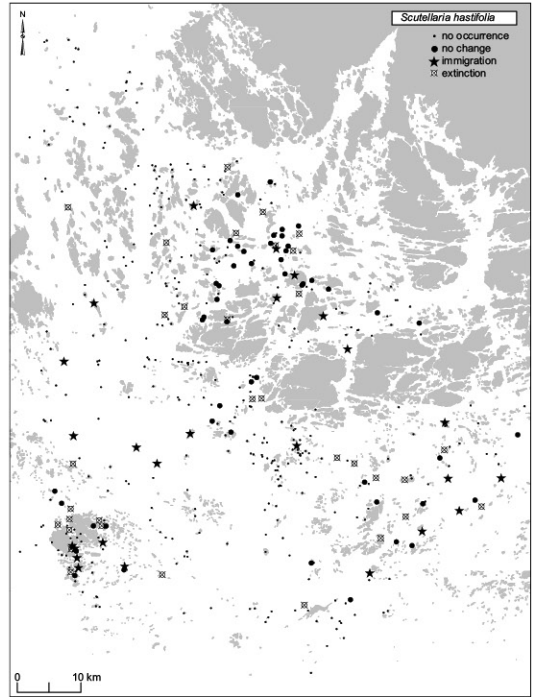


Fig. 17. Changes in the distribution of *Scutellaria hastifolia*.

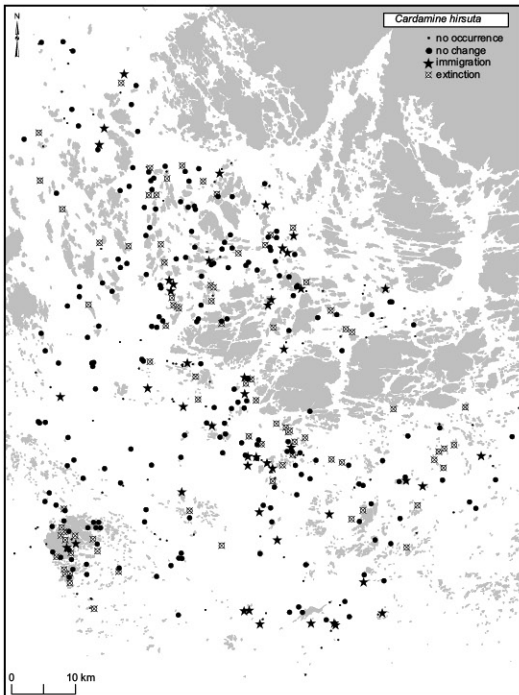


Fig. 18. Changes in the distribution of *Cardamine hirsuta*.

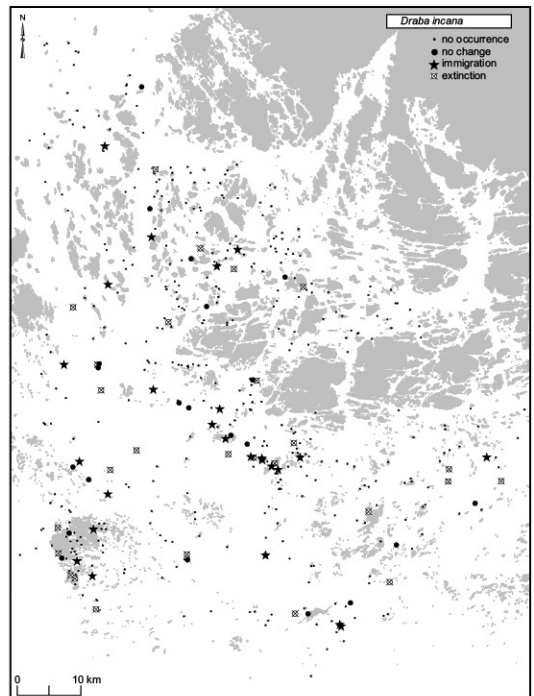


Fig. 19. Changes in the distribution of *Draba incana*.

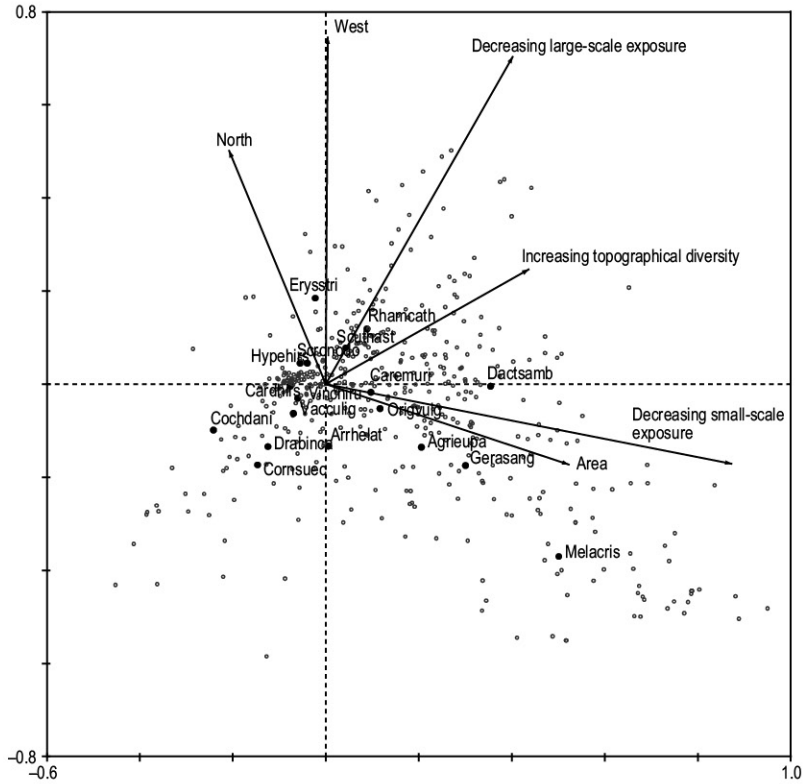


Fig. 20. Canonical correspondence analysis (CCA) ordination plot of the 493 species of the 436 islands. The 18 island plant species are marked with black dots. The predictors in the CCA are the same as those used in the binary logistic regression analyses.

Table 3. Predictors significantly contributing to the binary logistic regression model when islands with absences are compared with islands with presences for each of the species. Predictors contributing most strongly according to the Wald value are indicated with ++ or --.

	Area	West-east	South-north	Topographic diversity	Large-scale exposure	Local exposure
<i>Agrimonia eupatoria</i>		-	-	+		-
<i>Arrhenatherum elatius</i>	+	--	-			
<i>Cochlearia danica</i>	-	-	-		++	+
<i>Cornus suecica</i>	+	-	-	+	++	+
<i>Erysimum strictum</i>			++	-	-	
<i>Geranium sanguineum</i>	+	-	-	+		--
<i>Hypericum hirsutum</i>				+		
<i>Rhamnus cathartica</i>				++	-	
<i>Scrophularia nodosa</i>			+	++		-
<i>Vaccinium uliginosum</i>	+	-	+	+	++	
<i>Vincetoxicum hirundinaria</i>	++	-			+	
<i>Carex muricata</i>	+	-		+		--
<i>Dactylorhiza sambucina</i>	+	-			--	-
<i>Melampyrum cristatum</i>	++	-	-	+		
<i>Origanum vulgare</i>	+	-		+		--
<i>Scutellaria hastifolia</i>	+	+				--
<i>Cardamine hirsuta</i>	+			-		
<i>Draba incana</i>					++	

ally supports the results of the logistic regression analyses based on the current data. It is noteworthy that, in relation to the rest of the species of the islands, the plants, except *Cochlearia danica*, are not situated at the extreme ends of the gradients. *Carex muricata*, *Origanum vulgare*, *Dactylorhiza sambucina*, *Agrimonia eupatoria*, *Geranium sanguineum* and *Melampyrum cristatum* are associated with decreasing local exposure and increasing area. *Vaccinium uliginosum*, *Draba incana*, *Cornus suecica* and *Cochlearia danica* are associated with increasing large-scale exposure. *Cochlearia danica* is, in addition, associated with decreasing local exposure. *Rhamnus cathartica* and *Dactylorhiza sambucina* are most strongly associated with a high topographical diversity, whereas *Erysimum strictum* is associated with a northern position.

Discussion

As is evident from the results, there is no unambiguous response of the island plants to the predictors and the results seem contradictory. The number of island plant observations increased

(8.4%), but not as much as that of the shore plants of the same islands (22.7%; von Numers 2011). The increase in the number of observations of all plant species occurring on the studied islands (436) is 10.6% (own unpubl. data), which is also more than for the island plants. Unexpectedly, the species with a generally northern distribution in Finland (*Draba incana*, *Erysimum strictum*, *Cornus suecica* and *Vaccinium uliginosum*) increased more (17.1%) than the thermophilic species (the rest of the species; 6.0%).

Of the species with a northern distribution, only *Draba incana* marginally decreased; the three other species increased. Large-scale exposure is a good predictor of increased probability of occurrence of *Draba incana*, *Cornus suecica* and *Vaccinium uliginosum*, whereas a northern position is a predictor of the occurrence of *Erysimum strictum*. This is also seen in Figs. 19, 5, 11 and 6, respectively). Interpretation of the reasons for the changes for these four species is not straightforward. For *Draba incana*, no usable logistic regression model was obtained. The distribution map (Fig. 19) shows no clear pattern in colonizations and extinctions, nor did the distribution range of the species changed mark-

Table 4. Predictors significantly contributing to the binary logistic regression model for each species when islands with extinctions are compared with islands with colonizations (e/c) or islands with preserved occurrences are compared with islands with colonizations (p/c). n.s. = non-significant model. The most strongly contributing predictor according to the Wald value is indicated with ++ or --.

	Area	West-east	South-north	Topographic diversity	Large-scale exposure	Local exposure
<i>Agrimonia eupatoria</i> e/c	-			-	++	-
<i>Arrhenatherum elatius</i> p/c		++	-	-		
<i>Cochlearia danica</i> p/c		++	+	+		-
<i>Cornus suecica</i> p/c		+				--
<i>Erysimum strictum</i> p/c					++	
<i>Geranium sanguineum</i> p/c	-	++	-		-	
<i>Hypericum hirsutum</i> e/c	--					
<i>Rhamnus cathartica</i> e/c	--				+	
<i>Scrophularia nodosa</i> p/c	--			+		
<i>Vaccinium uliginosum</i> p/c		+		-	-	
<i>Vincetoxicum hirundinaria</i> p/c		+	++	-	+	
<i>Carex muricata</i> e/c		-				
<i>Dactylorhiza sambucina</i> n.s.						
<i>Melampyrum cristatum</i> n.s.						
<i>Origanum vulgare</i> e/c						--
<i>Scutellaria hastifolia</i> n.s.						
<i>Cardamine hirsuta</i> e/c	+	+	+	-	+	
<i>Draba incana</i> n.s.						

Table 5. Statistics (number of islands except for the last column) regarding the 18 island plant species on the 436 islands.

	No occurrence	Extinction	Preserved	Colonisation	Historical total	Current total	Change	Turnover	Historical frequency	Current frequency	Change (%)
<i>Agrimonia eupatoria</i>	330	23	54	29	77	83	6	32.5	18.12	19.53	7.8
<i>Arrhenatherum elatius</i>	278	16	93	49	109	142	33	25.9	25.65	33.41	30.3
<i>Cochlearia danica</i>	205	8	184	39	192	223	31	11.3	45.18	52.47	16.1
<i>Cornus suecica</i>	255	26	106	49	132	155	23	26.1	31.06	36.47	17.4
<i>Erysimum strictum</i>	391	8	14	23	22	37	15	52.5	5.18	8.71	68.2
<i>Geranium sanguineum</i>	379	4	44	9	48	53	5	12.9	11.29	12.47	10.4
<i>Hypericum hirsutum</i>	350	14	53	19	67	72	5	23.7	15.76	16.94	7.5
<i>Rhamnus cathartica</i>	371	13	35	17	48	52	4	30.0	11.29	12.24	8.3
<i>Scrophularia nodosa</i>	105	23	248	60	271	308	37	14.3	63.76	72.47	13.7
<i>Vaccinium uliginosum</i>	110	11	259	56	270	315	45	11.5	63.53	74.12	16.7
<i>Vincetoxicum hirundinaria</i>	101	11	245	79	256	324	68	15.5	60.24	76.24	26.6
<i>Carex muricata</i>	280	42	84	30	126	114	-12	30.0	29.65	26.82	-9.5
<i>Dactylorhiza sambucina</i>	415	7	9	5	16	14	-2	40.0	3.76	3.29	-12.5
<i>Melampyrum cristatum</i>	417	5	11	3	16	14	-2	26.7	3.76	3.29	-12.5
<i>Origanum vulgare</i>	272	42	110	12	152	122	-30	19.7	35.76	28.71	-19.7
<i>Scutellaria hastifolia</i>	331	33	48	24	81	72	-9	37.3	19.06	16.94	-11.1
<i>Cardamine hirsuta</i>	110	76	203	47	279	250	-29	23.3	65.65	58.82	-10.4
<i>Draba incana</i>	363	27	21	25	48	46	-2	55.3	11.29	10.82	-4.2

edly. Among all the studied species, the increase in *Erysimum strictum*, relative to its historical frequency, was the strongest, and according to the model this increase was towards the islands with a higher large-scale exposure. The center of its distribution remained in the north, however. *Cornus suecica* and *Vaccinium uliginosum* increased towards the east, but also towards the islands with lower exposure. As a conclusion, the changes in the distribution of the boreal island plants do not indicate uniform trends. An obvious negative effect of climate warming cannot be seen, but rather the contrary, as the total number of occurrences of these species increased. Note, however, that partly in opposition to the result in this study, Maad *et al.* (2009) found a decrease in the frequency of species with a northern distribution in the Uppland area in Sweden, which also contains islands. Here, the frequency of *Draba incana* decreased clearly, and the frequencies of *Erysimum strictum* and *Cornus suecica* remained the same during a period of about 80 years.

Cochlearia danica is the most maritime and maybe the most representative of the island plants. It is apparently also a thermophile as its northernmost occurrences are about 100 km to the north of the present study area (Vaahstoranta 1964). It is the only species whose probability of occurrence increases with decreasing island area and with both increasing local and large-scale exposures. *Cochlearia danica* markedly increased in frequency and expanded its distribution range to the east and north, and to the islands with lower local exposure. This increase in frequency might be explained by a more favorable climate.

The remaining part of the island plants are thermophiles. An increasing trend among these species is thus to be expected because of a climate warming. This is the case for some of them. Of these species, *Arrhenatherum elatius*, *Vincetoxicum hirundinaria* and *Scrophularia nodosa* increased the most. *Arrhenatherum elatius* had had a western distribution in the study area, but it spread eastwards. It also showed a marked increase in Uppland (Maad *et al.* 2009). Today, *Vincetoxicum hirundinaria* is common in the study area and it has spread northwards (Fig. 12 and Table 4). *Scrophularia nodosa* was very common in the entire study area to begin with,

but increased further, and has colonized smaller islands. The behavior of these three species could thus indicate an effect of a more favorable climate.

Agrimonia eupatoria and *Geranium sanguineum* slightly increased. The probability of occurrence increases for both species with decreasing local exposure, but they are indifferent to large-scale exposure. The changes in their distributions seem very modest, but *Agrimonia eupatoria* colonized islands with a high degree of large-scale exposure. Whether this is a result of climate warming or increasing overgrowth of the sheltered islands on one hand and appearance of suitable habitats on the maritime islands on the other remains unclear. Both species benefit from man-made open habitats. As these decreased, a potential larger increase in frequency of these two species might have been suppressed.

Carex muricata, *Scutellaria hastifolia* and *Origanum vulgare* decreased slightly. They resemble *Agrimonia eupatoria* and *Geranium sanguineum* as their probability of occurrence increased with decreasing local exposure (and an indifference to large-scale exposure). The maps alone (Figs. 13, 17, 16, respectively) do not reveal changes in distribution patterns, and the results of the logistic regression models are not easy to interpret.

Hypericum hirsutum was given much attention by Eklund (1935, 1947), as he claimed that it was increasing in the area. This thermophilic species, occurring mostly on dry southern slopes of the islands, has its center of distribution in Finland in the present study area. It does not occur, or is very rare, in the area bordering the study area in the northeast (own observations). The slight increase in frequency and the colonization of smaller islands is at least not in contradiction with an effect of a more favorable climate. An expansion of the distribution northwards is not seen.

Cardamine hirsuta was common all over the study area, usually occurring on open, low and flat islands, which was also indicated by the model. It somewhat decreased, and more on islands with higher topographical diversity. As an annual species, usually growing on open thinly soiled ground, overgrowth and the cessation of livestock grazing have probably contributed to the decrease on some islands.

The occurrence of *Rhamnus cathartica* is benefiting from high topographical diversity. It increased slightly, and the colonizations took place on smaller islands than the extinctions, which might indicate a favorable effect of a change in climate. *Dactylorhiza sambucina* and *Melampyrum cristatum* are both rare and decreased somewhat. Both are dependent on man-made habitats, such as pastures and meadows, and it is likely that overgrowth has contributed to make them rarer.

This study was based on data that was collected on an island scale, thus with fairly low resolution. Within the islands, the species are patchily distributed because of environmental gradients and habitat availability (von Numers & van der Maarel 1998, Hannus & von Numers 2010) and other factors such as dispersal potential and coincidence (e.g. Palmgren 1915–1917). According to Ackerly *et al.* (2010), spatial variability in temperature at scales as little as tens or hundreds of meters can potentially constitute buffers in ecosystem responses to climate change. This phenomenon is discussed further in Gillingham *et al.* (2012a, 2012b) and Leinor *et al.* (2013). Fine-grained thermal variability is attributed to physical processes such as air motion and solar radiation interacting with topographic complexities (Geiger & Aron 2003).

The pattern of microclimates on small islands can be very intricate, e.g. enabling thermophile species of sunny, southern slopes to co-occur with boreal species on northern shady slopes on the same island. It is thus obvious that small-scale topography and the mosaic of different microclimates within islands will buffer the effect of a large-scale climate warming.

Perennial species probably show considerable lags in their response to climate variability and other types of environmental change. Of the island plants, all species are perennials except *Cochlearia danica*, *Cardamine hirsuta*, *Melampyrum cristatum*. Of these species, *Cardamine hirsuta* shows a very high turnover. The seeds of *Erysimum strictum* germinate in spring, develop into a rosette during the first summer, and flower during the second. These annuals do not show coherent trends in relation to a climate change.

Most of the perennial species probably reach very old age: e.g., Solbreck (2012) observed individuals of *Vincetoxicum hircundinaria* recorded

already around 1970. Individuals can probably become much older than that. Longevity and the ability to tolerate both open and shady conditions (Knight *et al.* 2007) might explain the success of *Rhamnus cathartica* on small islands. Established, long-lived species will not easily disappear from an island even if the conditions become suboptimal. This might explain the very low extinction rate of e.g. *Geranium sanguineum* and *Vincetoxicum hircundinaria*. Palmgren (1915–1917, 1925), one of the pioneers in island biogeography, and alongside Eklund the most prominent expert on plants of the archipelago of SW Finland, emphasized the effect of coincidence when plant communities form in small-scaled habitat fragments on islands. Species that are established early, rapidly propagate vegetatively, thus effectively preventing establishment of later newcomers. This effect, in combination with persistence, probably efficiently buffers rapid changes in many of the species of the islands.

Tietäväinen *et al.* (2009) showed that the annual mean temperature rose in Finland during the last 100 years. This observation is supported by phenological events (Linkosuo *et al.* 2009). The results of this study show that an undisputed effect of a climate warming on the selected island plants is not evident, at least as compared with other more noticeable factors such as overgrowth or decline in traditional land use (von Numers & Korvenpää 2007, Hannus & von Numers 2010). This might be a consequence of factors hiding a real effect mentioned above, or then the changes in climate are still too small to result in unambiguous effects.

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Appendix 1. Results of the logistic regression analyses for the species; the final models. Islands with absences are compared with islands with occurrences (current data).

		B	SE	Wald	df	p	Exp(B)
<i>Agrimonia eupatoria</i>	west–east	–0.046	0.010	20.766	1	< 0.001	0.955
	south–north	–0.016	0.007	5.521	1	0.019	0.984
	topogr. diversity	0.200	0.100	3.983	1	0.046	1.221
	local exposure	–0.527	0.078	45.974	1	< 0.001	1.694
	constant	–1.487	0.610	5.943	1	0.015	0.226
<i>Arrhenatherum elatius</i>	area	0.053	0.011	21.588	1	< 0.001	1.054
	west–east	–0.052	0.007	47.893	1	< 0.001	0.949
	south–north	–0.014	0.005	7.721	1	0.005	0.986
<i>Cochlearia danica</i>	constant	0.563	0.414	1.850	1	0.174	1.756
	area	–0.043	0.013	11.317	1	0.001	0.958
	west–east	–0.026	0.008	9.805	1	0.002	0.975
	south–north	–0.027	0.007	15.379	1	< 0.001	0.973
	large-scale exposure	0.011	0.005	4.996	1	0.025	0.989
<i>Cornus suecica</i>	local exposure	0.660	0.098	45.686	1	< 0.001	0.517
	constant	4.679	0.615	57.849	1	< 0.001	107.665
	area	0.026	0.013	4.133	1	0.042	1.026
	west–east	–0.036	0.009	18.259	1	< 0.001	0.964
	south–north	–0.013	0.007	3.337	1	0.068	0.987
	topogr. diversity	0.462	0.106	19.019	1	< 0.001	1.587
	large-scale exposure	0.044	0.007	36.189	1	< 0.001	0.957
	local exposure	0.193	0.074	6.841	1	0.009	0.825
	constant	1.350	0.497	7.368	1	0.007	3.856
	south–north	0.037	0.009	15.117	1	< 0.001	1.037
<i>Erysimum strictum</i>	topogr. diversity	–0.389	0.149	6.805	1	0.009	0.678
	large-scale exposure	–0.012	0.005	4.840	1	0.028	1.012
	constant	–4.939	0.968	26.045	1	< 0.001	0.007
	area	0.017	0.010	2.760	1	0.097	1.017
	west–east	–0.036	0.012	9.211	1	0.002	0.964
<i>Geranium sanguineum</i>	south–north	–0.022	0.009	6.490	1	0.011	0.978
	topogr. diversity	0.431	0.127	11.563	1	0.001	1.539
	local exposure	–0.358	0.072	24.875	1	< 0.001	1.430
	constant	–2.667	0.748	12.732	1	< 0.001	0.069
	topogr. diversity	0.183	0.078	5.478	1	0.019	1.201
<i>Hypericum hirsutum</i>	constant	–2.296	0.314	53.294	1	< 0.001	0.101
	topogr. diversity	0.310	0.089	12.217	1	< 0.001	1.364
	large-scale exposure	–0.010	0.004	5.413	1	0.020	1.010
<i>Rhamnus cathartica</i>	constant	–3.724	0.435	73.466	1	< 0.001	0.024
	south–north	0.014	0.005	7.355	1	0.007	1.014
	topogr. diversity	0.421	0.083	25.382	1	< 0.001	1.523
	local exposure	–0.089	0.053	2.853	1	0.091	1.093
<i>Scrophularia nodosa</i>	constant	–1.529	0.440	12.057	1	0.001	0.217

continued

Appendix 1. Continued.

		B	SE	Wald	df	p	Exp(B)
<i>Vaccinium uliginosum</i>	area	0.166	0.034	24.569	1	< 0.001	1.181
	west–east	–0.035	0.010	13.482	1	< 0.001	0.965
	south–north	0.020	0.009	4.583	1	0.032	1.020
	topogr. diversity	0.309	0.117	6.940	1	0.008	1.362
	large-scale exposure	0.048	0.008	40.739	1	< 0.001	0.953
	local exposure	–0.148	0.086	2.955	1	0.086	1.159
<i>Vincetoxicum hirundinaria</i>	constant	0.624	0.615	1.028	1	0.311	1.866
	area	0.081	0.020	16.152	1	< 0.001	1.084
	west–east	–0.015	0.007	5.040	1	0.025	0.985
	large-scale exposure	0.007	0.003	4.587	1	0.032	0.993
<i>Carex muricata</i>	constant	1.152	0.267	18.555	1	< 0.001	3.164
	area	0.023	0.010	5.152	1	0.023	1.024
	west–east	–0.023	0.008	8.390	1	0.004	0.978
	topogr. diversity	0.195	0.091	4.648	1	0.031	1.215
	local exposure	–0.204	0.053	14.934	1	< 0.001	1.226
<i>Dactylorhiza sambucina</i>	constant	–2.027	0.311	42.428	1	< 0.001	0.132
	area	0.027	0.011	5.684	1	0.017	1.027
	west–east	–0.050	0.028	3.303	1	0.069	0.951
	large-scale exposure	–0.029	0.012	6.107	1	0.013	1.030
	local exposure	–0.215	0.095	5.092	1	0.024	1.240
<i>Melampyrum cristatum</i>	constant	–5.699	0.898	40.265	1	< 0.001	0.003
	area	0.042	0.013	11.321	1	0.001	1.043
	west–east	–0.098	0.030	11.050	1	0.001	0.907
	south–north	–0.050	0.022	5.261	1	0.022	0.951
	topogr. diversity	0.680	0.247	7.583	1	0.006	1.974
<i>Origanum vulgare</i>	constant	–2.884	1.463	3.889	1	0.049	0.056
	area	0.021	0.011	3.935	1	0.047	1.021
	west–east	–0.028	0.008	12.131	1	< 0.001	0.973
	topogr. diversity	0.171	0.092	3.477	1	0.062	1.187
	local exposure	–0.339	0.060	31.928	1	< 0.001	1.404
<i>Scutellaria hastifolia</i>	constant	–1.976	0.313	39.843	1	< 0.001	0.139
	area	0.017	0.008	3.871	1	0.049	1.017
	west–east	0.026	0.008	11.049	1	0.001	1.027
	local exposure	–0.184	0.056	10.671	1	0.001	1.202
<i>Cardamine hirsuta</i>	constant	–2.763	0.311	78.793	1	< 0.001	0.063
	area	0.055	0.014	16.032	1	< 0.001	1.057
	topogr. diversity	–0.255	0.074	11.764	1	0.001	0.775
<i>Draba incana</i>	constant	0.702	0.236	8.841	1	0.003	2.018
	large-scale exposure	0.016	0.006	7.743	1	0.005	0.985
	constant	–1.414	0.269	27.686	1	< 0.001	0.243

Appendix 2. Results of the logistic regression analyses for the species; the final models. Islands with extinctions are compared with islands with colonisations (e/c), or islands with preserved occurrences are compared with islands with colonisations (p/c).

		<i>B</i>	SE	Wald	df	<i>p</i>	Exp(<i>B</i>)
<i>Agrimonia eupatoria</i> (e/c)	area	-0.061	0.035	3.061	1	0.080	0.941
	topogr. diversity	-1.053	0.400	6.927	1	0.008	0.349
	large-scale exposure	0.069	0.025	7.757	1	0.005	0.933
	local exposure	-0.351	0.173	4.140	1	0.042	1.421
	constant	7.760	2.514	9.529	1	0.002	2345.049
<i>Arrhenatherum elatius</i> (p/c)	west-east	0.038	0.012	10.060	1	0.002	1.039
	south-north	-0.019	0.008	4.967	1	0.026	0.981
	topogr. diversity	-0.275	0.136	4.118	1	0.042	0.759
	constant	1.075	0.741	2.104	1	0.147	2.930
<i>Cochlearia danica</i> (p/c)	west-east	0.036	0.014	6.900	1	0.009	1.037
	south-north	0.037	0.010	12.853	1	< 0.001	1.038
	topogr. diversity	0.397	0.144	7.575	1	0.006	1.488
	local exposure	-0.437	0.166	6.931	1	0.008	1.548
	constant	-6.670	1.111	36.022	1	< 0.001	0.001
<i>Cornus suecica</i> (p/c)	west-east	0.023	0.010	5.013	1	0.025	1.023
	local exposure	-0.258	0.098	6.930	1	0.008	1.295
	constant	-1.594	0.331	23.159	1	< 0.001	0.203
<i>Erysimum strictum</i> (p/c)	large-scale exposure	0.033	0.016	4.476	1	0.034	0.967
	constant	2.778	1.173	5.611	1	0.018	16.088
<i>Geranium sanguineum</i> (p/c)	area	-0.127	0.070	3.291	1	0.070	0.881
	west-east	0.133	0.062	4.669	1	0.031	1.142
	south-north	-0.318	0.154	4.264	1	0.039	0.727
	large-scale exposure	-0.158	0.084	3.538	1	0.060	1.171
	constant	7.167	4.038	3.149	1	0.076	1295.479
<i>Hypericum hirsutum</i> (e/c)	area	-0.070	0.041	2.945	1	0.086	0.933
	constant	1.058	0.576	3.379	1	0.066	2.881
<i>Rhamnus cathartica</i> (e/c)	area	-0.148	0.060	6.107	1	0.013	0.863
	large-scale exposure	0.047	0.026	3.336	1	0.068	0.954
	constant	6.016	2.588	5.403	1	0.020	409.802
<i>Scrophularia nodosa</i> (p/c)	area	-0.043	0.020	4.505	1	0.034	0.958
	topogr. diversity	0.194	0.102	3.653	1	0.056	1.214
	constant	-1.750	0.369	22.504	1	< 0.001	0.174
<i>Vaccinium uliginosum</i> (p/c)	area	-0.030	0.021	2.188	1	0.139	0.970
	west-east	0.032	0.010	9.778	1	0.002	1.033
	topogr. diversity	-0.299	0.140	4.560	1	0.033	0.742
	large-scale exposure	-0.021	0.006	12.955	1	< 0.001	1.021
	constant	-1.833	0.446	16.891	1	< 0.001	0.160
<i>Vincetoxicum hirundinaria</i> (p/c)	west-east	0.025	0.010	6.549	1	0.010	1.025
	south-north	0.045	0.009	22.720	1	< 0.001	1.046
	topogr. diversity	-0.232	0.103	5.049	1	0.025	0.793
	large-scale exposure	0.031	0.008	16.992	1	< 0.001	0.969
	constant	-2.564	0.648	15.663	1	< 0.001	0.077
<i>Carex muricata</i> (e/c)	west-east	-0.030	0.014	4.529	1	0.033	0.970
	constant	0.172	0.318	0.291	1	0.590	1.187
<i>Dactylorhiza sambucina</i> (n.s.)							
<i>Melampyrum cristatum</i> (n.s.)							
<i>Origanum vulgare</i> (e/c)	local exposure	-0.279	0.115	5.892	1	0.015	1.321
	constant	-2.029	0.519	15.284	1	< 0.001	0.131
<i>Scutellaria hastifolia</i> (n.s.)							
<i>Cardamine hirsuta</i> (e/c)	area	0.082	0.029	8.236	1	0.004	1.085
	west-east	0.052	0.016	10.355	1	0.001	1.054
	south-north	0.022	0.012	3.303	1	0.069	1.022
	topogr. diversity	-0.923	0.225	16.906	1	< 0.001	0.397
	large-scale exposure	0.025	0.008	8.842	1	0.003	0.975
	constant	0.795	0.990	0.644	1	0.422	2.214
<i>Draba incana</i> (n.s.)							