Turnover of Vascular Plant Species on Small Islands in Lake Möckeln, South Sweden 1976–1980

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Summary. In 1976, 1978 and 1980 plant species were recorded on 41 forested islands. Apparent species turnover was much higher than true turnover, as was confirmed by recording the age of trees and shrubs in 1980. Extinction rate was negatively correlated with island area and the number of immigrations declined with distance to the mainland. No clear differences in turnover were found for species with different dispersal systems. The proportion of the species populations on an island that consisted of only one individual declined with increasing island area. Conversely, species with 75 or more individuals made up about 17% of the floras on the smallest but about 32% on the largest islands. The results of this study suggest that MacArthur and Wilson's theory of island biogeography is applicable to plants.

Introduction

The theory of island biogeography proposed by MacArthur and Wilson (1967) has been the theoretical framework of many recent empirical studies. However, few of these have tested the theory on plants. Only about 9% of the papers reviewed by Simberloff (1974) concern plants. In a later review (Gilbert 1980) the bias towards animal studies is equally strong.

Gilbert (1980) suggested that 'to demonstrate unequivocally that the MacArthur-Wilson model applies in any particular situation' three criteria must be fulfilled: (i) species number is closely positively correlated with island area; (ii) the number of species on an island does not change with time; (iii) species turnover is occurring.

The first criterion has been repeatedly demonstrated to hold for plants (e.g. Johnsson et al. 1968, Whitehead and Jones 1969, Power 1972, Abbott 1977, Järvinen 1977, McNeill and Cody 1978, Nilsson and Nilsson 1978). The low correlation found by Abbott (1974) between area and number of plant species presumably was caused by his inclusion of islands with different climates in the same correlation analysis.

The second criterion was verified by Abbott (1977) on islands off Australia over a 16–19 year period. Vartiainen (1967) found that the number of plant species increased over a period of 8–10 years on islands in the Gulf of Bothnia, Finland. The reason was that island areas increased due to land elevation (6–7.5 cm in the study period). This, then, was an example of a non-equilibrium situation.

Changes in plant species composition on islands have been recorded (Vartiainen 1967, Whitehead and Jones 1969, Heatwole and Levins 1973, Abbott 1977, 1980, Abbott and Blake 1980).

The study by Abbott (1977) fulfills all Gilbert's (1980) three criteria. However, Abbott (1977) failed to demonstrate the relations suggested by MacArthur and Wilson (1967) between rate of extinction and immigration and island area and isolation, respectively. In theory, extinction rate should decrease with increasing island area and the number of immigrations should decrease with distance from the mainland. It seems clear that detailed studies of species turnover must be made to test the hypothesis of MacArthur and Wilson's theory to see if the theory is applicable to plants or if Abbott's (1977) results could be due to methodological problems (see discussion). Here we report such a study of all vascular plant species on small islands in a lake in South Sweden.

Study Area and Methods

We studied 41 islands, identified on a map in Nilsson (1978), in the central part of Lake Möckeln (about 56°26′N, 14°02′E). Most of the islands are about 125 years old, because the water level of the lake was lowered about 1.8 m in the 1850s. All islands, except the two largest ones, which were grazed until a few decades ago, are covered with densely growing trees. The islands are from 0.03 to 2.19 ha large. Regardless of their area there are three major habitats on the islands. Along the shores there is a belt of a few metres of riparian vegetation with *Alnus glutinosa, Betula* spp. and *Populus tremula* in the three layer and *Myrica gale, Salix* spp. and tree saplings in the shrub layer. The ground is mostly covered with dead leaves and debris that has floated ashore. Sedge *Carex* spp. and other shore species (listed in Nilsson and Nilsson 1978) also occur here or in the second habitat on the very narrow exposed shore outside the trees. Stones are a dominating feature on this poorly vegetated belt. The third major habitat occurs inside the shore and riparian belts. It consists of a dense wood dominated by *Betula* spp., *Populus tremula, Picea abies* and *Pinus sylvestris*. The canopy reaches 15–20, occasionally 25 m high. Tree saplings, *Sorbus aucuparia* and *Rhamnus frangula* are common in the shrub layer. Stones are very frequent all over the islands, covering 5 to 80% of the ground. Characteristics of each island are given in Nilsson and Nilsson (1978).

We surveyed all the islands in the first half of July in 1976, 1978 and 1980. One of us walked around each island along the shore and thereafter searched the inner part of the islands. This was done all the time by the other observer. Each island was searched for about 100 man-minutes per ha, but the five smallest islands were investigated somewhat longer. The census time was a little shorter in 1976 than in the two later years.

In 1978 and 1980 the number of individuals, as seen above ground, of each species on an island was recorded in five abundance categories: a) 1 ind., b) 2 to 9 inds., c) 10 to 25 inds., d) 26 to 74 inds. and e) 75 or more inds. In 1980, if only few individuals of a species were present on an island, a rough estimate of the minimum age of the oldest individual was made in order to ascertain whether that species had been present on the island during our earlier surveys. Obviously, it was impossible to make such estimates for annual species, which, however, made up only a small proportion of the flora (see species list in Nilsson and Nilsson 1978).

When we analysed the data it became apparent that a large proportion of the recorded 'turnover' was, in fact, pseudoturnover, *sensu* Lynch and Johnson (1974). To eliminate this some basis for judgement is needed. We used one of many possible ways to eliminate pseudoturnover. Our procedure will be checked below with regard to its effect on our conclusions and the amount of 'turnover' eliminated. We proceeded as follows:

If a species was recorded in 1976 and 1980 on an island, but not in 1978, it was considered present all the years 1976–80 (98 cases). If a species was recorded in 1976 and 1978, but not in 1980 (110 cases), or recorded in 1978 and 1980, but not in 1976 (134 cases), the species was considered present 1976–80. Thus, if a species was recorded on any 2 out of the 3 visits it was considered to be present at all times. Note that there are about the same number of cases of all three combinations. If 10 or more individuals of a species were recorded in 1978 (7 cases) or 1980 (67 cases) but not in the other years the species was considered present in 1976–80. If a species was only recorded with less than 10 individuals in 1980 on an island, but the oldest individual apparently was more than 3 years (30 cases), it was obviously present 1976–80. Species that were recorded on an island in 1978 only, with 1 to 10 individuals, were considered present in 1976–80 (54 cases). Also, some species that are difficult to see during a census, small species that did not flower during the census period and ferns, grasses and sedges, but were only recorded in 1980 in small (2–9 inds.) populations, but with well developed individuals, were considered present 1976–80 (55 cases).

A species was considered as a certain immigrant if only a small seedling(s) was recorded in 1980, and the species had not been recorded in earlier years on the island. Probable immigrants were species that were recorded on an island only in 1980 with one or a few, small individuals. Possible immigrants were species, which were recorded only in 1980, with one established (flowering) individual on an island. For conspicuous species, also 2 to 9 individuals seen only in 1980, were classified as possible immigrants. Species that were recorded on an island only in 1976, but not in subsequent years, were considered as probably extinct in the period 1976–80 if they were conspicuous, and as possibly extinct if they were inconspicuous (ferns, sedges, grasses and small species that did not flower during the census period).

Extinction rate (ER) was calculated as $ER = 100 \, E/0.5(S_1 + S_2)$ where E is number of extinctions, and S_1 and S_2 is the estimated number of species present on the island in 1976 and 1980, respectively. These estimates were based on all available information from 1976–80 (see above). Turnover rate (TR) was calculated as $TR = 100(E+I)/(S_1 + S_2)$, where I is the number of immigrations. S_1 and S_2 are the same as above, except in the calculations of 'crude turnover', where S_1 and S_2 are number of species seen in 1976 and 1980, respectively. If not otherwise stated, E and I are the sums of certain, probable and possible numbers of extinctions and immigrations, respectively. In the

estimate of 'crude turnover' E is the number of species seen in 1976 but not in 1980 and I is number of species seen in 1980 but not in 1976.

Results

Area-Species Correlations

Our census procedure in 1976 apparently was more efficient on small than on large islands. To see if this affected our conclusions from our previous analysis of the data from that year (Nilsson and Nilsson 1978), we recalculated the regressions between area and number of species estimated to be present in 1980. In addition, we studied the correlation between island area and number of species, with both variables untransformed, because Abbott (1977) reported that he then obtained better fit than when using transformed variables. However, our previous conclusion that log area against number of species best fits our data remained unaltered (cf. Connor and McCoy 1979). The coefficient of determination was unchanged ($r^2 = 0.76$) when we included all species; it was higher (0.79 versus 0.72) when only strictly terrestrial species as well as only shore species (0.36 versus 0.25) were included in the regression analysis using estimated number of species in 1980 instead of the number seen in 1976. The z-values (the slopes of the regression lines between log area and log species number), using number of species in 1980, were 0.319, 0.682 and 0.149 for all, strictly terrestrial and shore species, respectively. The old values (Nilsson and Nilsson 1978) were 0.301, 0.726 and 0.133, respectively, which means that our earlier conclusions of the magnitude and differences between the z-values are unchanged.

Pseudoturnover and its Confirmation

Crude turnover (see methods) is about 15%, much higher than the estimated true turnover (Table 1). Apparently species that are present on an island are not recorded on some censuses.

A check of our classification of pseudoturnover was possible for shrubs and trees. For these 34 species, 20.0% of the total number of species recorded on the islands, fairly accurate estimates of the populations' minimum ages were available for 1980. Of 630 populations, only 78% were recorded on all three census occasions (Table 2). Of the remaining 140 populations 91 were seen in 1980 and estimated to be more than four years old. Only in two cases, one for *Rhamnus frangula* and one for *Vaccinium uliginosum*, was the classification 'pseudoturnover' considered uncertain. Thus, of the cases of apparent turnover that

Table 1. Turnover (%) of plant species populations on the islands between 1976 and 1980. Arithmetic mean with one standard deviation in parenthesis is given

Island size range (ha)	No. of islands	Certain + probable turnover	Certain + probable + possible turnover	Crude "turnover"
0.03–0.12	10	1.64 (1.23)	5.45 (3.65)	15.17 (6.81)
0.12–0.26	10	1.28 (0.97)	4.64 (1.50)	16.81 (4.57)
0.26–0.54	10	1.01 (0.94)	3.53 (1.78)	14.13 (4.09)
0.56–2.19	11	0.93 (0.70)	3.42 (1.67)	13.20 (2.78)
0.03–2.19	41	1.21 (0.98)	4.24 (2.37)	14.78 (4.76)

Table 2. The distribution of pseudoturnover, immigrations and extinctions among trees and shrubs (including dwarf shrubs). A species present on one island was considered as one population

Species	No. of populations	Pseudoturnover		Immigrations	Extinctions
		Species found in 1980	Species not found in 1980		
Picea abies L.	38	0	1	0	0
Pinus sylvestris L.	38	2	3	2	0
Juniperus communis L.	18	5	0	0	0
Populus tremula L.	35	1	0	0	0
Salix aurita L.	41	1	0	0	0
Salix cinerea L.	41	10	0	0	0
Salix caprea L.	4	2	1	0	1
Salix pentandra L.	27	5	5	0	0
Myrica gale L.	41	0	0	0	0
Betula verrucosa Ehrh.	41	0	0	0	0
Betula pubescens Ehrh.	37	18	6	0	1
Alnus glutinosa L.	41	0	0	0	0
Fagus sylvatica L.	4	0	2	0	0
Quercus robur L.	19	7	0	2	1
Quercus petraea Mattuschka	12	4	0	0	1
Ulmus glabra Huds.	1	1	0	0	0
Ribes uva-crispa L.	2	1	0	0	0
Prunus avium L.	3	1	0	0	0
Rubus saxatilis L.	5	2	1	0	0
Rubus idaeus L.	22	1	0	0	0
Rubus nessensis W. Hall	10	3	0	0	1
Sorbus aucuparia L.	33	3	5	2	2
Acer platanoides L.	2	0	0	1	1
Rhamnus frangula L.	22	10	0	1	1
Tilia cordata Mill.	4	3	0	0	0
Vaccinium vitis-idaea L.	21	3	0	1	0
Vaccinium uliginosum L.	24	2	3	0	0
Vaccinium myrtillus L.	28	2	1	0	0
Calluna vulgaris L.	5	1	1	0	0
Empetrum nigrum L.	2	0	0	0	0
Fraxinus excelsior L.	1	0	0	0	1
Solanum dulcamara L.	4	1	0	0	0
Sambucus racemosa L.	1	0	1	0	0
Viburnum opulus L.	2	2	0	0	0
Total	630	91	30	9	10

Fig. 1. Extinction rate on each island in relation to the island's area

Fig. 2. Number of immigrations to each island in relation to the distance of the mainland (only certain plus probable immigrations)

were classified as pseudoturnover and could be checked, at least 98% were correctly classified.

Obviously, some species are more easily overlooked than others (Table 2). Some species of Salix, Betula and Quercus are superficially similar to each other, as is also indicated by the frequent occurrence of pseudoturnover for these species (Table 2).

Extinctions, Immigrations and Turnover

Extinction rate was significantly ($\tau = -0.19$; $p < 0.05$) negatively correlated with island area (Fig. 1), but not with distance to the mainland. In the four-year period of 1976–80 on average 0.54 species (range 0–2) per island were probable extinctions. If we add possible extinctions, 2.85 species (0–8) went extinct on each is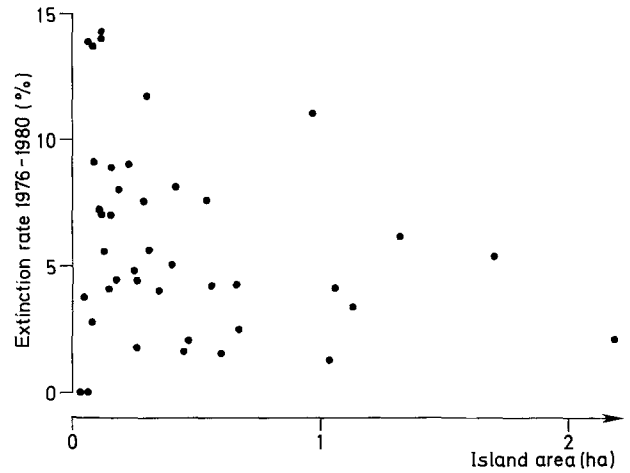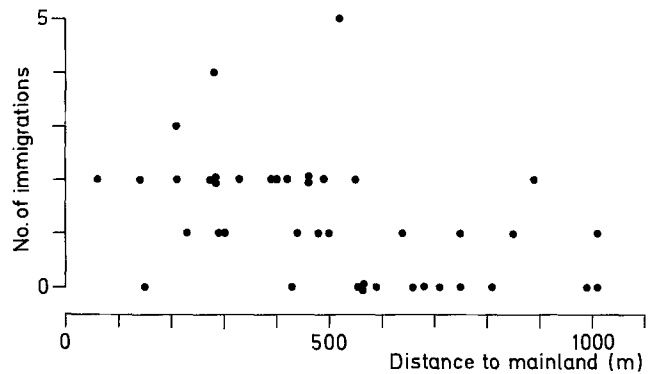land in the same period. There were no statistically significant correlations between either estimate of the number of extinctions and island area (Kendall rank correlation), respectively.

The number of immigrations declines with increasing distance to the mainland (Fig. 2; $\tau = -0.39$: $p < 0.0002$). The number of certain immigrations on average was 0.59 species (range 0–2) on the islands in the period 1976–80. Certain and probable immigrations combined were only slightly higher, 0.73 (0–2). If possible immigrations are included the figure increases to 1.32 (0–5) species per island. Neither measure of immigration was significantly correlated with island area.

The estimated true turnover declines with increasing island area ($\tau = -0.23$; $p < 0.02$) but is not significantly correlated with distance to the mainland ($\tau = -0.10$; $p \approx 0.18$).

Species Population Sizes

On average there were 2.3 (range 0–7) "one-individual-populations" on the islands, this number being independent of island size. However, the proportion of the species populations on an island that consisted of only one individual declined with increasing island size (Table 3; Kendall rank correlation, $\tau = -0.19$; $p < 0.05$). Populations with less than 10 individuals made up about 25% of the species on the smallest and about 21% on the largest islands studied (Table 3). Conversely, species with 75 or more individuals made up 17% only on the smallest islands but 32% on the largest ones.

Table 3. Distribution (%) of species population sizes on different sized islands. Arithmetic mean with one standard deviation in parenthesis. The highest number of individuals that was seen in 1978 or 1980 was used as an estimate of the population size

Size of islands (ha)	Species population size				
	1	2–9	10–25	26–74	≥75
0.03–0.12	5.95 (3.94)	19.73 (4.31)	25.87 (9.20)	31.61 (12.16)	16.83 (11.61)
0.12–0.26	5.30 (3.66)	20.06 (8.44)	26.80 (9.50)	26.19 (5.07)	21.66 (7.40)
0.26–0.54	3.01 (2.47)	17.56 (3.75)	24.34 (5.52)	26.70 (5.37)	28.39 (5.25)
0.56–2.19	3.76 (2.92)	17.74 (2.60)	23.20 (4.54)	22.87 (6.83)	32.43 (8.01)

Table 4. Population parameters in relation to means of dispersal of the species. A species present on one island was considered as one population

Means of dispersal	No. of species on all islands	No. of populations on all islands	No. of colonizations			No. of extinctions		Colonization rate (%)	Extinction rate (%)
			Certain	Probable	Possible	Probable	Possible		
Mechanical disseminations	3	3	0	0	0	0	0	0	0
Ants	10	89	0	0	3	0	8	3.5	9.3
Birds and mammals	24	252	4	2	1	0	9	2.9	3.7
Wind (very small seeds)	15	121	0	3	3	2	3	5.2	4.3
Wind (over snow and ice)	40	427	3	0	2	1	11	1.2	2.8
Wind (pappi)	19	236	6	1	3	12	2	4.4	6.2
Water	59	1,112	8	1	11	10	57	1.8	6.1
All	170	2,240	21	7	23	25	90	2.3	5.3

Appendix 1. Area, distance to mainland, estimated number of species in 1980 (see text), number of probable plus possible extinctions 1976–80, extinction rate, turnover rate and number of certain plus probable plus possible immigrations on the islands in 1976–80

Island no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Area (ha)	0.03	0.05	0.06	0.07	0.08	0.09	0.09	0.11	0.12	0.12	0.12	0.13	0.15	0.16	0.16	0.18	0.19	0.23	0.25	0.26	0.26
Distance to mainland (m)	280	990	660	850	330	420	560	430	140	750	560	280	460	640	490	290	750	230	500	60	710
No. of species	33	32	36	34	36	35	21	40	26	28	42	53	25	42	44	66	24	43	41	57	45
Terrestrial species	2	2	8	11	12	9	6	7	8	7	12	21	12	19	15	38	7	19	18	22	14
No. of extinctions	0	1	0	5	1	5	2	3	4	4	3	3	1	3	4	3	2	4	2	1	2
Extinction rate	0	3.08	0	13.9	2.82	13.7	9.09	7.23	14.3	14.0	7.06	5.61	4.08	6.98	8.89	4.48	8.00	8.99	4.82	1.77	4.35
Turnover rate	3.13	1.54	0	8.33	4.23	9.59	4.55	3.61	10.7	8.77	3.53	6.54	6.12	4.65	6.67	2.99	4.00	5.62	3.61	2.65	2.17
No. of immigrations	2	0	0	1	2	2	0	0	2	1	0	4	2	1	2	1	0	1	1	2	0

Island no.	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41
Area (ha)	0.29	0.30	0.31	0.35	0.40	0.42	0.45	0.47	0.54	0.56	0.60	0.66	0.67	0.97	1.04	1.06	1.13	1.32	1.70	2.19
Distance to mainland (m)	460	590	480	300	210	150	810	560	1,010	390	680	1,010	280	280	520	890	550	400	440	210
No. of species	52	40	52	49	58	47	62	48	63	70	64	69	79	70	82	72	87	79	91	95
Terrestrial species	24	23	17	14	22	20	35	22	31	31	33	34	42	33	48	33	50	38	53	54
No. of extinctions	4	5	3	2	3	4	1	1	5	3	1	3	2	8	1	3	3	5	5	2
Extinction rate	7.55	11.8	5.66	4.04	5.08	8.16	1.63	2.06	7.63	4.26	1.55	4.29	2.52	11.0	1.25	4.14	3.39	6.21	5.38	2.11
Turnover rate	5.66	5.88	3.77	3.03	5.08	4.08	0.81	1.03	3.82	3.55	0.78	2.86	3.14	7.59	3.75	3.45	2.82	4.35	3.23	2.11
No. of immigrations	2	0	1	1	3	0	0	0	0	2	0	1	3	3	5	2	2	2	1	2

Turnover and Means of Dispersal

The species present on the islands are mainly dispersed by water or wind (Table 4), which also are the most easily dispersed species (Nilsson and Nilsson 1978). We found no clear difference in colonization and extinction rates between these easily-dispersed species and animal dispersed species (Table 4). However, all 'turnovers' of ant-dispersed species was only classified as possible (Table 4).

Discussion

Sampling Problems in Plant Turnover Studies

We found that it was easy to overlook species on an island even if it was searched thoroughly. This problem is not generally recognized. However, Vartiainen (1967) admitted that "In some cases the disappearance of a species may have been apparent because a species was not noticed". Another problem is that

individuals of some species may not appear above ground every year (e.g. Gilbert and Lee 1980). The former problem is clearly the most important in our study as was confirmed by the estimates of the age of the populations. Furthermore, we surveyed six of the islands twice in July 1980 and found a pseudoturnover of about 8% (Nilsson and Nilsson, in prep.). Therefore, our measure referred to as crude turnover overestimates true turnover very considerably. It should be noted that crude turnover is the measure used to estimate turnover in other studies. Exceptions are Lynch and Johnson's (1974) and Simberloff's (1976) studies of birds and insects, respectively. They also suggested that true turnover was lower than apparent turnover. Obviously, more attention to methodological aspects is needed in turnover studies.

Effect of Data Manipulation on the Conclusions

How does our data manipulation procedure affect our conclusions? We checked this by using the unmanipulated data to test the two general predictions that extinction rate should decrease with increasing island area and that the number of immigrations should decrease with distance from the mainland. Both these predictions were supported using the unmanipulated data ($\tau \approx -0.309$, $p < 0.005$ and $\tau \approx -0.283$, $p < 0.005$) as well as the manipulated data (see above). Thus, our conclusions seem to be robust and not an effect of our data manipulations.

Population Sizes and Extinction Rate

We found that the proportion of the species populations that consisted of only one individual declined with increasing island area. Such populations clearly have a much higher probability of going extinct than large populations (e.g. Jones and Diamond 1976). We propose that the higher extinction rate on small islands is due to their having a higher proportion one-individual-populations than larger islands. That is, we suggest that, the fact that the proportion of species with only one individual is very similar to the estimated extinction rates (mean = 5.9%) and turnover rates (Table 1), is not just a coincidence.

General, Local and Random Factors

The predictions of MacArthur and Wilson (1967) that the number of immigrations should decline with distance to the mainland, and that the extinction rate should decrease with increasing island area, were confirmed in this study. However, only a small proportion of the total variation in immigration and extinction is statistically explained by these factors. Unaccounted variation may stem from sampling errors and other factors. If random sampling errors are prominent in estimates of extinction and/or immigration of plants, large samples of islands are needed to test the hypothesis. Therefore, the reason why Abbott (1977) did not find the patterns predicted to exist could be his rather small sample size (20). Also, some of the islands studied by him were frequented by sea birds, while others were not, making it even more difficult to test the theory since the two categories of islands were combined. Finally, different observers were responsible for the collection of the data in different periods. This would probably add to the variability in Abbott's data.

Many different factors locally affect the number of plant species per unit area on mainlands (see e.g. Harper 1969, Grime 1973, Harner and Harper 1976, Grime 1979). Therefore, when testing a *general* theory of biogeography, local factors should be eliminated as far as possible. The islands in Lake Möckeln are superficially very similar to each other, even if differences in stoniness and canopy density may explain some of the variations in species number (Nilsson and Nilsson 1978). There are no seabird colonies on the islands studied, and all three major habitats (see above) are present on all islands. Even so, we were only able to explain a small proportion of the variation in immigration and extinction on the basis of a general theory. However, we consider this to be an improvement over the one situation — one explanation approach advocated by Gilbert (1980). His statement "The apparent lack of conformity of the (MacArthur-Wilson) model when any taxon other than that of birds is considered points to a major flaw in its derivation..." is refuted by this study.

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