Temporal and spatial dynamics of waterfowl populations in a wetland area — a community ecological approach

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The temporal (long-term and short-term) and spatial dynamics of the waterfowl populations in the Siikalahti wetland area was studied in the light of competition theory. This theory predicts that in a saturated, resource-limited community ecologically closely related species will show compensatory population dynamics. When considering the southern part of Siikalahti the total pair number of the waterfowl community increased considerably from the period 1946—54 to the period 1980—83, the most successful species being the Coot *Fulica atra,* Pochard *Aythya ferina* and Slavonian Grebe *Podiceps auritus.* Taking the Siikalahti area as a whole two species immigrated between the study periods but none became extinct. In the period 1980—83 considerable yearly variation was observed in both the total density and total biomass of the community, whereas the species diversity (H') and the evennes component (J') of the diversity were rather stable. Diving ducks were the species group that varied most in both total density and total biomass, and grebes the group that varied least. Dabbling ducks and the Coot were intermediate between these groups and had almost the same coefficients of variation for both density and biomass. Compensatory population dynamics, both temporal and spatial, between two species belonging to the same ecological group were rare; the few negative associations found in the spatial relations between two species could be reasonably well explained by the species-specific response to differences in the habitat structure between the sub-areas. The overall spatio-temporal dynamics did not fulfil the prediction that opposite trends will be shown by two species overlapping greatly in two-dimensional (feeding habitat and feeding method) niche space. Altogether the results suggest that in the waterfowl community studied the sizes of the breeding populations of the species are not in resource-defined competitive equilibrium.

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Introduction

The number and abundance of the species that constitute an ecological community are often assumed to be at a certain equilibrium or saturation level. This assumption is based on the competition theory, which stresses the role of interspecific competition in shaping community structure (e.g. MacArthur 1972, Cody 1974, Schoener 1974, 1983, Diamond 1978, Grant & Grant 1982; but for the opposite view see e.g. Wiens 1977, Birch 1979, Rotenberry & Wiens 1980a, b, Wiens & Rotenberry 1980, Simberloff 1982). Community equilibrium has been emphasized especially in studies concerning island biotas (e.g. Diamond 1979, Terborgh & Faaborg 1980). The theory of island biogeography (MacArthur & Wilson 1967) predicts that the number of species in isolated island communities has reached a definite equilibrium level, which is maintained by compensatory local immigration and extinction. Accordingly, in stable resource-limited communities the numbers and abundance of species should be fairly fixed parameters, and the species composition and densities could change only through compensatory events.

The theory of island biogeography was developed for real, well-isolated oceanic islands and archipelagos. Many of its ideas, together with the predictions of the niche theory, can, however, be applied to habitat islands or patchy environments as well (for examples see Haila et al. 1982), although some caution is necessary in applying some of its assumptions to, for instance, bird communities in 'archipelagos' of habitat islands of restricted area (e.g. Coleman et al. 1982, Haila 1983 and papers therein). One can easily imagine that inland lakes and wetland systems function as patchy habitat islands to waterfowl species. There is thus justification for analysing the stability of waterfowl communities of inland lakes within the framework of ideas derived from theories of competition and island biogeography.

The aim of this study is twofold. Firstly, to ascertain whether a condition of equilibrium is suggested by the long-term changes in the structure of the waterfowl community in the southern part of the Siikalahti wetland area, studied by Lindeberg (1957) during the period 1946—54 and by me during four consecutive breeding seasons some 30 years later (1980—83). Secondly, to determine whether the short-term temporal and spatial population dynamics of different waterfowl species indicates any competitive interactions in species abundances and distribution in the wetland area. The niche relations among the waterfowl species breeding at Siikalahti have been considered elsewhere (Pöysä 1983a, b, c). The results of these earlier papers have been used in forming ecologically meaningful groups or guilds (*sensu* Root 1967) of all the 13 species belonging to the community and in predicting competitive relations among the species within each guild.

Study area

Siikalahti, a closed arm of Lake Simpele in SE Finland (61°33'N, 29°33'E), is about 500 ha in total area, including ca. 310 ha of wetland. The water depth does not exceed 1 m at any place and the mean depth in summer ranges from 0.5 to 0.7 m. About 1/5 of the shoreline is bordered by cultivated fields, from which nutrients are washed into the bay, fertilizing the water continuously. The vegetation in Siikalahti has been studied by Venäläinen (1980). The emergent vegetation consists chiefly of extensive stands of *Typha latifolia, Phragmites australis* and *Equisetum fluviatile.* The submerged and floating-leaved vegetation of the open-water areas consists of many plant species, the most important of which are *Sparganium friesii, Potamogeton natans, P. rutilus, P. obtusifolius, Elodea canadensis* and *Drepanocladus tenuinervis.* The dominant plants in the shore meadows are *Carex* spp. and *Salix* spp.

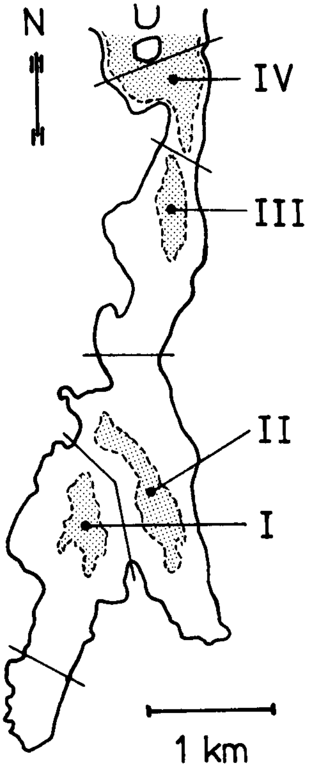

Fig. 1. Siikalahti and its division into four (I—IV) subareas. The dotted areas represent open water and the white areas emergent wetland vegetation.

Siikalahti can be divided into four main open-water areas (together ca. 65 ha), which are surrounded by a varying amount of wetland vegetation (altogether ca. 245 ha) (Fig. 1). The four sub-areas have some differences in their habitat structure (Table 1; see also Pöysä 1983d Table 1). The feeding habitat diversity, which indicates both the luxuriance and the vertical layering of the submerged and floating-leaved vegetation in the open-water areas (see Pöysä 1983a, d) is higher in sub-areas I, II and III than in sub-area IV. The wetland-vegetation area/open-water area ratio is highest in sub-area III and smallest in sub-area IV, sub-areas I and II being fairly similar in this respect. All in all, sub-areas I and II are similar in habitat structure, while sub-areas III and IV differ from them and from each other (see also Pöysä 1983d).

Material and methods

The waterfowl data for the period 1946—54 are derived from Lindeberg (1957) who gives pair numbers for the southern part of Siikalahti (sub-areas I and II in this paper, see Fig. 1). Unfortunately, he does not present the methodology he used in the bird censuses, but his pair numbers are based on five visits to Siikalahti during the study period (see Lindeberg 1954). Furthermore, since Lindeberg's visits to Siikalahti were very late as regards the optimal census period of the waterfowl species, much caution is needed in drawing conclusions about the long-term changes in the community structure. This being the case, only the least questionable changes will be pointed out here.

The data for the period 1980—83 are from my own censuses. Bird censuses were made in 1980 from 2 May to 13 June (16 visits), in 1981 from 7 to 30 May (9 visits), in 1982 from 5 May to 2 June (10 visits) and in 1983 from 3 to 30 May (6 visits). From the census series in 1980 (3 consecutive mornings; repeated 6 times during the census period), an optimal census period was determined for each species on the basis of the size and structure of its population during each series. These periods were used in estimating the size of the breeding populations of waterfowl species in the years 1981—83; the choice of optimal census periods also took account of between-year differences in the break-up of the ice cover and the timing of spring migration. The numbers of breeding pairs were interpreted using the criteria mentioned in Pöysä (1983b, d).

All the diversities were measured using the Shannon function (H'):

Table 1. Feeding habitat diversity (FEHADI) and the ratio of wetland vegetation area to open water area (WEVEAR/OPWAAR) in the four sub-areas. FEHADI and the data for calculation of WEVEAR/OPWAAR are derived from Pöysä (1983d).

	Sub-area			
	I	II	III	IV
FEHADI	1.48	1.51	1.32	0.60
WEVEAR/OPWAAR	4.299	4.322	6.882	1.114

Table 2. Pair numbers of the waterfowl community in the southern part of Siikalahti during the periods 1946—54 and 1980—83. For the period 1946—54 pair numbers are given in the same way as in Lindeberg (1957); for the total pair number mean pair numbers are calculated from the range values; + indicates small population size and ? breeding uncertain.

	1946—54	1980—83	
		mean	range
Great Crested Grebe (GCG), *Podiceps cristatus*	5—10	6.0	5— 7
Slavonian Grebe (SG), *Podiceps auritus*	5	12.8	10—18
Mallard (Ma), *Anas platyrhynchos*	15—20	8.8	5—12
Teal (Te), *Anas crecca*	10—15	16.0	11—23
Garganey (Ga), *Anas querquedula*	10	9.3	9—10
Wigeon (Wi), *Anas penelope*	20—50	16.5	9—29
Pintail (Pi), *Anas acuta*	5	6.3	2— 9
Shoveler (Sh), *Anas clypeata*	5—15	7.0	3—12
Tufted Duck (TD), *Aythya fuligula*	15—20	7.3	5—10
Pochard (Po), *Aythya ferina*	15—30	37.5	24—45
Goldeneye (Go), *Bucephala clangula*	?	2.0	1— 3
Coot (Co), *Fulica atra*	+	62.5	42—92
Total	142.5	192.0	

$$H' = -\sum_{i=1}^{S} p_i \ln p_i,$$

where p_i is the proportion of species i among all the pairs and S is the total number of species in the sample. The evenness component (J') of the diversity was measured with the ratio H'/lnS.

The data from the period 1980—83 were used to compare the waterfowl communities of the four sub-areas over all the four years with the index presented by Järvinen & Väisänen (1976):

$$rD=100\,(\exp(DIV_{diff}-1)),$$

where $DIV_{diff}=H'_{A+B}-1/2(H'_A+H'_B)$. H'_A and H'_B are the diversities of the waterfowl communities in sub-areas A and B, respectively. H'_{A+B} is the diversity of the pooled (A+B) waterfowl community. The value of rD ranges from 0 (communities exactly the same) to 100 (communities completely dissimilar). This over-sub-areas and over-seasons (n= 16) comparison was intended to show how permanent (year-to-year) and relevant were the differences revealed between the sub-areas by the one-year (1980) data of Pöysä (1983d).

The relationships between the population dynamics of two species were analysed using product-moment correlation coefficients. In many cases the sample size was so small (i.e. n=4) that it was practically impossible to demonstrate significant patterns, even if they appeared to exist. In such cases the general trend of the correlations (r= + or —) was noted. Factor analysis (principal axes method, e.g. Cooley & Lohnes 1971) was used to explore the overall spatio-temporal dynamics of the waterfowl populations at Siikalahti. The analysis was performed on a correlation matrix calculated using the densities of the species as variables (n=13) and the different years/sub-areas (n=16) as observations, i.e., the population density of each species in each sub-area and year. With this procedure it was possible to find groups of species that are either associated or disassociated in terms of spatio-temporal population dynamics.

Results

Long-term changes in community structure. The data compared between the periods 1946—54 and 1980—83 are presented in Table 2. The number of regularly breeding waterfowl species in the southern part of Siikalahti was 10 in the earlier period and 12 in the latter. The status of the Goldeneye *Bucephala clangula* and Coot *Fulica atra* is a little uncertain during the earlier period, since both these species may have bred in the southern part of Siikalahti, although they had very small populations. In recent years the Gadwall *Anas strepera* has established a population (1 pair?) at Siikalahti (Koskimies 1983), probably in sub-area I (own observations). The population of the Coot has increased dramatically since the period 1946—54, other species that show an increasing trend being the Pochard *Aythya ferina* and Slavonian Grebe *Podiceps auritus.* The decreasing trend shown by the numbers of the Tufted Duck *Aythya fuligula* also seems to be real, but as regards other species it seems too hazardous to draw any conclusion about long-term changes in population size. However, all in all, it seems warranted to conclude that the total pair number has increased in the southern part of Siikalahti during the period from 1946—54 to 1980—83. In all probability this conclusion also holds true in the northern part of Siikalahti. It may be mentioned here that the Red-necked Grebe *Podiceps grisegena* is a new breeder in the northern part (especially sub-area IV) of Siikalahti (see Koskimies & Sojamo 1976); in summer 1982 this species bred in sub-area III as well.

Short-term changes in community structure. Both total density and total biomass varied considerably between the years in 1980—83, ranging from 82.6 to 122.8 pairs km^{-2} and from 123.3 to 184.4 kg km^{-2}, respectively (Table 3). In terms of both total density and biomass, diving ducks were the species group that varied most and grebes the group that varied least. Dabbling ducks and the Coot had almost the same coefficients of variation for both density and biomass. Species diversity

Table 3. Total densities (pairs km^{-2}) and biomasses (kg km^{-2}), species diversity indices (H') and evenness components of diversity (J') in four years and their coefficients of variation (CV; 100 x (S.D./$\bar{x}$)) for the whole waterfowl community and for different species groups. Weights are derived from Cramp & Simmons (1977).

	1980	1981	1982	1983	CV
Total density					
Whole community	122.8	96.6	82.6	92.3	17.4
Grebes	9.0	8.0	10.6	9.4	11.8
Dabbling ducks	37.0	29.4	21.6	29.7	21.4
Diving ducks	30.2	25.4	22.8	15.4	26.4
Coot	46.6	33.8	27.6	37.9	21.9
Total biomass					
Whole community	184.4	142.0	123.3	133.3	18.4
Grebes	13.7	11.5	13.9	13.7	8.3
Dabbling ducks	46.1	34.6	27.2	35.1	21.8
Diving ducks	54.3	45.0	40.5	27.3	26.8
Coot	70.3	50.9	41.7	57.2	21.8
Diversity (H')	2.009	2.057	2.086	1.985	2.3
Evenness (J')	0.779	0.802	0.813	0.774	2.4

and the evenness component of the diversity were fairly stable during the four-year period, their ranges being 1.985—2.086 and 0.774—0.813, respectively.

Temporal population dynamics. Table 4 summarizes 120 possible species-to-species bivariate correlations calculated on the basis of the yearly densities of each species in the four sub-areas. Since the sample size is small (n=4 years) I have arbitrarily chosen the 0.750 level (positive or negative) for the correlation coefficients presented here. Only 7 of the 120 correlations are statistically significant and of these only 2 are significantly negative, namely those for the Mallard *Anas platyrhynchos* and Pintail *Anas acuta* and for the Teal *Anas crecca* and Pintail in sub-area II within the dabbling ducks group; this is, however, less than would be expected on the basis of chance alone at the $P \leq 0.05$ level: 2/60=0.033. The proportions of negative correlations ($r<0$) among all the possible bivariate correlations within each species group are: 0.750 for grebes; 0.483 for dabbling ducks; 0.500 for diving ducks and 0.386 for the Coot vs. other species. Due to the small sample size it is, however, again possible that a negative (or positive) correlation is the result of chance. Only among grebes is the proportion of negative correlations greater than the binomial probability (P=0.5) allows one to expect, but even in this case it is not significantly greater ($P<0.309$). The negatively associated grebes are the Great Crested Grebe *Podiceps cristatus* and the Slavonian Grebe in sub-areas I and II (not seen in Table 4). Furthermore, there is only one species pair, that of the Coot and Slavonian Grebe, in which a negative association always exists; in the other species pairs the densities show a compensatory effect in some of the four sub-areas, but not in the others (see Table 4).

Table 4. Correlations between yearly densities of some waterfowl species pairs within different species groups in four sub-areas. Only correlation coefficients ≥ 0.750 (+ or —) are given, otherwise only trends (+ or —) are indicated. Species pairs whose correlation coefficients do not reach the 0.750 level in any sub-area have been excluded. The total number of negative correlations ($r<0$) is also given for each species group. The significance levels for the correlation coefficients are: * = $P<0.05$, ** = $P<0.01$, *** = $P<0.001$; (n = 4 in all cases). For species abbreviations, see Table 2; RnG = Red-necked Grebe.

	Subareas			
	I	II	III	IV
Grebes				
GCG—RnG			—	1.00***
Negative/all	1/1	1/1	1/1	0/1
Dabbling ducks				
Ma—Te	—0.788	0.974	+	—
Ma—Wi	—0.922	—	—	0.828
Ma—Pi	—0.855	—0.986*	0.843	—
Ma—Sh	—0.807	—	+	—
Te—Ga	—	—	+	0.816
Te—Pi	+	—0.979*	—	0.000
Te—Sh	+	—	—	0.816
Ga—Wi	—0.866	—	+	+
Ga—Sh	—0.895	0.876	—	+
Wi—Pi	0.827	0.806	—	—
Wi—Sh	0.968*	—	—0.870	+
Pi—Sh	0.807	+	0.778	—
Negative/all	8/15	10/15	6/15	5/15
Diving ducks				
Po—Go	—	—	0.996**	0.992**
Negative/all	3/3	3/3	0/3	0/3
Coot vs. other species				
Co—GCG	+	+	0.856	+
—SG	—	—0.909		
—Ma	—0.883	—	+	+
—Te	0.927	—	—	+
—Ga	—	0.957*	0.856	+
—Pi	+	+	+	—0.808
—Sh	+	+	+	0.808
—TD	—	—	+	—0.905
—Po	0.873	+	—	—
Negative/all	5/11	4/11	4/11	4/11

Spatial population dynamics. In this section, instead of comparing the yearly densities of two species in a certain sub-area, I will compare the distribution of two species among the four sub-areas in different years, again using population densities as dependent variables. Table 5 summarizes the results. The densities of the species in the sub-areas correlate significantly in 6 of the 132 possible comparisons and all of these correlations are positive. Negative correlations ($r<0$) formed the following proportions: 0.667 for gre-

Table 5. Correlations between sub-area densities of some waterfowl species pairs within different species groups in four years. For further explanations, see text in Table 4, and for species abbreviations, see Table 2; RnG = Red-necked Grebe.

	1980	1981	1982	1983
Grebes				
GCG—RnG	0.997***	0.999***	0.989***	0.997***
Negative/all	2/3	2/3	2/3	2/3
Dabbling ducks				
Ma—Te	—0.781	+	0.882	+
Ma—Ga	—	0.757	0.936	0.896
Ma—Wi	—0.927	+	+	+
Ma—Pi	—	0.846	0.843	0.905
Ma—Sh	—	0.839	+	—0.831
Te—Pi	0.900	—	0.827	+
Te—Sh	+	+	—	—0.765
Ga—Pi	+	+	0.915	+
Ga—Sh	+	0.991**	—	—0.852
Wi—Pi	0.886	+	—	+
Wi—Sh	+	+	0.883	+
Pi —Sh	0.814	+	—	—
Negative/all	5/15	1/15	5/15	5/15
Diving ducks				
TD—Po	+	—0.839	—	—
TD—Go	0.756	+	0.998**	+
Po—Go	+	—0.785	—	—0.919
Negative/all	0/3	2/3	2/3	2/3
Coot vs. other species				
Co—GCG	—0.896	—	—	—
—RnG	—0.864	—	—	—
—Te	+	0.915	—	+
—Sh	0.813	+	+	+
—TD	—	—0.938	—	+
—Po	—	0.942	—	+
—Go	—0.783	—	—	—
Negative/all	6/12	6/12	10/12	4/12

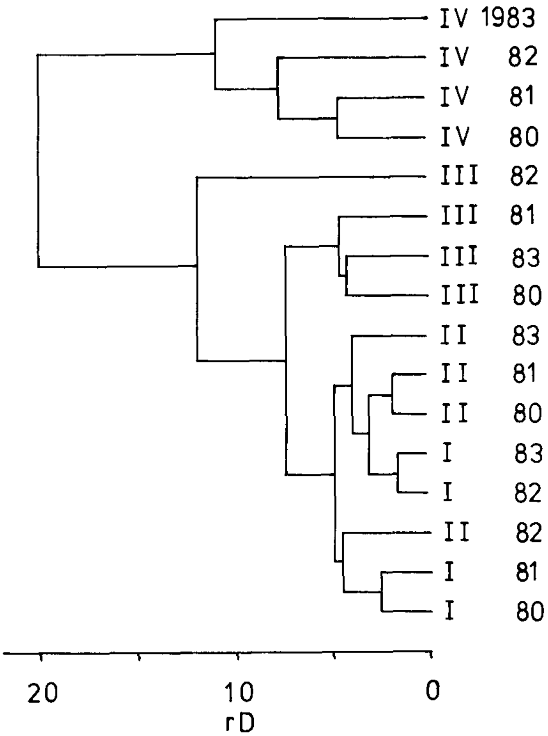

Fig. 2. Similarity of the waterfowl communities of the sub-areas in four different years. Similarity measured with the index rD, explained in Material and methods.

bes, 0.267 for dabbling ducks, 0.500 for diving ducks, 0.542 for the Coot vs. other species. However, for both grebes and the Coot vs. other species the deviation from the binomial expectation is not statistically significant ($P<0.194$ and $P<0.450$, respectively). By contrast, among dabbling ducks the deviation from the binomial expectation toward positive associations is statistically significant ($P<0.0002$). Completely negative series (indicating compensatory changes in densities in every year) were found in the comparisons between the Coot vs. Great Crested Grebe, Red-necked Grebe and Goldeneye, and a largely negative serie between the Coot and Tufted Duck (see Table 5).

Spatio-temporal population dynamics — an overview. We have so far considered the temporal and spatial aspects of the population dynamics as separate phenomena. Before taking an overview of these patterns, let us examine the year-to-year constancy of the differences in the waterfowl community structure between the four sub-areas. Fig. 2 shows that sub-areas IV and III remain distinct from year to year, but that there is some confusion between sub-areas I and II. However, in no case are sub-areas I and II grouped together in the same year. Accordingly, since the major groups are formed on the basis of the sub-areas rather than on the basis of the study years, the four sub-areas can be considered separate, although not independent, sets of populations of waterfowl species in a given year.

The overall pattern of the spatio-temporal dynamics of the waterfowl populations in the space defined by four sub-areas and four years was analysed with factor analysis, and Fig. 3 shows the distribution of the species along the first two factor axes (with eigenvalues of 5.2 for factor 1 and 1.1 for factor 2; which together account for 49.0 % of the total variance in the original data matrix). Two main groups, composed of species with similar spatio-temporal dynamics, can be recognized: A) all dabbling ducks plus the Slavonian Grebe, Pochard and Coot; B) the Great Crested Grebe, Red-necked Grebe, Tufted Duck and Goldeneye. Within group A), the Slavonian Grebe and the Coot behaved somewhat differently from the other species, and in group B) the Tufted

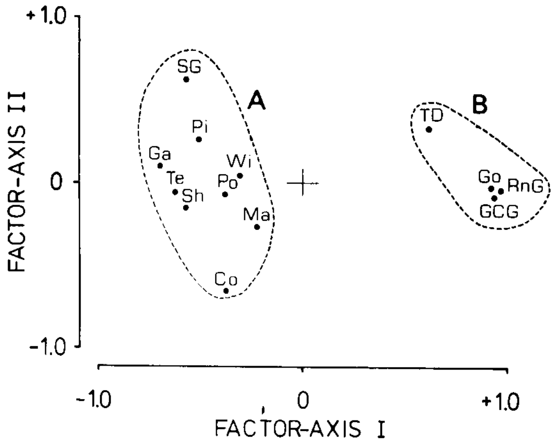

Fig. 3. Distribution of waterfowl species along the first two factor axes describing patterns of spatio-temporal population dynamics. For further explanations, see text and Material and methods, and for species abbreviations, see Table 2; RnG = Red-necked Grebe.

Duck also differed from the other members. In other words, the spatio-temporal population dynamics of two species in the same group (A or B) generally shows a positive association whereas, the association between two species in different groups is generally negative.

Finally, we can examine whether the species that are the most probable competitors from the point of view of niche overlap have the most 'compensatory' spatio-temporal population dynamics. This can be done by comparing the two-dimensional niche overlap values between the species in the niche space defined by the feeding habitats and feeding methods (derived from Pöysä 1983a; Table 5) with the spatio-temporal correlation coefficients calculated for each species pair. In this comparison I will calculate the spatio-temporal correlation coefficients not only for all the four sub-areas (one year/ one sub-area, n=16; the same matrix used in the factor analysis above), but also for sub-areas I and II alone (n=8). This is because differences in habitat structure between the sub-areas may confuse the results when all the areas are considered together. If the spatio-temporal population dynamics shows any competitive interactions, we may expect a negative correlation between the spatio-temporal correlation coefficients and the two-dimensional niche overlaps. Table 6 shows that among grebes and among dabbling ducks there is no support for competitively determined spatio-temporal population dynamics and that even among diving ducks and the Coot vs. other species the support is weak and not statistically significant.

Table 6. Relationship (r) between two-dimensional niche overlaps and correlation coefficients of spatio-temporal population dynamics within different species groups, calculated for all four sub-areas and for sub-areas I and II alone. N indicates the number of species pairs in each species group. None of the correlation coefficients are significant. For further explanations, see text.

	All sub-areas		Sub-areas I and II	
	r	N	r	N
Grebes	0.101	3	—	—
Dabbling ducks	0.508	15	0.011	15
Diving ducks	—0.980	3	0.750	3
Coot vs. other species	—0.072	12	—0.411	11

Discussion

Considerable long-term changes, immigrations, extinctions and fluctuations in population sizes, seem to be a general phenomenon in northern avifaunas (e.g. von Haartman 1973, 1975, Helle & Helle 1979, Järvinen & Väisänen 1977, 1978, Järvinen 1978, Soikkeli & Salo 1979, Järvinen & Ulfstrand 1980). The main factors connected with these changes are alterations of the habitat caused by eutrophiction and cessation of grazing on wetlands, modern forestry and reduced grazing in forests. In at least one case, however, the Heikinjärvenneva peatland area, the bird community has become much richer during the period 1954—74, although the habitat has not changed (Järvinen 1978). As immigrations have dominated over extinctions and population increases over population decreases, the general conclusion may evidently be drawn that the northern bird communities have been unsaturated in the sense of competitive equilibrium (e.g. Järvinen 1978, Haila et al. 1979, Järvinen & Ulfstrand 1980).

What is the position in the Siikalahti wetland area? Although the results may be affected by methodological differences in waterfowl censuses between the two study periods, at least one point seems unquestionable: the waterfowl community in the southern part of Siikalahti has become much richer in terms of the total pair number since the period 1946—54. Some species have immigrated, but none have become extinct. These conclusions also seem to be valid for the waterfowl community of the whole Siikalahti area. The structure of the habitat has changed considerably at Siikalahti during the period 1954—1980. Eutrophication has been accompanied by an increase in the amount and area of the submerged and emergent aquatic vegetation. The cessation of grazing on the shore meadows has allowed the emergent vegetation to grow higher and *Phragmites communis* and *Typha latifolia* stands to increase without check. Luxuriant *Salix* spp. bushes have also become established on the abandoned shore meadows. The cessation of grazing has surely been disadvantageous to the Wigeon, which uses shore meadows with low vegetation as feeding places early in the breeding season (see also von Haartman 1975). It may also have been disadvantageous to the other *Anas* species, as suggested by von Haartman (1975) and Soikkeli & Salo (1979). However, this effect may have been outweighed, or at least balanced, by the increase of the wetland vegetation area in relation to the open water and the increase of the submerged vegetation. This assumption is supported by the fact that the densities of all the dabbling duck species are positively correlated with feeding habitat diversity and the ratio wetland vegetation area/ open water area (Table 7), and with the fact that dabbling ducks in general favour lakes and water areas with extensive and well-developed wetland vegetation (e.g. Danell & Sjöberg 1978, Kaminski & Prince 1981, Murkin et al. 1982, Hudson 1983). The Coot has benefited similarly from these habitat changes (see Pöysä 1983b, d), although the overall increase of this species in southern Finland during the last few decades has certainly also contributed to the population increase at Siikalahti. On the other hand, the increase in the proportion of wetland vegetation has probably made the area less attractive to the Tufted Duck and may be responsible for the slight decrease in its density since the period 1946—54 (see also Table 7).

Table 7. Correlation coefficients for the relationship between the mean densities of the waterfowl species and the two habitat structure variables feeding habitat diversity (FEHADI) and wetland vegetation area/open water area (WEVEAR/OPWAAR) calculated for the four subareas. The significance levels are: * = P<0.05, ** = P<0.01.

	FEHADI	WEVEAR/OPWAAR
Great Crested Grebe	—0.982*	—0.852
Red-necked Grebe	—0.988*	—0.835
Slavonian Grebe	0.719	0.076
Mallard	0.778	0.987*
Teal	0.993**	0.687
Garganey	0.918	0.422
Wigeon	0.848	0.319
Pintail	0.727	0.401
Shoveler	0.920	0.692
Tufted Duck	—0.896	—0.939
Pochard	0.888	0.711
Goldeneye	—0.977*	—0.856
Coot	0.326	0.875

To sum up, the long term changes in community structure have been accompanied by a clear increase in the total pair number from the period 1946—54 to the period 1980—83. The population sizes of the Coot, Pochard and Slavonian Grebe have increased most clearly, while no compensatory changes were found in the population sizes of other species. Accordingly, there was no support for the assumption that the waterfowl community studied was saturated in the sense of the competition theory. As the changes have been so dramatic, it seems unlikely that the waterfowl populations at Siikalahti were able to increase only because the carrying capacity of the area has been raised by eutrophication, i.e. that they were "following" environmental resources (e.g. Herrera 1980).

When comparing the species densities between the two study periods, we are, of cource, faced with the problem that negative species interactions may be masked by similar responses of the species to changes in the habitat structure. If the change in the habitat is advantageous to both the species being compared, then the densities of both species will increase, showing a positive interaction between them, although in reality the species may compete with each other. Accordingly, conclusions concerning competitive interaction that are drawn from long-term changes in community structure may be confused by concurrent changes in habitat structure and productivity. This pitfall can be largely avoided by examining the dynamics of different community parameters and the populations of the constituent species within a reasonably short period. Studies on the short-term dynamics of local avifaunas are not very numerous (but see Järvinen 1979 for the stability of European land bird communities, Karr 1980, 1982 for the stability of bird communities in the tropics, Rotenberry & Wiens 1980b and Wiens & Rotenberry 1980 for the stability of bird communities in shrub steppes). A common message of the analyses made in the tropics and shrub steppes is that the dynamics of the populations and communities do not take place under conditions of equilibrium, i.e. the birds are not existing at their maximum densities, as they should under competitive conditions.

At Siikalahti considerable yearly variation in the total density and biomass of the waterfowl community was observed. Different species groups showed the same pattern. Furthermore, clear, though not statistically significant, compensatory trends in the population densities were found only among grebes and in the species pair of the Coot and Slavonian Grebe. Accordingly, the whole community and its constituent species populations are dynamic on a short-term basis, as well, but compensatory population dynamics between two species are extremely rare. With the short-term dynamics also, one can, of course, speculate that the densities of the populations may be following the environmental resource conditions, i.e., following the shifting competitive equilibrium determined by varying but continuously limiting resources (see e.g. Cody 1980). In the restricted wetland area studied here, the change in resource conditions may be expected to be of nearly the same magnitude in all the four sub-areas. This would mean that the magnitude of the year-to-year changes in total waterfowl density should be similar in the different sub-areas, but the following tabulation shows that this is not the case:

		%	
Sub-area	1980—81	—82	—83
I	-5.5	-5.1	-10.7
II	-10.0	-26.2	-4.3
III	-25.6	-7.5	+59.7
IV	-39.1	-3.6	+18.5

Similarities can be found only in the directions of the changes (note, however, the changes between 1982 and 1983), not in their magnitudes. Although the test used here is indirect and not very rigorous, these findings suggest that the waterfowl populations in the area studied are not closely following changes in the resources via competitive interactions. On the other hand, if we assume that the resources do not change drastically from year to year at Siikalahti, we are compelled to conclude that in view of the great differences in total density and biomass between the study years (e.g. 1980 vs. 1982, Table 3) the community is not in resource-defined competitive equilibrium, or at least not in every breeding seasons (for the so-called "crunch" years hypothesis see Wiens 1977, but see also Schoener 1983).

Examination of the spatial population dynamics is slightly complicated by the fact that there are some differences between the species in the response to the habitat structure, which changes from area to area. This is especially important when one wants to interpret the negative spatial correlations found between the Coot and the four other species, viz., the Great Crested Grebe, Red-necked Grebe, Tufted Duck and Goldeneye (see Table 7). It seems to me that these four species do not respond negatively to the increase in the Coot density itself, but to different structural features of the sub-areas. The high diversity of the feeding habitat and its very dense and well-developed submerged vegetation (in places) are surely disadvantageous to large-sized diving birds, and the smallness of the open-water area in relation to the wetland vegetation area is presumably not very attractive to these species.

With the other species pairs, examination of spatial relations did not give clear evidence of compensatory changes in population densities. On the contrary, the results suggest that the compensatory changes, if any, are more products of chance than the results of negative species interactions. This conclusion is also supported by consideration of the overall spatio-temporal population dynamics of the species and its correlation with niche relations among the species. The correlation was not of the kind predicted by competition theory. Among diving ducks, the seemingly high negative correlation when all the sub-areas were used is evidently a consequence of differences in the species-specific responses to the habitat structure (the Pochard differs from the Tufted Duck and Goldeneye, see Table 7). This is supported by the fact that the same comparison made with data from sub-areas I and II (fairly similar in habitat structure) gave a positive correlation between two-dimensional overlap and the spatio-temporal population dynamics correlation coefficient.

Concluding remarks

In this analysis of the temporal (long-term and short-term) and spatial dynamics of waterfowl populations in a wetland area, I have examined the patterns observed in the light of competition or community theory, attempting to find evidence of competitive interspecific interactions. In general, the results suggest that the system studied is not in competitive equilibrium as regards the densities of the breeding waterfowl populations. The populations of different species appeared to be more or less dynamic both temporally and spatially, but in many cases the patterns observed could be reasonably well interpreted as species-specific or group-specific responses to changing environmental conditions (i.e. habitat structure). Local breeding populations of waterfowl species fluctuate yearly and these fluctuations are mainly the consequences of the weather and water conditions during different stages of the breeding cycle, or of hunting pressure (e.g. Fiala 1972, 1982a, b, Siira & Eskelinen 1983). The results reported here suggest that synecological competitive reasons are of minor importance, at least in the present wetland area.

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Selostus: **Vesilintupopulaatioiden ajallinen ja alueellinen dynamiikka Parikkalan Siikalahdella — yhteisöekologinen lähestymistapa**

Työssä tarkastellaan Parikkalan Siikalahden kosteikkoalueen vesilinnuston ajallista ja alueellista dynamiikkaa kilpailuteorian valossa. Lähtökohtana on kilpailuteoreettinen oletus, että Siikalahden vesilintuyhteisö olisi resurssien määräämässä kilpailullisessa tasapainossa, jolloin teorian mukaan lajistossa ja populaatioiden koossa esiintyvien muutosten, mikäli niitä havaitaan, tulisi olla vastavuoroisia, so. jonkin lajin runsastuessa toisen lajin (todennäköisin kilpailija) populaatiokoko pienenee.

Siikalahti koostuu neljästä erillisestä avovesialueesta ja niitä ympäröivistä kasvillisuusvyöhykkeistä (kuva 1), jotka poikkeavat toisistaan sekä ruokailuhabitaattidiversiteetin (ilmentää uposkasvillisuuden ja kelluslehtikasvillisuuden runsautta ja kerroksellisuutta) että ilmaversoiskasvillisuuden ja avoveden keskinäisen osuuden suhteen (taulukko 1).

Siikalahden eteläosan (osa-alueet I ja II) vesilintuyhteisön kokonaisparimäärä on kasvanut jaksolta 1946—54 jaksolle 1980—83 (taulukko 2). Vaikka menetelmälliset erot vaikeuttavatkin yksittäisten lajien populaatiokoon pitkäaikaismuutosten arviointia, niin selvemmin runsastuneina lajeina voidaan pitää nokikanaa, punasotkaa ja mustakurkku-uikkua ja taantuneena tukkasotkaa. Siikalahtea kokonaisuutena tarkasteltaessa uusia lajeja ovat härkälintu ja harmaasorsa. Kaiken kaikkiaan Siikalahden vesilintuyhteisö näyttää siten runsastuneen sekä laji- että parimäärältään viimeisten vuosikymmenten aikana.

Tarkasteltaessa yhteisön ja eri lajiryhmien lyhytaikaista (1980—83) dynamiikkaa havaitaan sekä kokonaistiheyden että kokonaisbiomassan vaihdelleen varsin voimakkaasti, sukeltajasorsien omatessa suurimman ja uikkujen pienimmän vuotuisen vaihtelun näiden tekijöiden suhteen (taulukko 3). Yhteisön lajidiversiteetti ja diversiteetin tasaisuus pysyivät näinä vuosina varsin vakaina.

Yksittäisten lajipopulaatioiden vastavuoroista lyhytaikaisdynamiikkaa tarkasteltiin laskemalla lajiparittaiset korrelaatiokertoimet vuotuisten tiheyksien suhteen eri osa-alueilla ja erikseen uikuille, puolisukeltajasorsille, sukeltajasorsille sekä nokikanalle suhteessa muihin lajeihin. Ainoastaan kahdessa tapauksessa (sinisorsa — jouhisorsa ja tavi — jouhisorsa) tiheydet korreloivat merkitsevän negatiivisesti, kuitenkin vain yhdellä osa-alueella (taulukko 4). Negatiivisten korrelaatioiden ($r<0$) osuus ei ollut yhdessäkään lajiryhmässä merkitsevästi positiivisten osuutta suurempi, ja kaiken kaikkiaan lyhytaikaisdynamiikkaan perustuva analyysi antoi hyvin vähän tukea kilpailuolettamukselle.

Lajipopulaatioiden vastavuoroista dynamiikkaa tarkasteltiin vastaavalla tavalla myös osa-alueiden suhteen; kahden lajin alueellisia tiheyksiä verrattiin kunakin tutkimusvuonna. Negatiivisten korrelaatioiden osuus oli jälleen samaa suuruusluokkaa tai jopa merkitsevästi pienempi kuin positiivisten korrelaatioiden osuus (taulukko 5). Silkkiuikun, härkälinnun ja telkän tiheydet korreloivat kuitenkin negatiivisesti nokikanan tiheyden kanssa kaikkina neljänä tutkimusvuonna ja tukkasotkankin tiheys kolmena tutkimusvuonna. Havaittujen negatiivisten korrelaatioiden katsotaan kuitenkin selittyvän nokikanan ja näiden neljän lajin erilaisilla (vastakkaisilla) habitaattivaatimuksilla (taulukko 7).

Ajallisen ja alueellisen populaatiodynamiikan yhtäaikaistarkastelussa yhteisön lajit jakaantuivat kahteen ryhmään: A) puolisukeltajasorsat, mustakurkku-uikku, punasotka ja nokikana; B) silkkiuikku, härkälintu, tukkasotka ja telkkä (kuva 3). Lopuksi esitetään kilpailuteoriaan pohjautuva oletus: lajien, jotka ovat suuresti samankaltaisia ruokailupaikkojen ja -tapojen suhteen, tulisi omata vastavuoroinen ajallis-alueellinen dynamiikka populaatioiden tiheyksien suhteen. Tulokset eivät tukeneet oletusta merkitsevästi missään lajiryhmässä (taulukko 6).

Kaiken kaikkiaan tulokset eivät tue olettamusta, että Siikalahden vesilintuyhteisö olisi lajien pesimätiheyksien suhteen resurssien määräämässä kilpailullisessa tasapainossa.

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