

Patterns and processes in species assemblages on Northern Baltic islands

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Studies on the ecological biogeography of Northern Baltic islands are reviewed. The emphasis is on population level explanations for patterns observed in assemblages of animal and plant species.

As in other archipelagoes, faunal and floral diversity tends to increase on Northern Baltic islands with increasing island area. However, even within a single group of species there is no general species-area relationship. For example, within an area studied in detail, species number in vascular plants was higher on clustered islands (0.1–1.0 ha) than on more scattered, similar-sized islands. For most taxa island colonization in the Northern Baltic area is easy owing to the short distances between islands and the mainland, whereas long-term persistence on the islands might be difficult either due to lack of suitable habitats or due to harsh climate (long droughts, occasional flooding, exposure to wind, etc.) and probably occasionally due to biotic causes.

Islands expand and new islands emerge in the Northern Baltic owing to the continuous postglacial uplift of the land masses. Pioneering species colonize small islets and shorelines emerging from the sea, but they disappear from the central areas where species of more mature communities displace them. It follows that species colonizing the smallest islets are also found on almost any other islands irrespective of island size. This pattern seems to hold for a number of taxa ranging from vascular plants to breeding birds.

Rock-pools, small island-like aquatic ecosystems on Baltic islands harbor a rich fauna and flora. Though many of the species occupy different parts of the salinity gradient found in different rock-pools, quite a number of them have overlapping preferences. Factors contributing to the coexistence of those species are mosaic-like distribution and dynamic disappearance (droughts) and reappearance (in rains) of the rock-pools. These characters promote coexistence of good colonizers and poor competitors with good competitors but poor colonizers. Zooplankton of the rock-pools is characterized by the presence of large herbivorous *Daphnia* species, apparently due to the general lack of vertebrate planktivores. Experimental evidence suggests that *Daphnia* grazing on phytoplankton enables the presence of filamentous algae in rock-pools.

Experimental analysis of species assemblages on Northern Baltic islands has gained a foothold in recent years. This trend is likely to continue.

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1. Introduction

“No two journeys to these islands are alike”, wrote the Irish playwright J. M. Synge in his superb little book *The Aran Islands* in 1907, referring of course to Aran. This review of plants and animals living on Northern Baltic islands has a similar emphasis: the systems encountered are highly dynamic.

We also endorse another theme raised by Synge, who, after having met an “old dark man” on Aran

observed that the old man “had great confidence on his own powers and talent, and in the superiority of his stories over all other stories in the world”. With the great naturalist tradition of Northern Europe behind us, we join the old dark man of Aran.

This review focuses on a number of different topics from intraspecific variation within or among insular populations to broad patterns on Northern Baltic islands, where thousands of islands are to be found in many archipelagoes. Moreover, the studies

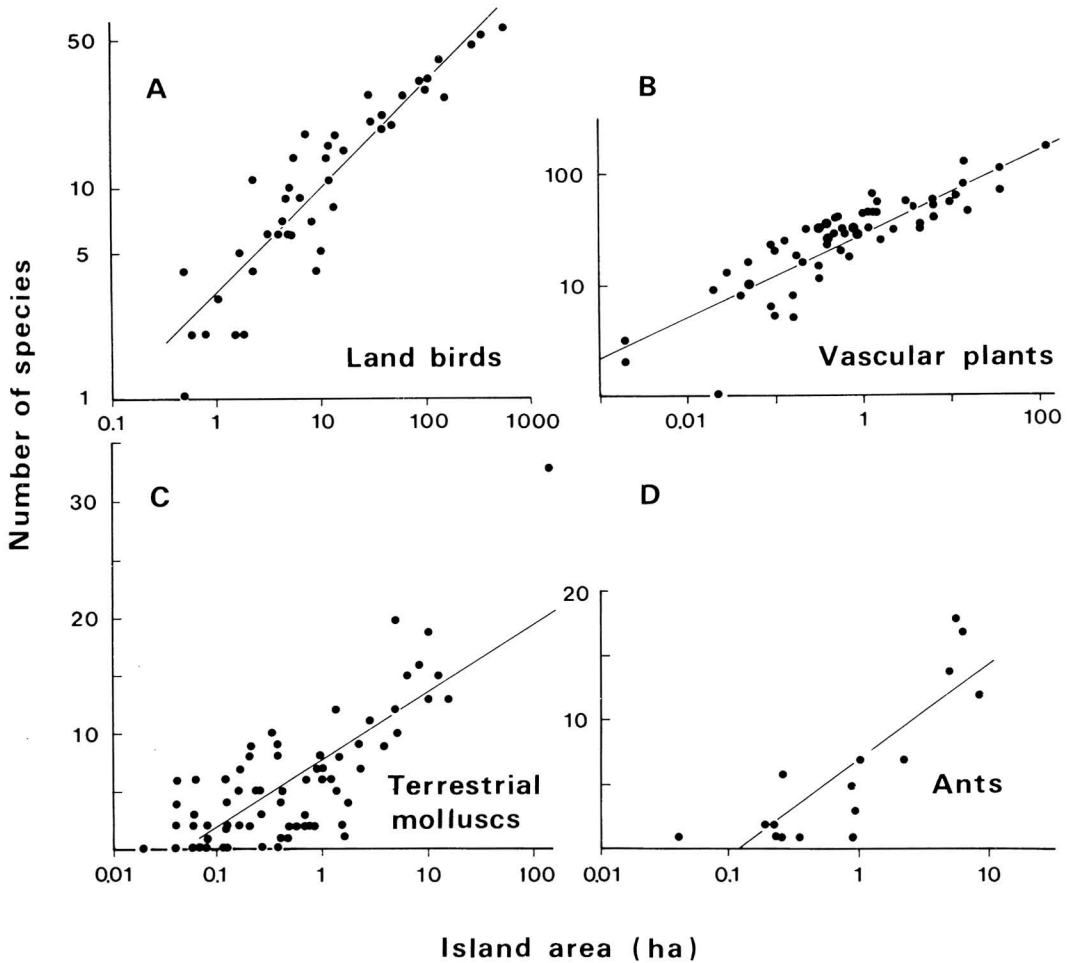


Fig. 1. Species-area diagrams for (A) land birds on the Åland Islands (Haila et al. 1982), (B) vascular plants in the Rönnskär archipelago (based on E. J. Valovirta 1937), (C) terrestrial molluscs in the Tvärminne archipelago (I. Valovirta 1977) and (D) ant species in the Tvärminne archipelago (Ranta et al., unpubl.).

reviewed range from 'snapshot' views of patterns to decade-long research on the dynamics of insular plant and animal assemblages. Since the diversity of taxa studied on Northern Baltic islands is remarkably high, this archipelago system seems to be among the best studied in the world.

In the following, we shall review certain topics and systems that have received particular attention in studies of species assemblages of plants and animals on Northern Baltic islands. We start with species-area relationships, which show well the fact that ecology starts after (and not with) the computation of species-area curves. The second topic — land birds — illus-

trates the consequences of the fact that dispersal difficulties may not constitute a major problem for certain taxa inhabiting Northern Baltic islands. We then review patterns of species turnover (immigrations and extinctions) on Northern Baltic islands in order to illustrate the dynamics of the species assemblages. As an example of an ecologically interesting special system found on Northern Baltic islands, we examine rock-pool systems that can be studied not only descriptively, but also experimentally, which is rare in field ecology. Finally, we briefly examine some evidence available on genetic variation in populations living on Northern Baltic islands.

2. Species-area relations on Northern Baltic islands

Two facts at least distinguish Northern Baltic islands from island ecosystems at lower latitudes: the importance of pronounced annual seasonality, and the low degree of isolation between islands and the mainland. For example, in response to seasonality, most birds breeding in Northern Europe (incl. islands) are migratory (Herrera 1978, Järvinen & Väisänen 1980), and each spring and autumn they cross straits separating the Northern Baltic islands from the mainland. Overwater dispersal is then not expected to be a problem for the bulk of Fennoscandian bird species. In contrast, plants, insects and other all-year residents have to tolerate the fairly harsh ecological and climatic conditions prevailing on the Northern Baltic islands, even though most organisms are dormant for several months in winter. Each spring the invertebrate populations, especially, start from numbers much reduced by winter mortality.

Faunal and floral diversity tends to increase on Northern Baltic islands with increasing area (Fig. 1). This is a world-wide phenomenon in different taxa and in different archipelagoes (Connor & McCoy 1979), but the superficial resemblance in results based on different data sets does not constitute a proof of identical causes. Attributing a positive cor-

relation between species number and island area, for example, to a dynamic equilibrium between immigration and extinction leads to oversimplifications or to misinterpretations, for the same relation may result for a variety of reasons (Connor & McCoy 1979). Therefore the actual biological mechanisms producing the species-area relationship are the main issue, not the regression itself.

The interrelation between species number and island area is a formal result and it must therefore be regarded as a starting point for future studies aimed at uncovering the biological, often population-level processes behind the pattern observed. We illustrate this point with a few examples.

Itäemies (1983) studied the distribution of vascular plants and Lepidoptera on the same islands off the coast of Rauma (Fig. 2) and found typical correlations between island area and species number (or island height and species number). However, the species number of Lepidoptera (many of which were monophagous or oligophagous in this data set) was even better accounted for by the species number of plants, which is consistent with the feeding ecology.

E. J. Valovirta (1937) thoroughly studied the flora of 63 islands belonging to the Rönnskär island group in the middle of the Gulf of Bothnia (Fig. 3). Ranta, Järvinen & L. Oksanen (unpubl.) selected two subsets of islands (0.1–1.0 ha) from his data (Fig. 3a). Group A encompasses a set of 11 islands scattered east of the 133-ha Storskär, while group B (13 islands) is situated within an archipelago of larger islands. Larger islands were excluded because we wanted to minimize habitat variation. As the two island groups cover the same size range, we calculated a common species-area regression for them.

In the equation $\log S = 1.57 + 0.44 \log A$ ($r^2 = 0.55$) the slope deviates significantly from zero ($P < 0.01$). We then calculated island-specific residuals and compared the two *a priori* subsets of islands. Islands B (within an archipelago) have significantly higher numbers of species (Mann-Whitney U test, $z = 2.81$, $P = 0.0025$; see Fig. 3b) than islands A (scattered). We conclude that even within such a small geographical area as the Rönnskär archipelago, no single species-area relationship prevails for the same taxon. Rather, the spatial structure (density of islands) of the archipelago has a significant effect on the emerging relationship.

The 219 vascular plant species observed by E. J. Valovirta (1937) on the 63 Rönnskär islands were classified (Ranta et al. unpubl.) into six biotope groups and four life cycle groups. Fig. 4 gives the

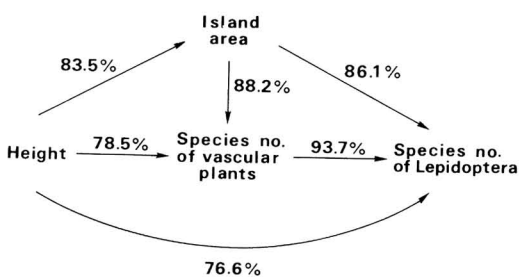


Fig. 2. Island area and height both affect species numbers of vascular plants on the islands off Rauma, as shown by the coefficients of determination ($100 \times r^2$) based on double-logarithmic correlations between the variables. The species number of Lepidoptera also correlates with these physical variables, but even better with species numbers of plants. Note that archipelago zones also influence the patterns. First, by restricting the distribution of different species (e.g. for habitat reasons) and second, by also affecting the physical characteristics of the islands (exposure to wind, island area, etc.). The diagram is modified from Itäemies (1983).

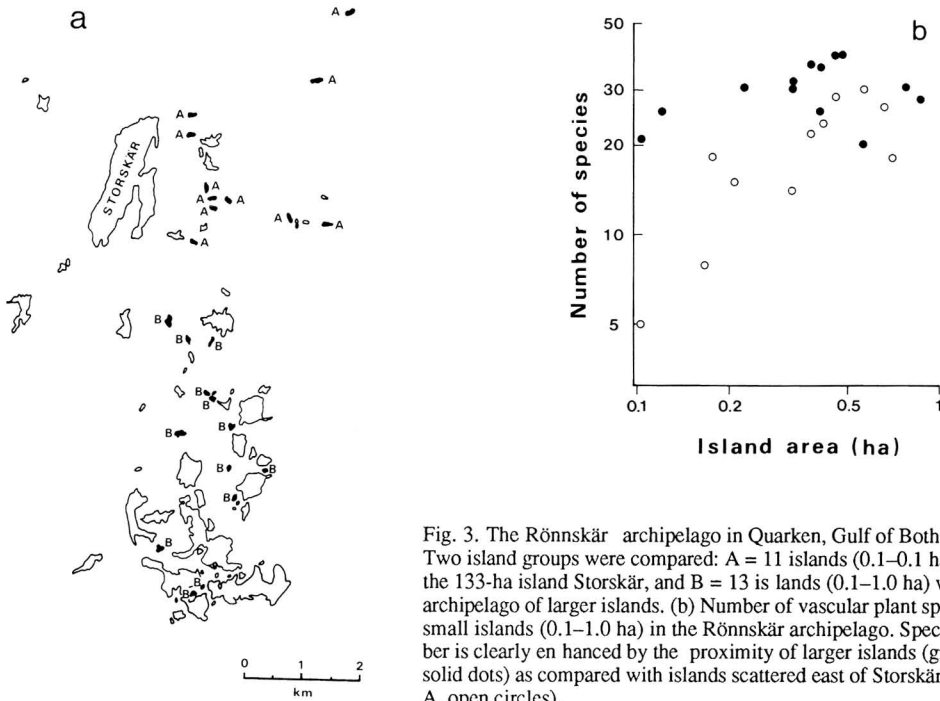


Fig. 3. The Rönnskär archipelago in Quarken, Gulf of Bothnia. (a) Two island groups were compared: A = 11 islands (0.1–0.1 ha) east of the 133-ha island Storskär, and B = 13 islands (0.1–1.0 ha) within an archipelago of larger islands. (b) Number of vascular plant species on small islands (0.1–1.0 ha) in the Rönnskär archipelago. Species number is clearly enhanced by the proximity of larger islands (group B, solid dots) as compared with islands scattered east of Storskär (group A, open circles).

species-area graphs for these groups. Several results emerge.

First, the slopes (parameter z) and correlation coefficients (r) differ significantly from zero.

Second, all slope values range from $z = 0.27$ to 0.44 , except that the littoral plants have a slope of $z = 0.12$. This is not surprising, because island area is obviously a poor estimator of the resources (area) available for littoral plants. We therefore exclude littoral plants below.

Third, the constant C in the regression equations varies from one species group to another (Fig. 4). This result would apparently suggest that vascular plant species belonging to different groups have differing minimum area requirements on islands. However, the result seems more likely to be a statistical artifact. As the slopes (z) of the regression equations do not differ statistically, the regression lines (Fig. 4) are parallel within the boundaries set by sampling error. If the numbers of plant species belonging to the different groups differ in the mainland species pool, one expects differences in the intercepts (C). This is evidently the case, for correlation coefficients between C and species number in the species pool of the nearby Finnish mainland (see Valovirta 1937: 53–57)

were extremely high: for biotope groups (littoral plants excluded) $r = 0.943$ ($P < 0.01$), and for life cycle groups $r = 0.983$ ($P < 0.05$).

In order to discover possible effects of island area on the species composition of vascular plants (in terms of species numbers in different biotope and life cycle groups), the 63 islands were grouped to (a) 11 islands less than 0.1 ha, (b) 28 islands ranging from 0.1 to 1.0 ha, (c) 16 islands ranging from 1.0 to 10 ha, and (d) 8 islands larger than 10 ha (Fig. 5; Ranta et al. unpubl.). It is clear that species composition on the smallest islands (a–c) differs from the species pool and among the island groups, while no differences were detected between the largest islands (d) and the species pool (Fig. 5). These data suggest that the availability of suitable growth sites on the islands decisively affects the species composition of vascular plants on the islands. Ecological conditions on the smallest islands favor perennial grasses and herbs (Fig. 5). As shown below (Sect. 3), this may be a consequence of the lower extinction rate among perennials than among (bi)annuals.

The biological reality behind the abstract species-area curves may often reveal a highly dynamic population system. In a thoroughly studied case, Pokki

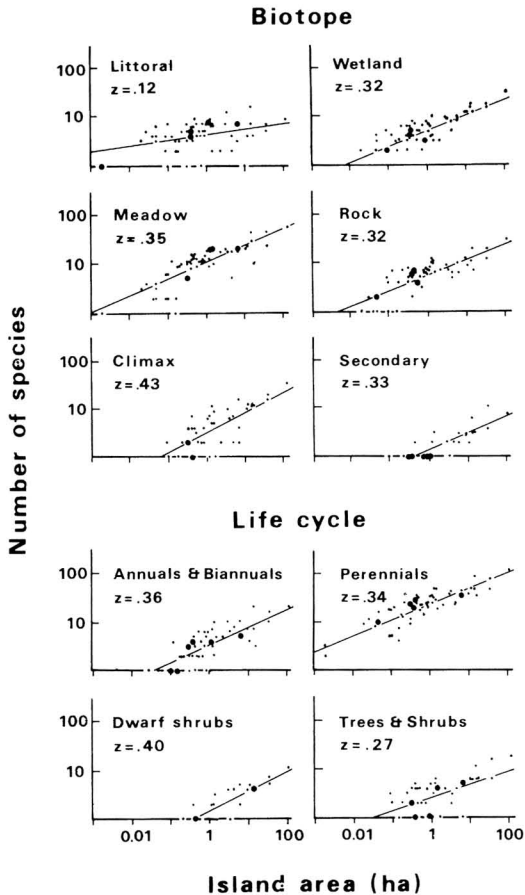


Fig. 4. Species-area relationships in six biotope and four life cycle groups of vascular plant species in the Rönnskär archipelago (slopes of the regression lines inserted). Large dots indicate that 3–5 data points coincide.

(1981) showed that field voles *Microtus agrestis* (L.) in the Tvärminne archipelago frequently disperse from one island to another mostly in summer and autumn. The longest swimming distances, based on trapping individually marked voles, exceeded 500 m. Populations were often established, but they also frequently became extinct: of the 71 islands studied, only three were occupied throughout the study period (1972–77) and only two were never inhabited. On the other 66 islands Pokki observed 165 turnover events (extinctions or immigrations).

For gaining understanding of the build-up of island communities we want to stress the importance of comparing particular communities on corresponding habitats on the mainland and islands. However, in these comparisons merely looking at presence/absence data of species occurrence may be misleading.

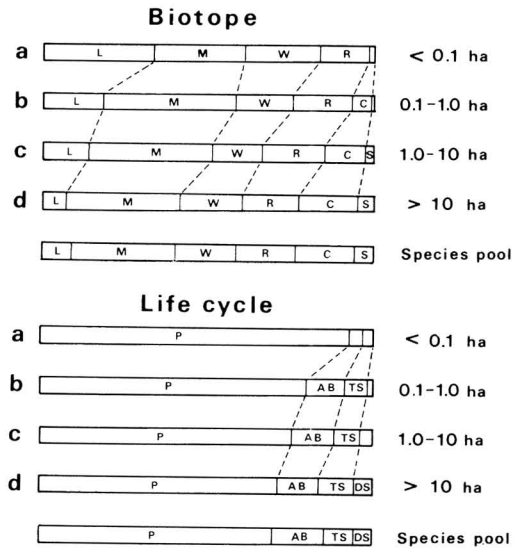


Fig. 5. Proportion of different biotope (L = littoral, M = meadow, W = wetland, R = rock, C = climax, S = secondary succession) and life cycle (P = perennials, AB = annuals and biennials, TS = trees and shrubs, DS = dwarf shrubs) classes of vascular plant species on four island size groups in the Rönnskär archipelago and in the neighboring mainland species pool. In the biotope classification the smallest islands (a–c) differ significantly both from each other and from the largest islands (d) and the species pool. In the life cycle classification the differences between island groups c and d and the species pool are statistically not significant, but other differences are significant.

A particularly demonstrative example was shown by Niemelä et al. (1985) who studied the distribution of carabid beetles on lush forest patches, both on the main island of the Åland archipelago and on small, nearby islands. What they found was that (1) with exactly the same sampling effort the number of individuals captured on the mainland sites was about fourfold that of the island sites. (2) No significant differences in species richness was found between the island and mainland sites when the effect of sample size differences was eliminated. (3) Striking differences were found in species abundance relationships between the mainland and the islands. The dominant species on the mainland (*Patrobis atrorufus*, Ström, 50% of the total mainland sample) was represented in the island samples by only two individuals, and several other abundant mainland species were scarce on the islands as well. Two species (*Cychrus caraboides* L., *Pterostichus niger* Schall.) were more abundant on the islands than on the mainland.

3. Land bird communities on Northern Baltic islands: sampling populations from the mainland universe

Haila et al. (1979) examined faunistic data and listed all land bird species that have colonized or disappeared from the Åland Islands during the preceding 50 years. Nearly all colonists had shown population increases and/or range expansions on the adjacent Finnish mainland in the period studied, while all the extinctions were in species that had decreased on the mainland. Åland therefore seems to be essentially part of the mainland for almost all land birds. As only long-term patterns were examined, short-term turnover may not have been detected. A reasonable hypothesis is that avian colonization tends to be most frequent during population highs, while extinctions may lag behind declines in the mainland populations because of site tenacity.

Extensive studies of islands in eastern Åland (Föglö) throw more light on this result. Censuses by Haila & Järvinen (1983) and Haila et al. (1983) give rise to a number of generalizations (modified from Haila 1983b):

(1) The abundant species tend to occur on the islands in numbers expected from the habitat composition of the islands and from the density of the species on the mainland (here the main island of Åland archipelago), namely the islands support bird communities that are quantitatively similar to those in equal-sized mainland areas with similar habitats. Density differences between the mainland and the islands can usually be traced to differences in habitat structure.

(2) Islands do support fewer species than large mainland areas, but most of the absent species are rare on the mainland and would be expected to be absent also from small areas on the mainland.

(3) Interspecific interactions seldom explain the absence or rarity of a species from many islands; rather, the lack of suitable breeding habitats is important here.

(4) Resource (food) availability is the main factor determining the structure of wintering land bird communities in this archipelago.

Based on the above generalizations, Haila (1983a, 1983b) concluded that land bird communities on northern islands can largely be regarded as samples taken from the mainland avifauna (see also Järvinen & Haila 1984). The islands are colonized each spring by migrants in a process that is similar to stochastic (Poisson) sampling, the important constraint being

the habitat structure of the islands. The species-area relations found (Fig. 1), therefore, are partly a result of the greater habitat diversity on large islands, but partly also a statistical consequence of the greater numbers of birds 'sampled' on them. In such systems annual turnover of bird populations is large but often ecologically trivial. In other words, land bird communities on Northern Baltic islands in the Åland archipelago are not restricted to single islands but to understand the dynamics of populations the scale of the study must be broader, e.g. the whole archipelago and the adjacent mainland. This conclusion is intended to be valid for most land birds in northern European archipelagoes, not necessarily for all taxa or all islands throughout the world.

Haila & Järvinen (1981) stress that quantitative data are essential in understanding the structure of island bird communities. We illustrate this by reviewing an analysis by Haila & Järvinen (1983; see also Järvinen & Haila 1984) of the land bird fauna of a fairly large island, Ulversö (about 5.8 km²), in Föglö. Excluding occasional visitors, Ulversö supported 68 species in 1976–80 (a typical value for a single season would be slightly lower). This is in marked contrast to the 121 species found on Main Åland (970 km²; Haila et al. 1979). How can the absence of 53 species be accounted for?

Haila & Järvinen (1983) regarded a species as 'rare' if it was observed five times at most in the line transect censuses made by Haila et al. (1979) on Main Åland. The number of such rare species totaled 45, and 63 observations were made of them in 213.7 km of transects. Assuming that rare species are equally dense on Ulversö (17.55 km of transects) as on Main Åland, one would expect 5.2 observations of these (17.55 km out of 213.7 km is 8.2%, and 8.2% out of 63 observations is 5.2). The observed number of rarities was 5, as close to the expectation as possible.

In quantitative terms, 74% (or 39 out of 53) of the species absent from Ulversö were rarities, in the sense defined above, and their absence can be understood as a statistical consequence of rarity. Equal-sized areas of Main Åland would not be expected to support a greater number of rarities than Ulversö did.

Relatively many nonpasserines are absent from Ulversö:

	Passerines	Non-passerines
Ulversö and Main Åland	49 spp.	19 spp.
Main Åland only	22 spp.	31 spp.

The difference between the two groups is significant (Haila & Järvinen 1983). Since many non-

passerines are large and have low population numbers (Haila et al. 1979), a random sample from the bird fauna of Main Åland would include more passerines than nonpasserines. However, if the rare species (in the sense defined above) are excluded, non-passerines and passerines have been able to colonize Ulversö equally well:

	Passerines	Non-passerines
Ulversö and Main Åland	48 spp.	14 spp.
Main Åland only	9 spp.	5 spp.

This result warns against conclusions about differential colonization abilities of different taxa being drawn from qualitative (presence-absence) data.

Haila & Järvinen (1983) further examined whether any of the 14 more abundant species absent from Ulversö could also be accounted for by the explanation based on rarity. The expected number of pairs on Ulversö can be calculated as the average density on Main Åland times the area of Ulversö. Assuming that the numbers of pairs is a Poisson variate – a reasonable hypothesis for rare species – the probability of having 0 pairs on Ulversö can be estimated. Haila & Järvinen (1983) concluded that 13 of the 14 absences are not attributable to rarity. Rarity thus accounts for the absence of 40 species altogether from Ulversö (75% of the cases).

This conclusion can be checked in another way. Data from censusing 16 habitats on Main Åland included 3134 pairs and 82 species of land birds (Haila et al. 1980). The censuses on Ulversö indicated that this island had approximately 2500 pairs and up to 65 species annually. Rarefaction analysis (Simberloff 1979) of census data from Main Åland indicates that a sample of 2500 pairs would include 80 species (77 to 82 as 95% confidence limits). Eliminating the 13 absences not attributable to rarity (mentioned above) thus gives 64 to 69 species, which fits well with the observed number of species.

Other reasons for absence include historical factors (a couple of species that have recently colonized the island group but not yet Ulversö), unavailability of suitable habitats (important), and interspecific interaction (competition and predation; a few probable cases). The absence of two species from Ulversö seems enigmatic.

Haila & Järvinen (1983) point out that rarity is not a long-term explanation for absence: that a rarity breeds on Ulversö is improbable but it will be observed in the long run unless there are other factors that prevent colonization. Haila & Järvinen (1983) observed that many rarities would also lack suitable

habitats on Ulversö, and therefore the tabulation of reasons for absence is substantially different depending on the time perspective adopted.

	Absences:	Short-term	Long-term
Rarity	40 spp.	(75%)	17 spp. (33%)
Dispersal difficulties*	1.5	(3%)	4.5 (9%)
Habitat unsuitable*	6.5	(12%)	25.5 (48%)
Interspecific interactions	3	(6%)	4 (8%)
Unknown reasons	2	(4%)	2 (4%)

*One species in two classes (0.5 species in each class).

Here 'short-term' refers to absences in one breeding season, while 'long-term' absences imply long study periods. A long-term absence due to rarity means that, in the long run, Haila & Järvinen (1983) would expect to observe the species breeding on Ulversö, as no obvious reasons seem to prevent at least temporary colonization.

The above figures naturally indicate only the main reason(s) for absence as identified by Haila & Järvinen (1983). In reality probably many different reasons are involved.

4. Immigration and extinction patterns in land uplift archipelagos

Land masses in the Baltic respond to the melting of the heavy ice sheet that covered Northern Europe during the Würm glaciation by continuing uplift. The present rate of land uplift ranges from 20 to 90 cm per 100 years on the Finnish coast (Kääriäinen 1953). The highest rates are in the northern parts of the Gulf of Bothnia where the effect of land uplift on island areas is particularly striking because of the generally flat topography. Owing to land uplift, new islets emerge continuously, and island area increases steadily until the island merges with the mainland (Fig. 6). The relative increase of land area is most important on small islands where the newly emerged shore constitutes a large proportion of the island area and thus ensures the availability of colonizable land.

Extensive botanical studies have been devoted to the primary succession following land uplift (Palmgren 1925, E. J. Valovirta 1937, 1950, Brunberg-Schwank & Bärlund 1948, Enholm 1949, Luther 1961, Palomäki 1963, Vaahtoranta 1964, Schwank 1974, Vartiainen 1980). Pioneering species are able to colonize small islets and shorelines emerging from the sea, but pioneers tend to disappear from central areas of islands which are characterized by species of

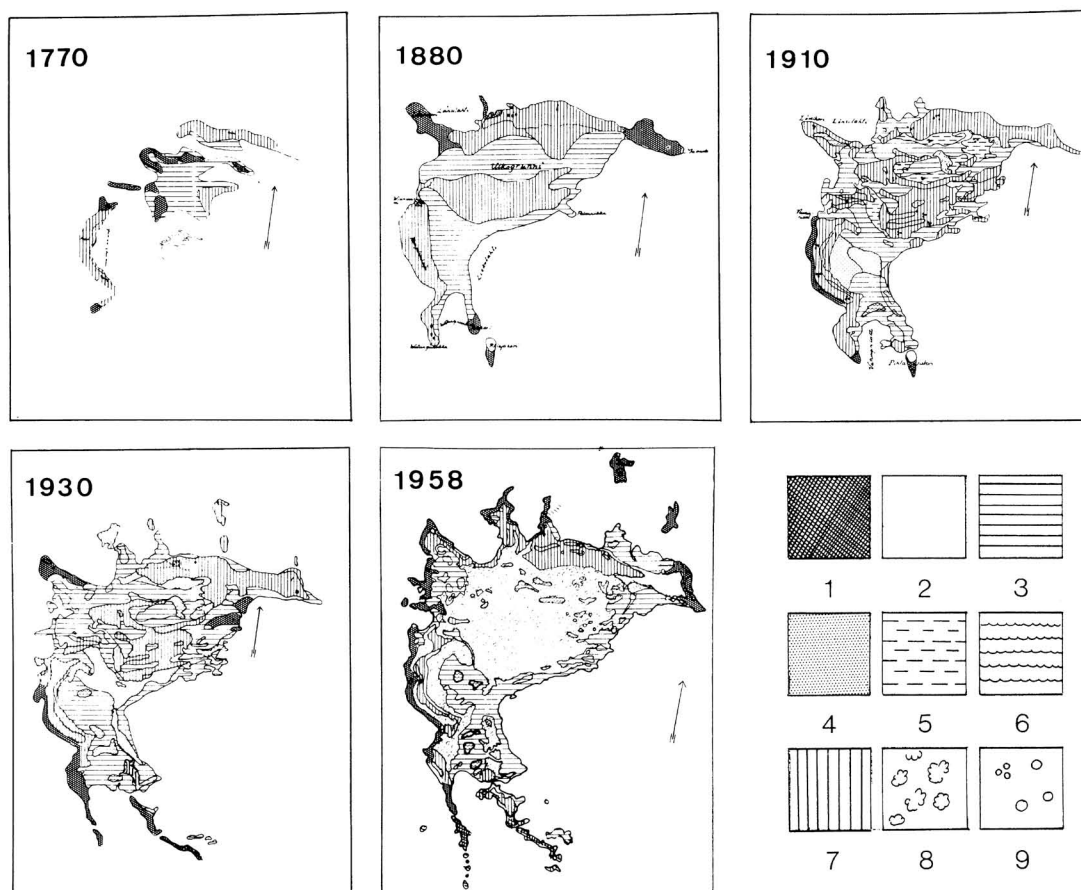


Fig. 6. Land uplift and succession of vegetation on Ulkokorunni 1770–1958 (from Vartiainen 1980). Key for the substrate and vegetation formation codes: 1 = boulder shore or stone crest, 2 = sandy shore or dune, 3 = shore meadow or interior meadowland, 4 = swampy land, 5 = fen (former lagoon), 6 = lagoon, 7 = heathy land (open or with some deciduous trees, pines or junipers), 8 = deciduous woodland, 9 = trees and bushes in the 1960s (mostly on heathy land).

later successional stages. Palmgren (1912) pointed out that rapidly growing species have a definite advantage in early successional phases immediately after the emergence of a new area. Species such as *Hippophaes rhamnoides* L. seem to persist mainly because of its ability to colonize newly emerged shores rapidly. In the inner parts of large islands it is usually outcompeted by other species.

Owing to continuous land uplift, vegetation on each island tends to show a clear zonation from outer, shoreline pioneer communities to inner, more mature plant communities (Table 1; see also Vartiainen 1980). Succession is rapid near the shoreline, but in the inner parts the process slows down in terms of

species replacement. The species on the smallest islands are but a subset of all species in any Northern European archipelago (E. J. Valovirta 1937, Vartiainen 1980) because of reduced habitat diversity on the smallest islands.

Another interesting pattern follows from the continuous emergence of new land. While mature communities develop in the central parts of the islands, pioneer communities still have a foothold along the shores. We therefore expect that immigration rates appreciably exceed extinction rates in typical land uplift archipelagoes because the area of all habitats, including the shoreline, tends to increase with time. The following review is based on our analysis of the data

Table 1. The most common plant species (represented by more than 90% of the sample plots) grouped according to their characteristic vertical ranges (converted to years). Modified from Vartiainen (1980). In land uplift archipelagoes, the vertical range of plant communities is an indicator of successional dynamics (even though succession is also affected by edaphic factors and exposure). In an archipelago (northernmost islands in the Gulf of Bothnia) studied by Vartiainen (1980), land uplift is approximately 73 cm/100 years.

11–20 years	<i>Potentilla anserina</i> coll. <i>Juncus gerardii</i> <i>Agrostis stolonifera</i>
21–30 years	<i>Eleocharis uniglumis</i> <i>Carex paleacea</i> <i>Glaux maritima</i> <i>Agrostis stolonifera</i> – <i>Calamagrostis stricta</i> – <i>Juncus gerardii</i> <i>Calamagrostis stricta</i> <i>Triglochin maritimum</i> <i>Deschampsia botnica</i>
31–40 years	<i>Phragmites australis</i> <i>Silene vulgaris</i> ssp. <i>maritimus</i> <i>Phalaris arundinacea</i> <i>Festuca rubra</i> <i>Vicia cracca</i> <i>Alnus incana</i>
41–60 years	<i>Sonchus arvensis</i> var. <i>maritimus</i> <i>Tanacetum vulgare</i> <i>Honkenya peploides</i> <i>Artemisia vulgaris</i> <i>Rubus saxatilis</i>
Over 60 years	<i>Rubus idaeus</i> <i>Deschampsia flexuosa</i> <i>Elymus arenarius</i> <i>Epilobium angustifolium</i> <i>Festuca ovina</i>

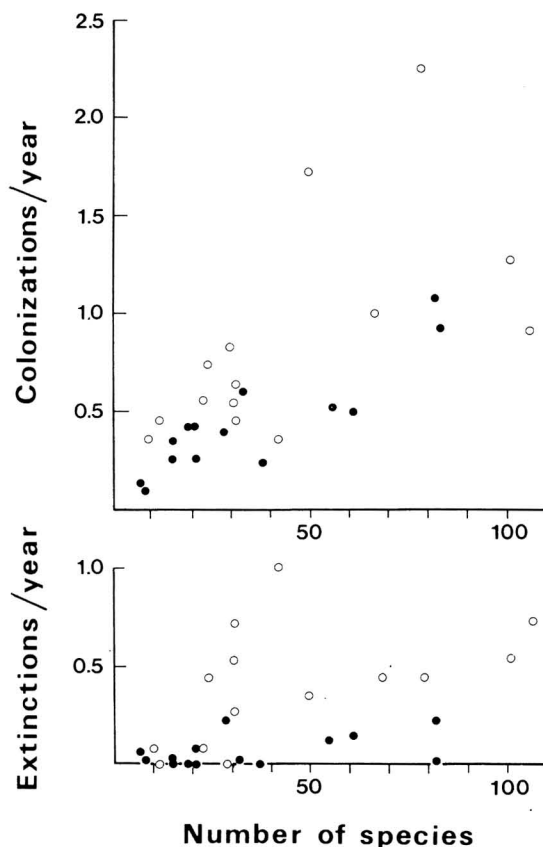


Fig. 7. Colonization and extinction rates (events/year) in the vascular plant communities on 14 islands in the Tvärminne archipelago. Two census intervals are distinguished (solid dots = period 1908/09 to 1949, open circles = period 1949 to 1960). Data from Haila et al. (1982).

published by Häyrén (1914) and Luther (1961) on the colonization and extinction of vascular plant species in the Tvärminne archipelago, SW coast of Finland.

Häyrén and Luther censused a total of 14 islands (0.1–1.5 ha) in three periods, 1908/09 (Häyrén 1914), 1949 and 1960 (Luther 1961). We are interested in the changes of floral composition on islands between two subsequent census periods. Colonization and extinction rates (events/year) for the whole vascular plant communities (Haila et al. 1982) show that in both census intervals colonization rates were markedly higher than extinction rates (Fig. 7). Furthermore, in the latter interval both colonization and extinction rates were significantly higher than during the first census interval. It is true that a difference in this direction can be expected because of the differences in the length of the intervals studied (Diamond

& May 1977), but examination of additional data from the 1930s (Luther 1961) indicates that relatively small errors stem from this source. Indeed, the high turnover rates for the interval 1949–60 have a good biological explanation (Luther 1961): severe droughts occurred in Tvärminne archipelago in 1955 and 1959.

It is particularly interesting to study whether all plant species behave similarly as regards colonization and extinction. Ranta et al. (unpubl.) classified the 186 vascular plant species on the 14 Tvärminne islands into 6 biotope and into 4 life cycle types, using the data base thus formed for turnover calculations. As in the pooled community data, both colonization and extinction rates are positively correlated with the number of species present on the islands.

Which species colonize, which species become extinct? We counted all colonization and extinction

Table 2. A summary of vascular plant colonizations and extinctions on 14 islands studied in 1908/09, 1949 and 1960 in the Tvärminne archipelago (for primary data, see Luther 1961). In this analysis plants were classified according to their biotopes and life cycles, and the frequency of colonization (Col.) and extinction (Ext.) events is given for each class. The results of χ^2 tests comparing the distribution of colonization or extinction events in the same period or between two study periods are given below.

	Number of species			Percent 1909–49		Percent 1949–60	
	1909	1949	1960	Col.	Ext.	Col.	Ext.
Biotope classes							
Littoral	21	29	30	26	24	24	25
Meadow	32	41	52	32	32	43	35
Wetland	23	25	30	19	32	13	19
Rock	12	18	19	8	3	7	5
Climax	13	22	23	10	11	4	11
Secondary	1	3	6	4	–	9	5
Life cycle classes							
Perennials	77	96	10	29	11	48	29
Annuals and Biannuals	15	24	37	63	71	44	68
Trees and shrubs	3	10	11	4	5	5	3
Dwarf shrubs	7	8	10	4	14	2	–
Total number of events				248	38	135	63

χ^2 tests:

Life cycle	Biotope			
	Col. 1909–49	Ext. 1909–49	Col. 1949–60	Ext. 1949–60
Col. 1909–49		n.s.	n.s.	–
Ext. 1909–49	p<0.05		–	n.s.
Col. 1949–60	p<0.01	–		n.s.
Ext. 1949–60	–	p<0.01	p<0.05	

events using the six biotope classes and four life cycle classes as basic units (Table 2). In the biotope classification, colonization and extinctions were more or less similarly distributed over the six different species groups in both periods, and no between-period differences were observed. In contrast, clear differences among the life cycle groups were observed both in colonization and in extinction totals. Second, colonizations totaled differently in the two intervals, and between-census differences were observed in extinction scores of the species groups (Table 2). The differences are attributable to perennials and to annuals and biannuals, though in the first period dwarf shrubs had proportionately more extinctions than colonizations.

The quantitative analyses above suggest the following conclusions. The dry summers 1955 and 1959 affected the plant communities on the Tvärminne islands not only because many annuals, thriving well on these islands before this 'crunch' (Wiens 1977) went extinct, but also because the densities of many populations were drastically reduced, often to as little as one-half or even to one-tenth of the former density (Luther 1961). The overall decrease in popu-

lation density enhanced the colonization possibilities of perennials, which seemingly have had poorer chances of invading during the first interval. In spite of the markedly higher extinction rate in the latter period, average rates of increase in the numbers of all species were nevertheless similar during the two periods, 0.38 and 0.39 species per island and year, respectively (Haila et al. 1982).

Dry summers are not the only source of extinction of plant populations on Northern Baltic islands, but snowless winters or flooding by brackish water can be equally disastrous (Hinneri 1972). Bergman (1970) reports that in winter the mountain hare *Lepus timidus* L. may destroy whole blueberry stands on small islands. Heavy grazing of birch seedlings *Betula pubescens* Ehrh. prevents renewal of birch populations when hare populations are dense. Similarly, grazing affects plant populations on islands in peak years of voles *Microtus agrestis* (Pokki 1981, Bergman 1982). For example, species such as *Quercus robur* L., *Corylus avellana* L., *Hepatica nobilis* Miller, *Saxifraga granulata* L. and *Ribes alpinum* L. suffered so much from vole and hare grazing that they were unable to establish populations on a 2.8-ha

wooded island in an introduction experiment (Bergman 1982).

Species turnover of bird populations in the island group of Krunnit (65°25'N, 25°00'E) in the northern Gulf of Bothnia — protected as a sanctuary since 1936 — shows another kind of dynamic pattern. Since 1939, quantitative censuses of breeding birds were made in 20 summers during 1939–72 (Väisänen & Järvinen 1977a, 1977b). After the human negative impact on birds decreased, the bird populations on the Krunnit Islands have changed considerably. Here, as almost everywhere, species number and island area correlate positively. More interestingly, the recovery process can be seen in the numbers of breeding species expected according to the species-area relationships on small islands (Väisänen & Järvinen 1977a):

Area:	0.1 ha	1.0 ha
1939	2.0 spp.	4.5 spp.
1949	2.6	5.6
1957	2.9	6.2
1963	4.0	7.5
1972	3.6	6.7

As regards the succession of bird species assemblages on the Krunnit Islands, Väisänen & Järvinen (1977b) compared annual bird counts on a number of islands. Based on botanical studies (Vartiainen 1980), the islands were classified into A) boulder skerries (elevation 1.3 m, area 0.4 ha, 17 vascular plant species), B) grassy skerries (2.1 m, 2.8 ha, 34 plant species), C) grassy islands (2.4 m, 5.7 ha, 61 plant species) and D) wooded islands (4.5 m, 34.6 ha, 108 plant species). A fairly good correspondence was observed between the bird assemblages and the botanical classification of the islands (Fig. 8).

Three features of the bird communities on Krunnit deserve emphasis. First, no species occurs on two of the more extreme types of islands without breeding on the intermediate type(s). Second, nearly all species breed on C and D, though often in low densities (Väisänen & Järvinen 1977b, their Table 3). Finally, only eight species breed on a single type of island. These observations correspond to what E. J. Valovirta (1937) found when he studied the flora of the Rönnskär archipelago in the central part of the Gulf of Bothnia. Here species colonizing the smallest islands were also found on almost all other islands. This distribution pattern implies that northern land uplift archipelagoes have few or no 'supertramps' (Diamond 1975) occurring abundantly on small islands but missing from the large ones. The lack of

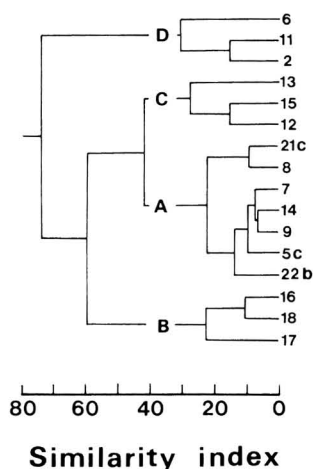


Fig. 8. Classification of breeding bird communities on the Krunnit Islands in 1972 (from Väisänen & Järvinen 1977b). The main branches of the dendrogram have been labelled using upper case letters according to the type of island, A = boulder skerries, B = grassy skerries, C = grassy islands, D = wooded islands (three exceptions from the generally regular clustering are indicated with lower case letters).

supertramps is also evident as one examines land birds on small islands (Haila et al. 1983), ants (Vepsäläinen & Pisarski 1982), terrestrial molluscs (I. Valovirta 1977), or ground beetles (Silfverberg 1968, Niemelä et al. 1987).

5. Rock-pools: islands on islands

Rock-pools on the Northern Baltic islands are islands on islands: mosaically distributed habitats characterized by unpredictable changes in their water content. Rock-pools usually form in shallow (15–30 cm) depressions in the rock and they tend to be small, often 2–20 m². Although the pools vary in their physico-chemical characteristics, it is easy to find pools of certain types on every island and almost on every islet. Many of the pools close to the shore receive their water mainly from the waves and surf, while the freshwater pools are maintained by rains and therefore they face a risk of desiccation during droughts. The probability of drying up varies from pool to pool, depending both on the volume of the pool and the frequency of rains.

Early studies on rock-pools focused on the paramount importance of salinity in governing the distribution of species (Levander 1900, Järnefelt

1940, Lindberg 1944, Droop 1953, Lagerspetz 1955, Björklund 1972). Different species occupy different parts of the salinity gradient, and in many groups of organisms the total number of species does not change substantially along the whole salinity gradient encountered in rock-pools (Ranta 1982). Superficially this would seem like an example of niche differentiation and neat species packing (*sensu* MacArthur 1972), but two examples, one on rotifers and the other on cladocerans, will illustrate that the real patterns are more complicated.

Björklund (1972) classified rotifers into three groups according to their occurrence in the surrounding brackish-water sea: common, rare and absent. If rock-pools are classified according to their proximity to the sea, the following species distribution emerges.

Occurrence in the sea:	Common	Rare	Absent
Wave and splash zone	49	11	5
Spray zone	41	46	84
Above the spray zone (freshwater)	6	22	53

It is understandable that species common in the sea dominate in the wave and splash zone, but, as regards salinity, it is not obvious why species absent from the sea are most frequent in the spray zone, where salinity is equal to that in the sea (periodically higher). Another interesting group of species is those that are rare in the sea. They occur fairly evenly in all the three zones. Clearly these species tolerate a wide amplitude of environmental conditions but are not able to build up high densities in the sea. Whether this is due to the marginality of the marine habitat, to poor competitive ability or to other factors, is not known. It is also apparent from the above tabulation that salinity niche differences do not wholly explain the distribution of rotifer species in rock-pools.

Three species of *Daphnia*; *D. magna* (Straus), *D. pulex* (deGeer) and *D. longispina* (O. F. Müller), occur commonly in Northern Baltic rock-pools. The niches of the species have been characterized by Ranta (1979) who observed their distribution in rock-pools with respect to four environmental variables (pH, organic carbon content, salinity, and size of pool). Even though the species niches overlapped considerably, no pool was inhabited by all three species, and the proportion of two-species pools was only about 10% of all pools inhabited by *Daphnia*. This finding was also confirmed by Pajunen (1986). Ranta suggested that the scarcity of coexisting populations is due to resource competition. *Daphnia* are

filter feeders, and the size of ingested particles is relative to body length (Burns 1968). The body sizes of the species overlap considerably (*D. magna* ranges from 0.9 to 5 mm, *D. pulex* 0.7–3.5 mm, *D. longispina* 0.6–2.5 mm), which, together with laboratory experiments (Frank 1952, 1957, Neill 1975), supports the competition hypothesis (but see Bengtsson 1986).

Immigration and extinction are major factors in theories of population processes in heterogeneous environments (Levin 1976, Roughgarden 1979, Hanski 1982, 1983). Levins (1969) modeled changes in the number of local populations of one species instead of changes in its local abundance, and this approach has been extended to two or more interacting species (Slatkin 1974, Christiansen & Fenchel 1977, Hanski 1983, Hanski & Ranta 1983 are but a few examples) or to two differentially dispersing morphs of one species (Järvinen 1976).

The mosaic-like distribution of rock-pools and their durational instability make the persistence of aquatic organisms unpredictable. When pools dry up, the rock-pool organisms either have to migrate or spend the unfavourable period in dormancy. Year-round residents, incapable of active dispersal, avoid desiccation either by dormancy or by burrowing into the bottom sediment. Active dispersal is largely restricted to insect imagoes that enter rock-pools in spring for oviposition. When conditions deteriorate, the individuals may leave the pool and move to larger (drought-resistant) pools.

In the spatio-temporally heterogeneous rock-pool systems *regional coexistence* in an 'archipelago' of rock-pools on one island may be possible (Ranta 1979). For example, in *Daphnia* spp. frequent local extinctions and colonizations (Pajunen 1986) of empty pools appear to maintain the observed pattern of regional (within-island) coexistence despite the fact that within-pool coexistence is unlikely owing to resource competition. Hanski & Ranta (1983) conclude from a theoretical analysis that the largest species *D. magna* is the best colonizer and the least successful competitor, and that the smallest species *D. longispina* is the best competitor and the least successful colonizer, *D. pulex* being intermediate in both respects. Their model predicts that the probability of regional coexistence increases with an increasing number of pools on an island. This agrees with field data since only the largest islands having numerous pools rear all the three species. Because of the colonization and competitive abilities of the three species, a priority effect is unlikely in this system. This is

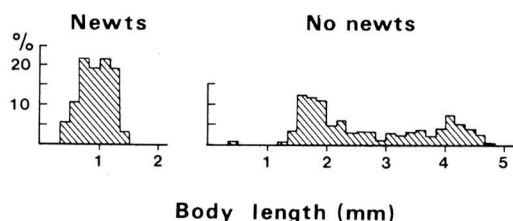


Fig. 9. Examples of the body size distribution of zooplankters in a rock-pool inhabited by smooth newts *Triturus vulgaris* and in a newt-free rock-pool (from Ranta & Nuutinen 1985).

supported by field data: all the single-species islands were occupied by *D. magna*, and all the two-species islands by *D. magna* and *D. pulex*.

Two species of corixids, *Arctocorisa carinata* (Sahlb.) and *Callicorixa producta* (Reut.), occur frequently in high numbers in rock-pools on Northern Baltic islands (Pajunen 1977). Vepsäläinen (1978a) contrasted the two species in terms of their life history strategies and concluded that *C. producta* is clearly the more *r*-selected species of the two. Pajunen (1979a) lists four facts that suggest strong interspecific competition between the species (see also Vepsäläinen 1978a): (1) the habitat utilization of the two species is similar, quantitative differences in the usage of different-sized pools occurring only in the late part of the season; (2) the species are almost identical in terms of their reproductive phenology; (3) no obvious possibilities for microhabitat differentiation between the species exist in rock-pools; and (4) densities of mixed populations are frequently high enough to result in considerable mortality of larvae. Pajunen (1979b) gives evidence indicating that in stable situations *C. producta* would be excluded by *A. carinata*. However, in a patchy and unpredictable environment *C. producta* is able to maintain its populations regionally because of its greater willingness to disperse. Late in the growing season, *C. producta* is also able to make use of smaller water bodies than *A. carinata*. In a field experiment Pajunen (1982) was able to show that the competition between these two species is for food. They completely overlap in resource use, and exploit resources with almost equal efficiency. An interesting aspect of their biology is that adults and larger larvae of both species are cannibalistic upon smaller larvae. Since *C. producta* is about half the size of *A. carinata*, interspecific interference clearly favors the larger species.

Ranta & Nuutinen (1985) measured the size distribution of zooplankters in large rock-pools inhabited

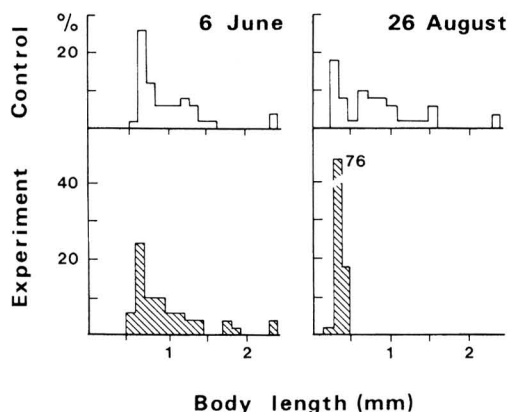


Fig. 10. Body size distribution of zooplankton in a rock-pool divided into two equal-sized halves (according to Ranta et al. 1987). The experimental half had introduced fish (*Tinca tinca*) while the control half had none. The left-hand side of the graph shows the frequency distribution of zooplankter sizes at the beginning of the experiment (6 June 1983) while the right-hand side compares size distributions in the control and experimental halves after 70 days (26 August 1983).

by smooth newts *Triturus vulgaris* L. and compared it with zooplankton sizes observed in rock-pools without newts. Large plankters were found in rock-pools without newts, but were excluded from newt pools apparently by predation (Fig. 9). The observation is in accordance with laboratory experiments showing that newts have a clear preference for zooplankters larger than 1 mm. Ranta et al. (1987) conducted a field experiment by introducing a fish, the tench (*Tinca tinca* L.), in rock-pools inhabited by large *Daphnia*. Pools were divided into two equal halves, and a small number of fish was put into the experimental half. Zooplankton in the control and experimental halves was sampled during 3 months at 10-day intervals. A clear reduction of zooplankton size could be attributed to fish predation in this experiment (Fig. 10). The elimination of *Daphnia* from the experimental halves of the rock-pools also resulted in the elimination of previously abundant filamentous algae from the phytoplankton. It seems that intensive grazing by *Daphnia* on small unicellular algae enhances the relative competitive advantage of filamentous algae (*Daphnia* are unable to feed on them) in the plankton community.

Zooplankters in lakes and ponds are vulnerable to fish and newt predation, while small water bodies usually lack the visually hunting vertebrates that prefer large-sized prey. However, small pools are occupied by invertebrate planktivores that increase the

mortality of small zooplankters (Hrbacek 1962, Brooks & Dodson 1965, Lynch 1980, Zaret 1980). It follows that in water bodies inhabited by fish and salamanders, small plankter sizes predominate, while in small water bodies large plankters, such as *Daphnia*, are common.

6. Genetic variation in insular populations

Insular populations may have special adaptations, as shown by the studies of wing dimorphism in water-striders *Gerris* by Vepsäläinen (1978b; see also Järvinen & Vepsäläinen 1976). The proportion of wing dimorphic species of carabid beetles is higher in Fennoscandia than elsewhere in the world (Lindroth 1949), and brachypters are more frequent on small islands than on large ones in the Åland archipelago and elsewhere (Lindroth 1949, Gillefors 1966, Ås 1984). Various adaptations to insular conditions have also certainly occurred in about 20 plant species having taxonomically distinct subspecies in the archipelago of the Northern Baltic.

We review some data on two polymorphic species which have been studied in detail in the Finnish Baltic archipelago.

Purple loosestrife, *Lythrum salicaria* L. (that even caught the attention of Charles Darwin because of its tristylous flowers), were studied on 16 islands in the Tvärminne archipelago by Halkka & Halkka (1974). Many of the populations were small (less than 100 individuals) and isolated, but all populations, including one comprising no more than 5 individuals, had all three morphs present. The pooled frequencies in the whole data set were 36% long-, 33% mid- and 31% short-style phenotypes. This is slightly, but significantly different from the 1:1:1 distribution derived from the assumption that the system has evolved to minimize inbreeding. It is striking that phenotype frequencies are almost identical in Great Britain, Germany, Switzerland and the United States (Halkka & Halkka 1974), which seems to suggest that island ecological factors are not responsible for fitness differences between the phenotypes.

Since all morphs were present in all the populations studied, Halkka & Halkka (1974) concluded that *Lythrum* disperses very effectively in the Tvärminne archipelago. Heuch (1980; see also 1979a, 1979b) has subjected tristylous to a theoretical analysis, and on the basis of his simulation studies he concludes that "a large amount of pollen or seed flow is

not necessary to maintain a population of size about $N=20$ with all three types." All except one of the populations studied by Halkka & Halkka (1974) exceeded this critical limit.

In another instance, various polymorphisms in the meadow spittlebug, *Philaenus spumarius* (L.), have been studied in great detail in the Tvärminne archipelago by Halkka and his co-workers. The spittlebugs live on small meadows on the islands and their populations are characterized by a great number of visually distinguishable colour morphs. Population size increases with increasing area of available habitat on the islands (Halkka et al. 1971). What is even more interesting is that colour variability (studied on 29 islands) correlates positively with population size and the area of available habitat (Halkka et al. 1971). Increasing isolation has a negative effect on variability perhaps because of the reduced numbers of founder individuals on remote islands. The same trend (summarized in Table 3), decreased polymorphism with increasing isolation, was also found in a study of enzyme gene polymorphism in the same archipelago by Saura et al. (1973).

Table 3. Genetic polymorphism in enzyme gene loci of *Philaenus spumarius* in the Tvärminne archipelago (data compiled from Saura et al. 1973). D = distance isolation index, N = size of population, P = proportion of polymorphic loci in the population, and H = average heterozygosity per locus per individual in the population. The populations are insular excepting Tvärminne. Genetic variation decreases with distance and increases with population size (see footnotes for our analyses of these data). The number of *Philaenus* colour morphs parallels the trend in enzyme genes, for all females on Segelskär belong to a single morph group in most years, while all seven morph groups are represented in Tvärminne (Halkka et al. 1974).

Island	D	N	P^1	H^2
Segelskär	17.7	1100	0.17	0.023
Flatgrund	0.7	90	0.39	0.063
Storsundsharun	2.4	500	0.42	0.071
Fyrholmen	0.6	1000	0.43	0.096
Skyffelskär	6.5	3000	0.50	0.099
Mellankobben	1.0	200	0.61	0.112
Tvärminne	0	30000	0.64	0.153

¹A multiple regression model for $P = 0.43 - 0.26 D + 0.022 \ln N$, which explains 66.2% of the variation in P . In this model N does not significantly increase the total variance explained, but D is statistically fairly significant ($P < 0.05$).

²A multiple regression model for $H = 0.47 - 0.07 D + 0.011 \ln N$, which explains 82.5% of the variance in H . In this model both variables are statistically significant, although distance is the more important of the two (excluding distance reduces the variance explained by 52%, but excluding N only by 25%).

The insular populations of *Philaenus* are often small and apparently derived from a small number of founders. Random genetic drift operates in small populations, which is shown by erratic and relatively large year-to-year changes in the morph frequencies (Halkka et al. 1970, 1976). The phenotypic composition of the populations also depends on subtle microhabitat differences, as shown by the fact that 'mini-meadows' situated only 5 m apart have been observed to differ considerably in their morph frequencies (Halkka et al. 1976). This is probably due to selective differences that are related to varying climatic tolerances of the morphs and to differences in their food plant selection (Halkka & Mikkola 1977).

A particularly fascinating chain of biological effects was found by Halkka et al. (1975) in their comparative study of *Philaenus* polymorphism on islands where voles had largely destroyed the vegetation as opposed to islands where they were unable to do so. On one island, grazing and burrowing by the voles caused injury to the vegetation which resulted in a population decline of *Philaenus*, and two polymorphism alleles were lost during the bottleneck phase of the population. When the vegetation recovered, the density of *Philaenus* increased and concomitantly the frequency of the most common colour morph increased. Halkka et al. (1975) suggested that this could have been due to density-dependent selection, although this is merely an inference. Voles may even indirectly cause population extinctions of *Philaenus* on islands where suitable meadows are small.

Remarkable small-scale differentiation has also been reported in the allele frequencies at one locus in an island population of the ant *Formica sanguinea* Latr. (Pamilo 1981). In the island population the frequencies of two alleles changed abruptly within a distance of some tens of meters. No such differentiation was observed in a comparable mainland study population of *F. sanguinea*.

We summarise these studies on population variability of island populations on Northern Baltic islands by pointing out that some evidence exists on the effects of random genetic drift and founder principle on the genetic constitution of the populations, but some selective agents operate even in very small populations. Selection on some polymorphic characters is so strong that it overrides the importance of stochastic fluctuations. Selection may involve both abiotic and biotic factors in the same population and regarding the same phenotypic feature. Even though isolation in the Northern Baltic archipelagoes is slight as compared with oceanic distances, it may appreciably reduce the

genetic diversity of populations inhabiting the outermost islands. It is clear that isolated populations on Baltic islands should receive more attention from this point of view, for example, we lack good data on patterns of morphological variation associated with continuously varying characters in isolated populations. Such data could throw light on the importance of founder effects on the evolution of insular populations at these northern latitudes.

7. Concluding remarks

A major tradition among studies of Northern Baltic islands can be called descriptive, for there are a large number of papers describing the insular distribution of different taxa. Usually these papers aim at a typification of islands, island zones, rock-pools, etc., or point out biogeographically interesting details, such as the occurrence of arctic birds or insects in the outer archipelago where the climate and openness of habitats resemble arctic conditions.

Researchers more interested in the processes creating patterns have tended to focus on the consequences of land uplift. Quite naturally, the primary succession of the vegetation has received most attention and has been carefully examined in many archipelagoes of the Northern Baltic. In such studies, as well as in papers examining the turnover of insular plant and animal populations, either the explicit or the implicit tenet has been that population processes, such as dispersal and reproduction, are important in affecting the co-occurrence of species and that, in fact, community patterns can often be traced to population-level phenomena. A case in point is Palmgren's (1912) study of the population biology of the sea buckthorn *Hippophaë rhamnoides* that preceded his many studies of Åland vegetation and was specifically thought of as a prelude to his many later studies. The scientific tradition has thus favored the Gleasonian tradition emphasizing populations instead of the holistic, 'supraorganismic' tradition in ecosystem ecology that has ecosystem energetics as its most recent outgrowth.

Our review also views population processes as explanations for the community patterns observed, even though apparently similar patterns often have different causes (cf. our discussion of species-area relationships in Sect. 2).

During the past few years there has been an increasing number of studies aimed at understanding ecological processes on Baltic islands with field ex-

perimentation (rock-pool biota, ant and carabid beetle communities). Approaches along the experimental lines are encouraging as executing carefully planned experiments are more likely to produce clear-cut answers to specific problems than merely collecting more field data.

Thus there is an interesting interplay of highly modern experimentalism and "old-fashioned" naturalism that can be observed in papers attempting to understand the biotas of the small and often desolate

islands of the Northern Baltic. Intelligent experiments cannot be made in a vacuum, but descriptive data are needed in order to make clear how the systems normally function. There are several areas for progress, and progress at its best combines different approaches.

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