GENETIC DIFFERENTIATION IN *SILENE DIOICA* METAPOPULATIONS: ESTIMATION OF SPATIOTEMPORAL EFFECTS IN A SUCCESSIONAL PLANT SPECIES

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Abstract.—*Silene dioica* is a diploid, dioecious, perennial, insect-pollinated herb and part of the deciduous phase of primary succession in Skeppsvik Archipelago, Gulf of Bothnia, Sweden. These islands are composed of material deposited and left underwater by melting ice at the end of the last ice age. A rapid and relatively constant rate of land uplift of 0.9 cm per year continually creates new islands available for colonization by plants. Because the higher deposits appear first, islands differ in age. Because it is possible to estimate the ages of islands and populations of plant species belonging to early stages of succession, the genetic dynamics occurring within an age-structured metapopulation can be investigated in this archipelago. Fifty-two island populations of *S. dioica* of known ages, sizes, and distances from each other were studied through electrophoretic data. A number of factors increase the degree of genetic differentiation among these island populations relative to an island model at equilibrium. Newly founded populations were more differentiated than those of intermediate age, which suggests that colonization dynamics increase genetic variance among populations. The very old populations, which decrease in size as they approach extinction, were more differentiated than intermediate-aged populations. Isolation by distance occurs in this system. Colonizers are likely to come from more than one source, and the migrant pool model best explains colonization events in the archipelago. Degree of environmental exposure also affects population differentiation.

Many natural populations are subdivided into a number of small demes with varying amounts of dispersal among them. Much theoretical work, most focusing on the opposing forces of genetic drift and migration (Hartl and Clark 1989), has been carried out to understand the evolutionary consequences of this subdivision. Genetic drift leads to deficiencies of heterozygotes in subdivided populations (Wahlund 1928), and when an equilibrium between drift and migration has been reached, the resulting degree of genetic differentiation between populations with respect to neutral loci is a simple function of the effective numbers of migrants between units (Wright 1943, 1951). This relationship, however, holds only for an island model (Wright 1943) in which a large array of "immortal" populations of finite size, each composed of N diploid, monoecious individuals, have an equal probability of exchanging migrants. Violations of some of these assumptions have been shown to have profound effects on levels of population differentiation. The

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first violation to be investigated was spatial variance in migration, which, in stepping-stone (Kimura 1955; Kimura and Weiss 1964; Weiss and Kimura 1964) and isolation-by-distance models (Wright 1943), increased population differentiation relative to an island model (e.g., Kimura and Weiss 1964; Crow and Aoki 1984; Whitlock 1992b; Goudet 1993; Slatkin 1993). A second and separate line of model development focused on deviations from population "immortality," since extinction and reestablishment of populations at vacated localities were found to be common in nature (e.g., Andrewartha and Birch 1954). To study the effects of extinction and recolonization (turnover) on differentiation, Slatkin (1977) introduced the ecological concept of metapopulations (Levins 1970) into population genetics. A metapopulation is an array of local populations that can exchange migrants. Each population has an equal probability of going extinct at any time, but each extinction is followed by immediate recolonization (Slatkin 1977). As a consequence, local populations vary in age, and the metapopulation, of which they are part, has an age structure.

Age structure has several implications for the degree of differentiation among local populations. One is that since founding events represent a source of genetic drift, populations from different age classes have different levels of genetic differentiation (F_{st}) due to the relative influences of founder events and continued migration on the gene frequencies of populations in each age class; this ultimately causes the genetic variance for the entire metapopulation to deviate from island model equilibrium values (Whitlock and McCauley 1990; Whitlock 1992b). A second indirect consequence is variation in population size, which enhances variance among populations relative to the case in which all populations are equally demographically mature and large (Whitlock 1992a). The degree of common origin of colonists also affects differentiation (Slatkin 1977; Wade and McCauley 1988; Whitlock and McCauley 1990; Whitlock 1992b). Initially, two extreme models of colony formation were investigated; the propagule pool model, in which colonizers are drawn from a single source population chosen at random from the metapopulation, and the migrant pool model, in which colonizers represent a random sample drawn from the metapopulation (Slatkin 1977; Wade and McCauley 1988). In the propagule pool model, colonization always increases genetic differentiation relative to an island model at equilibrium, while this relative increase occurs only if the number of colonists is less than twice the number of migrants under the migrant pool model (Wade and McCauley 1988). Whitlock and McCauley (1990) generalized these two models by including a new parameter, ϕ, which corresponds to the probability that colonizers have a common origin ($\phi = 0$ in the migrant pool model, $\phi = 1$ in the propagule pool model). Differentiation is enhanced in a metapopulation compared to an island model if the inequality

$$k < 2N_m/(1 - \phi) + 1/2, \tag{1}$$

where k is the number of colonists, N_m is the effective number of migrants, and ϕ is the probability of common origin of the colonists, is true (Whitlock and McCauley 1990). This inequality is always true for a propagule pool model since the right-hand side of inequality (1) approaches infinity as ϕ approaches 1. An important consequence of inequality (1) is that the standardized variances among

newly formed populations will be greater than among populations nearer or at equilibrium (Whitlock and McCauley 1990; Whitlock 1992a). Thus, if it can be shown or reasonably assumed that inequality (1) describes a system, and the F_{st} of young populations can be shown to be significantly greater than that of older populations, the hypothesis that colonization increases differentiation cannot be rejected.

One problem with testing this hypothesis is that it is seldom possible to age natural populations and therefore to describe the age structure of a metapopulation in a way that would facilitate analyzing changes in F_{st} with age. The first study of this kind was Whitlock's (1992a) study of the forked fungus beetle. He was able to show that inequality (1) holds, that the variances among younger populations were greater than among older populations, and thus that metapopulation dynamics increase genetic variance among populations relative to the equilibrium case. This article provides another example but in a plant species. We studied isozyme variation in 52 naturally founded island populations of *Silene dioica* in an archipelago where colonization and extinction dynamics occur. We examine the degree of genetic differentiation among populations of different ages for consistency with the consequences of the Whitlock-McCauley model. Since geographically restricted dispersal is known to increase differentiation, we also examine the patterns of association between genetic and geographical distances to see whether isolation by distance occurs within the archipelago. Since spatial variance has not been incorporated into models designed to investigate the effects of population turnover, the effects of spatial heterogeneity and population turnover on the degree of genetic differentiation cannot be disentangled. We discuss the possible effects of these two sources of variance on our results. Finally, information about isolation by distance among islands in different age-groups is used to draw inferences about ϕ in this archipelago.
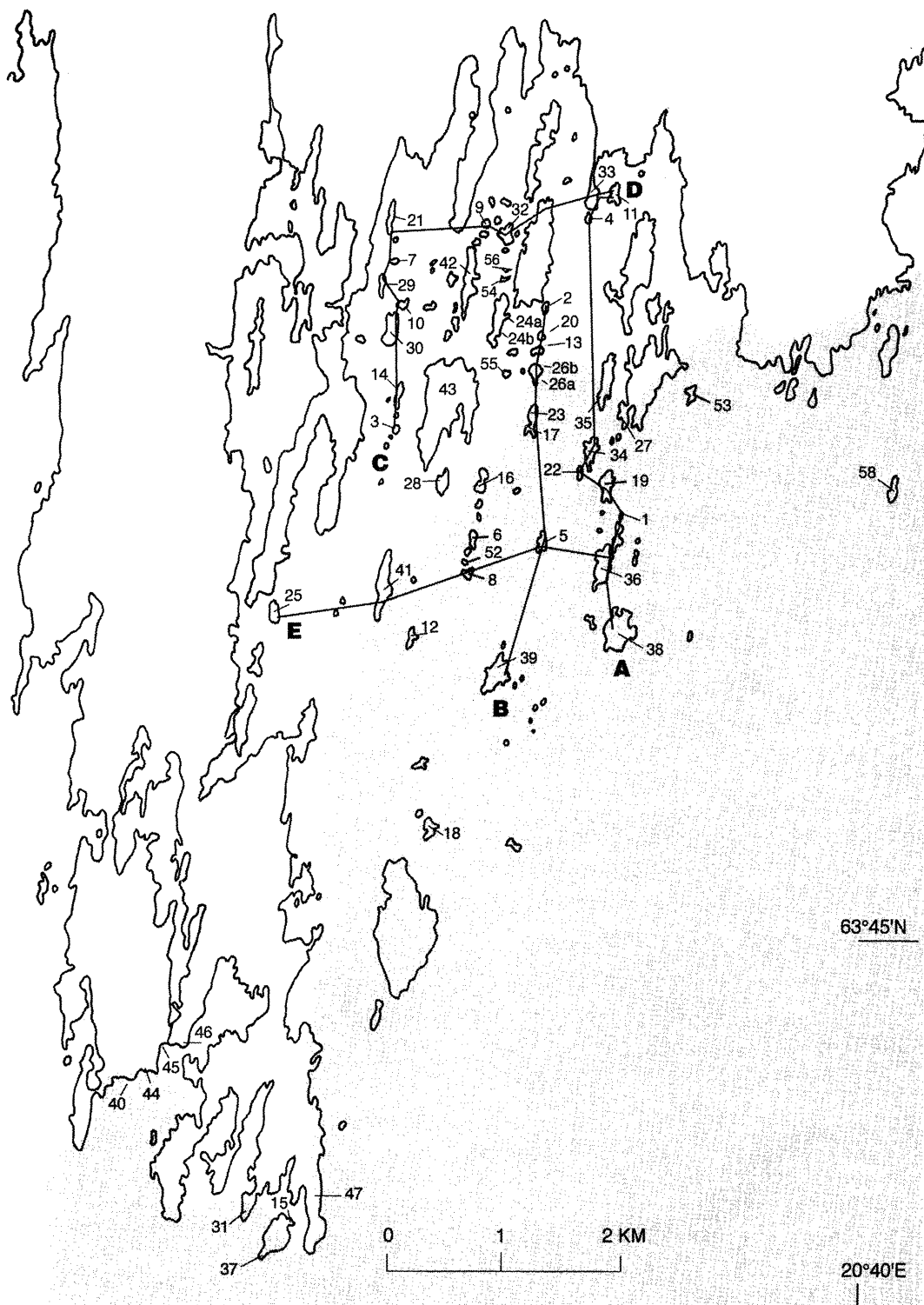
MATERIAL AND METHODS

Study Organism

The red bladder campion, *Silene dioica* (L.) Clairv. (Caryophyllaceae), is a perennial, dioecious, bumblebee-pollinated herb. Levels of vegetative spread are low, and the dynamics of population growth depend on sexual reproduction. Flowering occurs in June and July in northern Sweden. The seeds, which ripen in August, are dispersed by gravity and germinate the following spring. *Silene dioica* requires fertile, open habitats and is a member of the deciduous phase of primary succession in the study area. This species disappears from an area when successional processes close in the habitat and is never found in coniferous forests (B. E. Giles and J. Goudet, personal observation, consistent with the ecological descriptions of Baker 1947; see also Grime 1979).

Study Site

Skeppsvik Archipelago (fig. 1), located at the mouth of the Sävar River in the Gulf of Bothnia, Västerbotten province, Sweden (63°44′–48′ N, 20°34′–40′ E),

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63°45'N

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20°40'E

currently contains about 100 islands within its 20-km^2 area. The islands are composed of material deposited by glaciers and left underwater when the ice melted at the end of the last ice age. This area has been subject to the rapid and relatively constant rate of land uplift of 0.90 cm/yr for the last 7,700 yr (Ericson and Wallentinus 1979), and thus new land is continually made available for colonization by plants. Because the glaciers did not deposit equal amounts of material in all places and land uplift raises the highest points above the water first, the islands and their plant populations differ in age. The rate of uplift and the heights of islands above sea level were used to estimate the ages of the islands; knowledge of regional successional processes and the time required before islands can be colonized by plants was used to estimate the ages of the *S. dioica* populations (see Ericson and Wallentinus 1979; Carlsson et al. 1990). Even the mainland in figure 1 was formed by these processes and should be viewed as "fused" islands.

Colonization and Extinction Dynamics in Skeppsvik Archipelago

Individual diploid seeds bring about the colonization and establishment of *S. dioica* populations. Seeds are transported between islands over water in the drift material, which is moved around the archipelago by the prevailing winds, storms, and rising water levels each autumn. In the four new populations detected in the last 4 yr, colonizers were found growing in the decomposing drift material, and individuals were separated by distances, which suggested they did not arrive in the same capsule (B. E. Giles, personal observation).

The demographic histories of *S. dioica* populations follow a repeatable pattern on the islands, although succession proceeds more slowly in the outer part of the archipelago (Carlsson et al. 1990) owing to stronger wind, wave, and ice actions (*shaded area,* fig. 1). The ages given below reflect time differences between the inner and outer archipelagoes.

Seeds of *S. dioica* cannot establish populations on islands less than 70–150 yr old. This is the time required for sufficient soil and nutrients to accumulate and for islands to attain heights at which risks of habitat erosion by storm waves are low (Ericson and Wallentinus 1979). Successful colonization, the presence of flowering adults of both sexes with the first generation of seedlings under adult females, is not observed until individuals of the nitrogen-fixing *Alnus incana* are found in the centers of these islands (Carlsson et al. 1990; Carlsson 1995). These mats of seedlings, about 0.5 m in diameter, have not been observed under the female plants until four to six individuals representing both sexes have arrived and flowered simultaneously (B. E. Giles, personal observation).

FIG. 1.—Skeppsvik Archipelago, Gulf of Bothnia, Västerbottens Province, Sweden (63°44′–48′ N, 20°34′–40′ E). The shaded and unshaded areas are the exposed and protected parts of the archipelago, respectively, and reflect the boundary between (1) islands in the lee of other islands (*unshaded*) and those directly exposed to autumn storms (*shaded*), and (2) the area that is frozen solid during the winter (*unshaded*) or subject to pack ice driven by winds (*shaded*). A, B, and C are the outer, middle, and inner chains; D and E are the north and south transects, respectively.

Silene dioica populations expand rapidly on islands 120–250 yr old. Seedling establishment is high at the beginning of this stage (Carlsson 1995; B. E. Giles, unpublished data). *Silene dioica* and *A. incana* are gradually displaced from the centers of the islands by later successional species (*Sorbus acuparia* and *Betula pendula* in the deciduous phase, followed by *Picea abies* in the coniferous phase), and *S. dioica* populations form thick rings with high densities and numbers toward the shores (Carlsson et al. 1990). At this stage, *S. dioica* populations may be invaded by *Microbotryum violaceum,* a pollinator-borne, systemic, perennial, sterilizing anther-smut fungus and an obligate parasite of *S. dioica.* The incidence of infection varies from 5% to 60% in these middle-aged populations (Carlsson et al. 1990). There are no differences in longevity between infected and healthy individuals (Carlsson and Elmqvist 1992), and infected individuals continue to use habitat resources. Since infected individuals are sterile, disease reduces the number of reproducing individuals in a population.

Shading increases as later successional species invade a locality. Recruitment drops off sharply (Carlsson 1995; B. E. Giles, unpublished data), and if seeds germinate, seedlings turn yellow and die under the shaded conditions (B. E. Giles, personal observation). As coniferous forests spread over islands 200–400 yr old, *S. dioica* populations become increasingly restricted to the shores, and the rings become thinner and eventually break up into small patches or single individuals (Carlsson et al. 1990).

Coniferous forests occupy islands 250–500 yr old, and *S. dioica* populations go extinct, although single individuals can occasionally be found growing near the shores (Carlsson et al. 1990).

Skeppsvik Archipelago and the Metapopulation Model

This pattern of population development and the continual supply of new islands implies that Skeppsvik Archipelago is an age-structured metapopulation. The advanced successional status of the vegetation along the shores of the mainland suggests that the most likely sources of colonizers and migrants are islands within the archipelago. Colonization and migration dynamics must, however, satisfy inequality (1) if it is to be inferred that age structure resulting from founding events increases genetic differentiation relative to an island model at equilibrium. We assume that our system corresponds with the conditions in inequality (1) for the following reasons: Gene flow occurs among islands by seeds, which move by wind and water and by pollen transported by bumblebees. Only seeds can colonize, but seeds and pollen may contribute to gene flow. The observation that seedlings can be produced in new populations with fewer than 10 individuals suggests that k is small. Bumblebees fly between islands (followed by boat; L. Ericson, personal observation). One indication of the extent of pollen flow among islands may be obtained by regarding the pollinator-borne spores of *M. violaceum* as "natural" color markers for pollen and examining the proportion of flowers bearing spores in uninfected populations. Two such studies showed that 3%–5% of female flowers collected from uninfected populations bore smut spores (P. K. Ingvarsson and B. E. Giles, unpublished data). While the number of fertilizations will be lower than the number of pollen transfers, the magnitude of these "indica-

tor" transfer numbers, plus continued seed flow, suggest that the number of migrants is likely to be higher than the number of colonists.

Skeppsvik Archipelago, however, differs from the classical metapopulation model in which extinction processes are stochastic and independent of population age (Levins 1970; Slatkin 1977; Wade and McCauley 1988; Whitlock and McCauley 1990; Whitlock 1992b). Instead, extinction, influenced by successional processes, is deterministic and not a prerequisite for colonization. Colonization, however, is stochastic, and genetic differentiation among island populations should be enhanced by the continuous supply of new colonization sites in a manner similar to that predicted by extinction and recolonization models.

Sampling

Samples were collected in June (1991–1993) from flowering plants on 52 islands. The positions of the islands and information about their ages, population sizes, degree of exposure, and demographic stages are given in table 1. Our aim was to collect 50–100 individuals per population where possible (table 1). Islands with sample sizes over 100 were part of a larger study and sampled over more than one season (individuals were not scored more than once). Equal numbers of each sex were chosen so that any differences in allelic or genotypic frequencies between males and females could be detected. Plants were sampled at random throughout the area occupied by *S. dioica* on each island.

Electrophoresis

The youngest leaf was sampled from each plant in the field. Leaves were homogenized in an extraction buffer containing 0.01 M HEPES (pH 7.2), 1 mM ethylenediaminetetraacetic acid (EDTA), 2% Triton X-100, and 6 mM dithiothreitol (DTT). The supernatant was absorbed onto filter paper wicks that were frozen at −70°C until electrophoresis.

Electrophoresis was carried out in 10.5% starch gels with a discontinuous buffer system (electrode buffer = 0.21 M boric acid, 0.047 M lithium hydroxide, pH 8.4: gel buffer = 0.008 M citric acid, 0.05 M Tris, pH 8.1). Gels were stained for phosphoglucose isomerase (PGI, EC 5.3.1.9), phosphoglucomutase (PGM, EC 5.4.2.2), triosphosphate isomerase (TPI, EC 5.3.1.1), diaphorase (DIA, EC 1.6.99.-), and leucine aminopeptidase (LAP, EC 3.4.11.1) by using standard recipes (see Soltis and Soltis 1989) with some modification of substrate amounts. Six polymorphic loci were scored from these five enzyme systems. Homogenate from a single individual (divided into several clones) was placed at three positions on every gel to provide a control against which the relative mobility of the bands in the other individuals could be scored. The inheritance of the banding patterns was determined from crosses carried out on greenhouse material (data not shown; see also Prentice and Giles 1993), and no deviations from Mendelian patterns of inheritance were found.

Estimation of Population Differentiation and Statistical Tests

Genotypic and allelic compositions were analyzed with the program FSTAT V1.2 (Goudet 1995). Gene diversity (Nei 1975) was estimated at each locus. Devi-

TABLE 1

ISLAND DATA

ISLAND NUMBER	COORDINATES Horizontal	COORDINATES Vertical	EXPOSURE CLASS	POPULATION AGE	STAGE CLASS	POPULATION SIZE	SAMPLE SIZE	F_{is}
1	37.52	83.65	2	5	1	400	53	.093
2	36.72	85.40	1	5	1	500	94	.063
3	35.55	84.27	1	10	1	3,600	91	−.040
4	37.05	86.25	1	12	1	430	47	.050
5	36.89	83.40	2	13	1	1,500	93	.113
6	36.30	83.40	2	31	2	4,000	220	.000
7	35.39	85.68	1	35	1	400	150	.026
8	36.30	83.05	2	39	2	4,000	354	.152
9	36.23	86.12	1	41	2	16,000	256	.045
10	35.52	85.33	1	46	1	530	98	.084
11	37.25	86.50	1	53	2	5,000	168	.072
12	35.87	82.44	2	53	2	3,900	48	−.060
13	36.73	85.02	1	58	2	6,600	49	−.140
14	35.55	84.55	1	61	2	10,500	235	.112
15	35.25	77.25	2	63	1	800	90	.106
17	36.73	84.31	2	75	2	3,200	49	.168
18	36.18	80.80	2	80	2	15,000	35	.238
19	37.40	84.00	2	80	2	66,000	228	.094
20	36.73	85.15	1	84	2	2,000	49	.100
21	35.34	86.10	1	85	2	3,000	50	.096
22	37.20	84.00	2	91	2	3,000	50	.053
23	36.72	84.32	2	96	2	16,000	360	.096
24a	36.35	85.45	1	107	2	11,000	48	.100
24b	36.35	85.45	1	107	2	11,000	49	.047
25	34.65	82.55	1	111	2	4,900	181	−.050
26a	36.70	84.62	2	134	2	4,700	51	.152
26b	36.70	84.62	2	134	2	4,700	26	.120
27	37.43	84.34	2	156	2	4,600	27	.215
28	36.05	83.85	2	164	3	150	46	.133
29	35.32	85.50	1	178	2	15,000	50	.033
30	35.45	85.00	1	180	2	12,200	49	.034
32	36.35	86.00	1	185	3	2,400	45	.021
33	37.07	86.44	1	187	2	9,800	58	−.030
34	37.24	84.15	2	191	2	25,000	100	.098
35	37.33	84.80	2	196	2	8,500	46	.040
36	37.45	83.30	2	221	2	30,000	96	.160
37	35.10	76.90	2	265	3	600	28	.376
38	37.63	82.70	2	265	2	43,000	96	.104
39	36.63	82.47	2	276	2	18,000	60	.226
40	33.65	78.41	2	281	3	4,700	10	.000
41	35.60	82.90	2	300	3	1,500	30	.210
42	36.14	85.54	1	318	2	12,000	46	.000
44	33.80	78.35	2	360	3	960	58	.086
45	34.10	78.73	1	370	3	150	46	−.130
46	34.25	78.68	1	370	3	700	66	.063
47	35.55	77.42	2	381	3	600	29	.103
52	36.27	83.25	2	5	1	20	12	−.180
53	38.09	84.79	2	5	1	13	16	−.180
54	36.35	85.61	1	15	1	300	117	.077
55	36.47	84.79	1	5	1	18	18	.010
56	36.37	85.87	1	10	1	200	55	−.010
58	39.86	84.15	2	· · ·	2	· · ·	82	.188

NOTE.—Island number corresponds to location in fig. 1; coordinates specify island position on the national grid system.

ations from random mating for each locus and over all loci were assessed by means of F-statistics (F_{it} [F], F_{st} [θ], and F_{is} [f], where F_{it} is the degree of inbreeding in individuals relative to the total population and F_{is} is the degree of inbreeding in individuals relative to the subpopulation to which they belong), by the variance component method of Weir and Cockerham (1984). Standard errors for each F-statistic were obtained by jackknifing among populations for per-locus estimates and among loci for overall estimates. The value for F_{is} was also estimated within each island.

Considerable discussion has emerged over which method to use for testing the significance of F-statistics (Excoffier et al. 1992). We follow these authors (and Goudet 1995) and use the methods requiring the fewest assumptions, that is, permutation analyses of the null distributions of each F-statistic. For F_{is}, the null hypothesis is that random mating occurs within islands (H_0: $F_{is} = 0$), and alleles are considered to be drawn from the islands with variation due to random sampling in the construction of genotypes. We therefore allocated each allele at random and without replacement to a randomly chosen individual within each island. The F_{is} value was estimated from each of 5,000 random reallocations of alleles to individuals within islands generated by the program FSTAT. The observed value of F_{is} was then compared with the null distribution generated and tested against the alternative hypothesis, H_1: $F_{is} > 0$. If the observed value belonged to the highest 5% of the null distribution, it was deemed significant.

For F_{it}, the null hypothesis is that random mating occurs over the entire archipelago, and alleles are considered to be drawn at random from the archipelago with variations due to random sampling in the construction of genotypes. We therefore permuted alleles among individuals over the entire data set. Under the null hypothesis for F_{st}, individuals are considered to be drawn at random from the entire archipelago with variation among islands due only to random sampling of individuals. Note that considering alleles to be drawn at random from the entire archipelago would not be appropriate since alleles within individuals may not be independent (i.e., $F_{is} \neq 0$). We therefore permuted individuals among islands. If the observed values of F_{st} and F_{it} belonged to the highest 5% of their respective null distributions generated from 5,000 randomizations, they were considered to be significantly >0.

Changes in F_{st} with Age

The potential effect of turnover in the Whitlock and McCauley (1990) model, with equal extinction probabilities for all age classes and colonization rates equal to extinction rates, is to create small newly founded populations that are more differentiated. An additional model assumption, that all populations grow to carrying capacity in one generation, means that all populations surviving after one generation have reached carrying capacity and are approaching genetic equilibrium. In populations at carrying capacity, N_m is assumed to remain constant, and F_{st} should not be deflected from approach to equilibrium values. Thus, in empirical studies, population arrays have been divided into two groups—one containing only young populations and a second containing the rest—to see whether changes in F_{st} are consistent with the consequences of the Whitlock-

McCauley model (Whitlock 1992*a;* McCauley et al. 1995). In our metapopulation, however, extinction is driven by successional processes so that the probability of extinction is a function of population age, extinction is not instantaneous, and extinct patches are not recolonized. Compared with earlier stages, populations approaching extinction continually decrease in size, and there is a shift in the age distribution toward older individuals and a sharp reduction in recruitment (Carlsson 1995; B. E. Giles, unpublished data). Reduction in recruitment will ultimately reduce the number of migrants (N_m) able to enter a population. Together with the decrease in population size, this should lead to an increase in differentiation among these populations (Whitlock 1992*b*). Consequently, we did not include the oldest populations as part of a single group called "older" populations but treated them separately. We constructed three age-groups called young, intermediate, and old (table 1, stage classes 1, 2, and 3, respectively) by considering population sizes, ages, and shape of occupied area. The young group (age < 30 yr, size < 4,000 individuals) contains newly founded and expanding populations that occupy habitats from the centers to the shoreward edges of the islands. The intermediate group (30 yr < age > 280 yr, size > 4,000) contains those populations with the thick ring form, and the group of old populations (age > 280 yr, size < 4,000) were well into the decrease phase and had the broken ring form. We tested whether the F_{st} of young populations was larger than that of intermediate populations to see whether colonization increases genetic differentiation in correspondence with the Whitlock-McCauley model. We then separately tested whether the F_{st} of the old populations was greater than the F_{st} of the intermediate populations. This second test is not part of the Whitlock-McCauley model.

Standard statistical methods cannot be used to compare multilocus F_{st} estimates since there is only one value for each age class. To test whether the F_{st} values from two age classes differ, we adopted a randomization approach (Manly 1991; Crowley 1992). Our null hypothesis is that the observed F_{st} values from two age classes do not differ. To test this, we first took the difference between two observed F_{st} values. We then reassigned the samples at random to two groups identical in size to the original age-groups and calculated the differences in F_{st} between the two new groups. This procedure was repeated 5,000 times. The distributions of these differences are the distributions of our null hypotheses: (1) $F_{st,y} = F_{st,i}$, and (2) $F_{st,i} = F_{st,o}$ (y, i, o = young, intermediate, and old, respectively), and the locations of the observed differences in these null distributions provide an unbiased estimate of the probability of obtaining by chance a difference as large as or larger than that observed. Since our alternative hypotheses were (1) $F_{st,y} > F_{st,i}$, and (2) $F_{st,i} < F_{st,o}$, we concluded that the differences in F_{st} among age classes were significant if the observed values of the differences were in the highest or lowest 5% of the distributions of the null hypotheses (1) and (2), respectively.

Spatial Structure

In seeking evidence for isolation by distance in Skeppsvik Archipelago, we ignored the effects of age and limited our search to groups of islands that, on the basis of information about vectors of gene flow, are (or are not) likely to exchange

genes. We restricted analyses to these small island groups to come as near as possible to looking only at spatial restriction of migration even though the small sample sizes make detection of significant associations more difficult. Although temporal and spatial variances are confounded in these analyses, we believe that positive associations detected in these restricted analyses provide stronger, more conservative evidence of spatial restriction of migration than would a positive association at the archipelago level, where there would be total confounding between ages and distances and potentially "inflated" associations arising from inclusion of islands unlikely to exchange genes along with those likely to exchange genes.

From the time of seed release and onward into the autumn, the prevailing winds blow from the southwest, storms blowing from the southeast are common, and water moves into the archipelago as a result of the annual water cycle in the Baltic (Ericson 1981). Since the joint action of these vectors will be to move seeds from the south to the north of the archipelago, we constructed three "chains" of islands, the outer, middle, and inner chains, oriented in a south-north direction, based on the topology of the archipelago created by the retreat of the glaciers (labeled A, B, and C, respectively, in fig. 1). Isolation by distance was expected in all three chains. We also looked for isolation by distance where wind and water are not likely agents of seed flow by setting up two east-west transects. Since bumblebee movement occurs among islands and appears to be more frequent in the inner than the outer part of the archipelago (L. Ericson, personal observation), an effect in the north transect is not unexpected (fig. 1,D). The south transect, (fig. 1,E) was set up in the most exposed part of the archipelago as a contrast to the other four groups. Since we do not suspect these islands to be linked by known vectors of gene flow, we do not expect to find evidence of isolation by distance.

Evidence of isolation by distance among the islands was obtained by examining the correlations between matrices of pairwise genetic distances (F_{st}) and pairwise physical distances (Slatkin 1993). Mantel tests (Mantel 1967) were used to test the strength of the correlations between the matrices. Significance levels were calculated through sequential Bonferroni procedures that adjust α levels for the number of component tests (Rice 1989). Since there is no indication as to what type of transform of F_{st} and distance is appropriate, we have used three: untransformed F_{st} versus untransformed physical distances, Slatkin's (1993) $\ln[(1/F_{st} - 1)/4]$ (log of the number of migrants in an island model) versus log of physical distances, and ranked F_{st} versus ranked physical distances.

Source of Colonists

In models of isolation by distance, migration occurs between nearby populations. As a first attempt to understand the probability of common origin of the colonists, we looked for evidence of isolation by distance among young populations and among intermediate populations using Mantel tests. Isolation by distance detected among young populations, or among both young and intermediate populations, will be taken as suggesting that colonizers of new islands were drawn from a limited number of source populations and that a propagule pool model

TABLE 2

ALLELE NUMBERS AND GENE DIVERSITY FOR EACH LOCUS OVER ALL POPULATIONS

	Pgi2	Pgm1	Pgm2	Tpi1	Dia1	Lap1
Number of alleles	4	3	3	2	2	5
Effective number of alleles	2	1.4	1.1	1.3	1.1	3.9
Gene diversity	.51	.26	.09	.26	.09	.75

TABLE 3

F-STATISTICS PER LOCUS AND OVER ALL LOCI FOR THE ENTIRE
ARCHIPELAGO

Locus	F_{it}	F_{st}	F_{is}
Pgi2	.069 (.013)	.043 (.009)	.028 (.011)
Pgm1	.174 (.024)	.038 (.008)	.142 (.022)
Pgm2	.413 (.046)	.023 (.007)	.400 (.047)
Tpi1	.108 (.034)	.073 (.028)	.038 (.019)
Dia1	.330 (.081)	.057 (.019)	.289 (.088)
Lap1	.053 (.020)	.023 (.004)	.031 (.020)
All	.110 (.039)	.038 (.010)	.075 (.035)

NOTE.—Standard errors are in parentheses.

best describes the archipelago. If, however, isolation by distance is detected among intermediate but not among young populations, it is more likely that colonizers represent a sample of the metapopulation and a migrant pool model will be inferred. Rejection thresholds were adjusted by sequential Bonferroni procedures (Rice 1989). Old populations were not tested because of their clumped distribution (table 1; fig. 1).

RESULTS

Restricted Gene Flow in the Archipelago

Deviations from random mating were first assessed by using the data from all islands to see at what levels restrictions in gene flow occurred. The actual and effective numbers of alleles and gene diversity per locus are reported in table 2. No systematic differences in allelic or genotypic frequencies between males and females were detected.

The F-statistics per locus, and over all loci for the entire archipelago, are given in table 3. Over all loci, F_{it}, F_{st}, and F_{is} were significantly >0. There is thus strong evidence of restricted gene flow in the archipelago (F_{it}), both among (F_{st}) and within (F_{is}) islands.

We checked whether the significant F_{is} values were due solely to the contributions of Dia1 and Pgm2 since their per-locus F_{is} values were high (table 3). These loci were the least polymorphic, and thus their contributions to the overall F_{is} were low (table 2). The F_{is} values decreased to 0.048 after their removal but

TABLE 4

Two-Way ANOVA of Ranked F_{is} for Exposure
and Stage Classes (table 1)

Source	df	Mean Square	F	P
Exposure (E)	1	2,749.5	15.66	.0003
Age (A)	2	224.3	1.28	.2884
E × A	2	217.9	1.24	.2986
Residual	46	175.5		

remained significantly >0. The F_{is} values within each island range from -0.18 to 0.38 (table 1). Such heterogeneity suggests that structuring within islands may be the cause of the observed F_{is} value, since inbreeding is expected to give more uniform values of heterozygote deficit (Robertson and Hill 1984). One hundred patches (0.2 m^2) have recently been studied on islands 23, 35, and 39 (fig. 1). These data were partitioned as follows: $(1 - F_{it}) = (1 - F_{ip}) (1 - F_{pl})(1 - F_{lt})$, where p refers to patch and l to islands. Estimates of F_{ip} did not differ from 0, and the among-patch values of F_{pl} obtained for each island were very close to the within-island estimates of F_{is} reported in table 1 (B. E. Giles, E. Lundqvist, and J. Goudet, unpublished manuscript). Single islands thus consist of several random breeding units, and the appropriate partitioning of the heterozygote deficit in the archipelago is best described by the above expression. For the current study, this means that our estimator of the among-island Wahlund effect, F_{st}, corresponds to F_{lt} in this expression, but our estimator of F_{is} actually corresponds to $1 - (1 - F_{ip})(1 - F_{pl})$. While the total Wahlund effect, estimated by F_{pt}, will be underestimated by our F_{st}, any of our inferences based on these F_{st} values will be conservative (Goudet 1993).

One further aspect of the heterogeneity of the F_{is} values among the islands is of interest. Successional changes occur more slowly in the exposed parts of the archipelago. Exposure may also reduce the probability of colonization and increase that of local patch extinction due to destruction by waves and ice. Exposure could thus increase F_{is} in a way that is not completely independent of age. We therefore used age and exposure (stage and exposure classes, table 1) as factors in a two-way ANOVA on the ranked F_{is} values obtained from each island. Islands were grouped into two exposure classes, protected and exposed, according to their position within the shaded and unshaded sections of figure 1. Because of the survey nature of these data and imbalance arising from differing numbers of islands in the three age classes (islands within each age class were fairly evenly distributed into exposed and protected classes [table 1]), Type I sum of squares (SS) were computed (Milliken and Johnson 1992). Fitting exposure first, table 4 shows that the effect of exposure is significant, but those of age and the interaction between age and exposure are not. Slight numerical differences were observed when age was fitted first (not shown), but it remained clear that exposure is the dominant factor accounting for the variation in F_{is}. The F_{is} values for exposed islands are generally greater than 0.09 (table 1).

TABLE 5

F-STATISTICS OVER ALL LOCI FOR THE YOUNG, INTERMEDIATE,
AND OLD AGE-GROUPS

	N	F_{it}	F_{st}	F_{is}
Young	13	.105 (.061)	.057 (.028)	.052 (.046)
Intermediate	30	.107 (.033)	.030 (.006)	.080 (.032)
Old	9	.158 (.068)	.066 (.009)	.098 (.068)

NOTE.—Standard errors are in parentheses.

Changes in Genetic Differentiation with Age

All F-statistics estimated for the young, intermediate, and old age classes are significantly >0 (table 5). The F_{st} is high among young islands (0.057), decreases to 0.030 in the intermediate age class, and reaches its highest value of 0.066 among the old islands. The F_{st} of the young populations was significantly larger than that of the intermediate populations ($P = .05$). The F_{st} for the intermediate class was significantly lower than that of the old class ($P = .04$). Although table 5 suggests that F_{is} increases with age, these differences are not significant. It is therefore unlikely that the observed changes in F_{st} are artifacts of changes in F_{is}.

Spatial Structure

Table 6 shows the results of Mantel tests carried out on correlations between matrices of pairwise F_{st} and geographical distances for the three transformations. The correlation coefficients (R) between the two matrices were high, 0.40 or greater, for the outer and inner chains and the north transect for the untransformed and ranked data. At the level specified by the conservative sequential Bonferroni test, only the outer chain using untransformed F_{st} is significant. However, the number of observations (islands) in these transects were small, which makes detection of significance difficult and increases the risk of Type II error. If we consider the calculated probabilities (P) up to 5% to be indicating marginal significance, the outer chain is always in this category, as are the inside chain and northern transect in two cases. The probability values obtained for the middle chain and south transect were not significant.

Source of Colonists

The results of the Mantel tests within the young and intermediate age-groups are given in table 7. No effect of distance was detected in any of the tests for the young populations, while all three Mantel tests were highly significant for islands in the intermediate group.

DISCUSSION

Our study of 52 populations of *Silene dioica* in the Skeppsvik Archipelago metapopulation indicates that temporal, spatial, and environmental factors affect the degree of genetic differentiation among island populations.

TABLE 6

MANTEL TESTS OF ISOLATION BY DISTANCE IN GROUPS OF ISLANDS
FORMED ON THE BASIS OF HYPOTHESES ABOUT
VECTORS OF GENE FLOW

Group	N	R	P	Threshold
a:				
Inside chain	7	.4669	.019	.013
Middle chain	9	.0767	.327	.025
Outer chain	11	.4296	.008	.010
North transect	6	.5629	.054	.017
South transect	5	−.5034	.932	.050
b:				
Inside chain	7	−.3947	.052	.013
Middle chain	9	−.2548	.128	.017
Outer chain	11	−.3289	.021	.010
North transect	6	−.2275	.196	.025
South transect	5	.2922	.759	.050
c:				
Inside chain	7	.3961	.057	.017
Middle chain	9	.1681	.268	.025
Outer chain	11	.3980	.011	.010
North transect	6	.5673	.024	.013
South transect	5	−.3697	.868	.050

NOTE.—Threshold specifies the sequential Bonferroni level of sig-
nificance required for rejection of the null hypotheses. a = F_{st} vs.
geographical distances; b = $\ln[(1/F_{st} − 1)/4]$ matrix vs. $\ln$(dis-
tances); c = ranked F_{st} vs. ranked geographical distances.

TABLE 7

MANTEL TESTS FOR ISOLATION BY DISTANCE IN YOUNG AND
INTERMEDIATE ISLAND GROUPS

Group	N	R	P	Threshold
a:				
Young	13	−.0561	.405	.05
Intermediate	30	.3662	.002	.025
b:				
Young	13	−.0011	.43	.05
Intermediate	30	−.3231	.00	.025
c:				
Young	13	−.0032	.461	.05
Intermediate	30	.3298	.002	.025

NOTE.—See table 7 for definition of a, b, and c.

An array of populations connected by gene flow but that differ in age as a
result of population turnover will be more differentiated than populations that are
equally demographically mature and at equilibrium between gene flow and genetic
drift—as long as the number of colonizers is less than twice the number of mi-
grants (Wade and McCauley 1988; Whitlock and McCauley 1990; Whitlock 1992a,
1992b). Drift within the young, newly founded populations is the source of the

enhanced differentiation that can be demonstrated by showing that the standard-ized genetic variance of a group of young populations exceeds that of a group of older populations (Whitlock 1992a). Whitlock (1992a) obtained this empirical sup-port by dividing populations of forked fungus beetles into young and older groups using the size of the fungal resource as an indicator of demographic maturity. We divided our populations into three groups to capture the founding, increasing-maximum size, and decreasing phases of the demographic history of the island pop-ulations. We predicted that the F_{st} of young populations should reflect founding events and be higher than that of intermediate populations, which have been ex-posed to further migration and have presumably moved closer to equilibrium. In populations approaching extinction, size decreases and recruitment is reduced. Thus, the F_{st} of old populations should reflect this second perturbation from equilib-rium by increasing again. The latter is not part of the Whitlock-McCauley model. We found a significant decrease in F_{st} between young and intermediate populations and a subsequent significant increase between intermediate and old populations, which is consistent with these predictions. Thus, turnover dynamics in Skeppsvik Archipelago increase levels of genetic differentiation among populations relative to an equilibrium case, and two sources of perturbation from equilibrium, first found-ing events and later population decay, contribute to this increase.

Founder events are likely to contribute to the high F_{st} of the young populations, since the number of colonists able to establish populations on new islands is small. However, the accumulated effect of genetic drift also depends on the reciprocal of population size (Falconer 1989). Since the harmonic means of the census sizes of populations within the young and intermediate groups were 63 and 6,413, respectively (from data in table 1), the smaller sizes of the young populations could also contribute to their greater differentiation. The decrease in F_{st}, observed between the young and intermediate stages as the populations expand, is likely due to continued migration, which homogenizes the gene frequencies among pop-ulations. Homogenization does not reach completion since the F_{st} of the interme-diate group remains significantly >0. These inferences are supported by noting that the means and standard deviations of the numbers of alleles observed at all loci (maximum 20) in the young, intermediate, and old groups were 14.33 ± 3.39, 18.56 ± 0.73, and 15.25 ± 2.05, respectively.

The increase in F_{st} observed between the intermediate and old stages has never been reported and may be associated with the successionally driven extinction that characterizes our metapopulation. A number of factors that could increase genetic drift in the old populations can be identified. *Microbotryum violaceum,* which prevents its hosts from reproducing, usually invades *Silene* populations at the intermediate stage (Carlsson 1995). It seems unlikely, however, that the re-moval of reproductive individuals by disease alone changes the genetic composi-tion of the gene pool and thereby explains the observed changes in population differentiation between intermediate and old stages. With the same enzyme loci as in the current study, no differences in the allele or genotype frequencies were detected between infected (sterile) and uninfected (reproductive) fractions of pop-ulations from four islands with incidences of infection over 40% (T.-M. Pettersson and B. E. Giles, unpublished manuscript). Incidences of disease are also less

than 5% in most populations (Carlsson and Elmqvist 1992), again making it un-
likely that disease is the primary cause of the increased differentiation among
populations of the remaining reproductive individuals. A number of other factors
clearly contribute to a reduction in the size of the populations. The reproductive
output of *Silene* populations has been observed to be reduced in the presence of
disease (Carlsson and Elmqvist 1992; Antonovics et al. 1994). Later successional
species have expanded over large fractions of old islands. We observe (*a*) reduced
survival of seedlings in the presence of later successional species and (*b*) in-
creased mortality rates through displacement of adult individuals by trees (both
of which act without respect to *Silene* genotype). In addition, *Silene* populations
must become smaller as a result of the reduction of suitable habitat as succession
proceeds. Since (*a*) and (*b*) also reduce the probability of establishment of migrant
individuals, migration is not likely to counteract genetic drift in these populations.
It is thus more likely that small population sizes lead to increased genetic drift
within populations and therefore increased differentiation among populations.
Last, if these populations are moving away from equilibrium, as they appear to
be doing, our "old" populations do not meet the criteria for membership in the
"older" group implied by Whitlock and McCauley (1990). Thus, where local
extinction appears to be associated with age or a long deterioration phase such
as occurs in succession, we suggest removing these populations from the group
meant to represent populations nearest their demographic and genetic equilibria.
Any increase in F_{st} contributed by such decaying populations could obscure the
decrease expected between founding and "equilibrium" stages.

Two analyses reveal that isolation by distance occurs in this archipelago. The
first was limited to groups of islands believed to be connected by vectors of gene
flow. Gene flow among islands occurs by seeds and pollen. Bumblebees can move
in all directions; seeds must follow wind and water movements. We looked at
three north-south chains where we know that wind and water move from south
to north at the time of seed release, and two east-west transects where wind and
water are not likely agents of seed movement. Isolation by distance was observed
in the outer chain; the inner chain and northern transect closely approached
significance (table 6). No isolation by distance was detected along the south tran-
sect where connections through wind, water, and pollinators appear to be weak.
The analysis of the 30 populations in the intermediate age-group (table 7) also
provides evidence of isolation by distance. Since isolation by distance has been
shown to increase differentiation relative to an island model at equilibrium (e.g.,
Crow and Aoki 1984; Whitlock 1992*b;* Goudet 1993; Slatkin 1993), we conclude
that the degree of differentiation among islands in Skeppsvik Archipelago is also
affected by geographically restricted migration.

We looked for isolation by distance among young and intermediate populations
as a first attempt to examine the origin of colonists since the properties of the
founding group also determine whether colonization increases differentiation
(Whitlock and McCauley 1990). Finding isolation by distance among intermediate
but not among young islands suggests that the appropriate colonization model is
closer to the migrant pool than the propagule pool model (ϕ nearer 0). It also
highlights another difference between our system and the Whitlock-McCauley

model, although this difference strengthens our conclusion that founding events increase differentiation in this metapopulation. In the model, isolation by distance may occur in the colonization phase, but subsequent migration events are assumed to follow the island model. Our system does the opposite. Even though isolation by distance, which may inflate F_{st}, was observed among intermediate islands, the decrease in F_{st} between the young and intermediate age classes was still significant. This suggests that either founder effects are strong (k is small) and/or that subsequent migration rates are high as specified by the Whitlock-McCauley model. Too few studies of metapopulation systems have been carried out to know whether our observations of isolation by distance in relation to age are exceptional or common. However, since the combination of migrant pool colonization and subsequent isolation by distance patterns of migration could impede the detection of increased differentiation arising from colonization, it is possible that other metapopulations displaying migration patterns similar to our system may show no differences in F_{st} among age classes. Further development of the theoretical framework to include the effect of isolation by distance in addition to the effects of extinction and colonization is required.

The analytical form of the metapopulation model and information about age, distances, and gene flow vectors—specific to Skeppsvik Archipelago yet external to the genetic data set—were used to generate hypotheses to test the effects of age, geographical distances, and sources of colonists on the degree of differentiation among island populations of $S.\ dioica$. Turnover and spatial restriction of migration are likely to increase the genetic variances among populations relative to an island model at equilibrium. Environmental heterogeneity among islands arising from differences in the degree of exposure also affects the overall degree of differentiation which, in our case, is seen through the F_{is} values for each island. These results suggest that the sizes of the breeding units of $S.\ dioica$ are small and subject to ecological processes that prevent many of them from reaching demographic or genetic equilibrium. Theoretical models show that variances and covariances of population sizes and of migration and colonization rates can affect the average amount of genetic variance among populations (Whitlock 1992b) and that, ultimately, this will affect the rates and patterns of evolutionary change. Few empirical tests of these models exist, and many more are necessary to advance our understanding of these processes. Species influenced by successional dynamics may represent a rich source of case studies on the evolutionary impact of nonequilibrium processes.

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