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Breeding bird communities along Insular Mediterranean gradients

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ABSTRACT - Frequency, niche expansion, and adaptation of bird species were examined in six habitats sited along vegetational gradients in Corsica, Sicily, Crete and Cyprus (Mediterranean basin), in order to highlight possible patterns of species allocation. A peak in species diversity and total abundance is noticed in the shrubby habitats and an impoverishment in the mature ones. The number of species is proportional to the number of terrestrial breeding birds. Habitat breadth shows the highest values in the shrubby habitats of Corsica, Sicily and Cyprus, but since this pattern is slightly different at Crete, it does not seem to be correlated to isolation degree and island size. The percentage of sedentary species increases in mature habitats; an inverse correlation between habitat breadth and sedentariness seems to point out that sedentary species isolated in mature habitats should expand their ecological niche less than migrant breeders do. Succession rate follows a similar trend over the four gradients, but, according to the insularity degree, species turnover is more complete in Sicily (the largest island), less so in the other insular gradients. Correspondence analysis shows that communities are distributed along the tridimensional space of F_1-F_2-F_3 planes in such a way that F_2 separates the first three habitats from the following ones. In Sicily and Corsica a higher number of species is shared in mature habitats than in Crete and Cyprus; the different sedentary/migrant species ratio in mature habitats and the more xerothermic nature of the sclerophyll forest of the eastern islands might account for the differences in bird allocation recorded on F_1-F_2-F_3 planes.

KEY WORDS : *Successional gradients; Mediterranean islands; Breeding bird communities; Frequency of occurrence; Correspondence analysis*

INTRODUCTION

Studies of avifauna along successional gradients show an increased bird diversity during the first vegetational stages and reduced or stable diversity in the mature ones. The increase is not monotonous along the gradient, generally peaking in the pre-climax stages (e.g. Ferry *et al.*, 1976; Faaborg, 1980; Smith and Mac Mahon, 1981; Glowacinski and Weiner, 1983; Blondel *et al.*, 1988; Wiens, 1989). Therefore over different continental areas of Europe and America, bird density peaks in the mature forest (Helle and Monkkonen, 1990), in disagreement with theory predicting that density is generally correlated to habitat productivity, which in turn peaks in the pre-climax stages (Odum, 1969). In the Mediterranean area bird species diversity peaks in shrubby habitats and decrease in the mature ones (Ferry *et al.*, 1976; Blondel *et al.*, 1988; Lo Valvo and Massa, 1989; Massa, 1990). Contrary to the above pattern, Blondel *et al.* (1988) in the

Corsican shrubby habitats found both the highest species diversity and bird density. The impact of man on the Mediterranean vegetation started 10-12,000 years ago (Le Houérou, 1980), encouraging for several times the formation of garigues and different stages of the Mediterranean maquis, to the detriment of forests. Consequently forests are now relict and fragmented and hold only a restricted number of bird species, generally widespread in Europe, whereas birds inhabiting shrubby habitats are more numerous and well adapted. (Blondel *et al.*, 1988; Blondel, 1990). On the contrary, Central European forests were permanent formations for thousands of years, this accounting for the highest diversity observed there. The aim of our research was to detect the trend of bird diversity along insular Mediterranean gradients, in order to verify the existence of the above described pattern of space partitioning, habitat use and species turnover rate over lands affected by human presence since thousands of years ago.

STUDY AREAS

Bird communities were investigated in four islands, Corsica, Sicily, Crete and Cyprus (Fig. 1), and detected along a successional gradient toward mature forest of typically Mediterranean oaks belonging to *Quercetalia ilicis* association (*Quercion ilicis* alliance in Corsica and Sicily, *Quercion calliprini* alliance in Crete and Cyprus: Quezel, 1988). Each habitat is supposedly derived from the evolution of a previous one and presumably is evenly old in the four islands. The young habitats have their origin in clear felling while older habitats are of various origin, more or less in natural circumstances. Even if the vegetation structure is similar for the four islands, the compounding species are different. Some species (e.g.: *Ceratonia siliqua, Olea europea, Myrtus communis, Pistacia lentiscus*, etc.) are circum-mediterranean, others are widespread on central-western Mediterranean and absent or sporadic in the eastern area, or viceversa; *Quercus ilex*, for example, is episodic at Crete, absent in Cyprus and widespread in Sicily and Corsica; viceversa *Q. brachyphylla* (which some botanists consider to be a simple variety of *Q. pubescens*) is typically east-mediterranean and *Q. alnifolia* is endemic of Cyprus. In the island of Crete *Cupressus sempervirens* is common within some shrubby-arboreal vegetation, and thickets and woods in thermo- and meso-mediterranean stage are constituted by *Q. brachyphylla*, which is a deciduous species. *Q. calliprinos* of eastern Mediterranean is considered more thermophilous than *Q. ilex* (Le Houérou, 1980). The avifauna

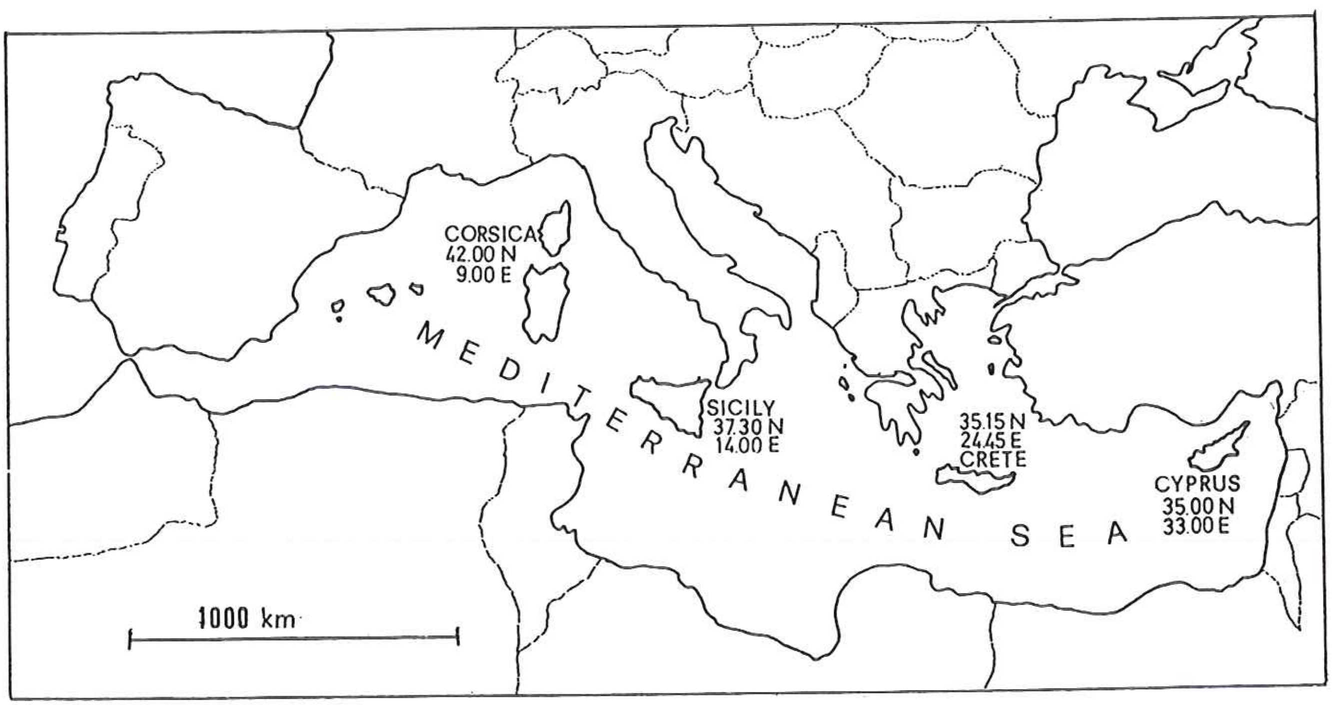

Fig. 1. Mediterranean basin and location of the four islands where bird species were censused.

Table I
Botanical species and vegetation physiognomy characterizing each habitat

Habitat		A	B	a	b	c	d	e	f	species characterizing
grassland										
Corsica	(C01)	1	0.5	+	0	0	0	0	0	*Asphodelus* sp.
Sicily	(SI1)	1	0.5	+	0	0	0	0	0	*Asphodelus* sp.
Crete	(CR1)	1	0.5	+	0	0	0	0	0	*Sarcopoterium* sp., *Asphodelus* sp.
Cyprus	(CY1)	1	0.5	+	0	0	0	0	0	*Stipa tortilis*, *Medicago* sp., *Sarcopoterium* sp., *Asphodelus* sp.
garigue										
Corsica	(C02)	2	0.8	-	-	0	0	0	0	*Cistus* spp.
Sicily	(SI2)	2	0.8	-	-	0	0	0	0	*Calicotome villosa*, *Euphorbia* sp.
Crete	(CR2)	1.8	0.8	-	-	0	0	0	0	*Pistacia* spp., *Euphorbia* sp.
Cyprus	(CY2)	2	0.8	-	-	0	0	0	0	*Cistus* sp., *Sarcopoterium* sp.
low matorral (= maquis)										
Corsica	(C03)	3	1	-	+	+	0	0	0	*Cistus* spp., *Myrtus communis*, *Pistacia lentiscus*, *Calicotome* sp., etc.
Siciliy	(SI3)	2.5	1	-	+	+	0	0	0	*Cistus* spp., *Myrtus communis*, *Pistacia lentiscus*, *Calicotome villosa*, etc.
Crete	(CR3)	2.5	1	-	+	+	0	0	0	*Rhamnus oleoides*, *Euphorbia* sp., *Pistacia* sp., *Cupressus sempervirens*, etc.
Cyprus	(CY3)	2.5	1	-	+	+	0	0	0	*Pistacia* sp., *Cistus* spp., *Genista sphacelata*, *Calicotome* sp., *Scutellaria cyprum*, etc.
high matorral										
Corsica	(C04)	4	3.5	-	-	+	+	0	0	*Arbutus unedo*, *Pistacia lentiscus*, *Erica* spp., etc.
Sicily	(SI4)	4	4	-	-	+	+	0	0	*Arbutus unedo*, *Pistacia lentiscus*, *Myrtus communis*, *Calicotome villosa*, *Quercus ilex*
Crete	(CR4)	3.5	3.2	-	-	+	+	0	0	*Calicotome* sp., *Genista* sp., *Pistacia* sp., *Quercus calliprinos*, *Q. brachyphylla*
Cyprus	(CY4)	4	3.5	-	-	+	+	0	0	*Pistacia* sp., *Olea europaea*, *Arbutus andrachne*, *Pinus brutia*, *Quercus calliprinos*
thicket										
Corsica	(C05)	5	8	-	0	-	-	+	+	*Quercus ilex*, *Pistacia lentiscus*, *Myrtus communis*, *Calicotome* sp.
Sicily	(SI5)	5	8	-	0	-	-	+	+	*Quercus ilex*, *Pistacia lentiscus*, *Myrtus communis*, *Calicotome villosa*
Crete	(CR5)	5	7	-	0	-	-	+	+	*Quercus calliprinos*, *Q. brachyphylla*, *Cupressus sempervirens*, *Chamaecytisus* sp., *Calicotome* sp.
Cyprus	(CY5)	5	7.5	-	0	-	-	+	+	*Quercus calliprinos*, *Q. alnifolia*, *Pinus brutia*, *Arbutus andrachne*
mature wood										
Corsica	(C06)	5	15	-	-	-	0	+	+	*Quercus ilex*
Sicily	(SI6)	5	15	-	-	-	0	+	+	*Quercus ilex*, *Q. pubescens*
Crete	(CR6)	5	15	-	-	-	0	+	+	*Quercus brachyphylla*, *Q. calliprinos*
Cyprus	(CY6)	5	15	-	-	-	0	+	+	*Pinus brutia*, *Quercus calliprinos*, *Q. alnifolia*

Columns a–f are layers.

A = mean number of layers; **B** = mean heigth of vegetation; **a** = grasses (0-0.5 m); **b** = shrubs (0-0.5 m); **c** = shrubs (0.5-1 m); **d** = shrubs (1-4 m); **e** = trees (4-16 m); + = more than 50% of cover; - = less than 50% of cover was censused in six habitats; table I reports botanical species and vegetation physiognomy characterizing each habitat.

MATERIALS AND METHODS

A total of 453 point-counts were carried out: in Corsica, between Ajaccio and Porto, in 1982; in Sicily, in the area of the Madonie Mts, among the villages of Gibilmanna, Collesano, Castelbuono and Cefalù, in 1982 and 1983 (cf. Lo Valvo and Massa, 1989; Massa, 1990); on the northern coast of Crete, between Chania and Sitia, in 1983 and 1984 (by BM); in Cyprus, in the area of Larnaca, Limassol, Paphos and Polis (cf. Massa and Catalisano, 1987; Massa, 1990), in 1986 (by BM in collaboration with A. Catalisano). All the point-counts were located between 50 and 1000 m a.s.l. To remove any bias due to the census area, and to heterogeneous diversity at the edge and central areas of the same habitat (cf. Stamps *et al.*, 1987), the point-count sites were chosen within homogeneous habitats, wide enough to allow comparisons, every effort being made to perform censuses within the habitat and not on its boundaries.

We used the EFP method (Blondel, 1975; Blondel *et al.*, 1981) to obtain the frequency of species occurrence in each habitat. The census technique was chosen for the following reasons: 1) available manpower of the censusing team; 2) mean richness yielded by this method is thought to be a reliable index of the total abundance in the community; 3) the aims of our research were to compare bird communities of similar extensive selected habitats in different areas (cf. Blondel *et al.*, 1981). Breeding birds were detected between 15 May and 15 July for 20 minutes in each point-count; the mere presence or absence of species in each habitat allowed us to achieve a frequency value per habitat. Point-count numbers varied from habitat to habitat and from island to island, with a minimum of 13 and a maximum of 27 per habitat (Table II). These numbers were fixed from the value of a/N, being a the number of species observed in a single point-count, and N the total number of point-counts performed within the same habitat (Ferry, 1976). In all cases a/N was lower than 0.1, thus assuring that differences in point-count numbers were not a bias source in the results (cf. Blondel *et al.*, 1988).

By considering bird species as a variable of the six successional habitats in each island, we performed four factorial analyses of correspondences (AFC) (Benzecri, 1973; cf. Reciprocal Averaging of Hill, 1973) on the species/habitat matrix containing in its lines species frequency for each habitat. This method,which is considered appropriate for ecological analyses of gradients (Legendre and Legendre, 1976; Prodon and Lebreton, 1981; Gauch, 1986; Digby and Kempton, 1987; Blondel *et al.*, 1988), enabled us to highlight on the F1-F2-F3 planes the point-species along the point-habitat gradient. Values on the factorial axes are a good measurement of the species turnover along the gradient: the higher the values, the more complete is the turnover (Prodon and Lebreton, 1981). Intraspecific variance on the F_1 axe corresponds to dispersal ability of each species in the different habitats of the gradient (Chessel *et al.*, 1982); thus we used it for a

Table II

Island area (km²); total number of terrestrial regular breeding birds **(A)**, total number of bird species censused along the whole succesional gradient (**B**), total (S) and mean (s̄) species richness detected in the six habitats selected in the four mediterranean islands; number of point-counts in each habitat (N)

	km²	A	B		HABITATS 1	2	3	4	5	6
CORSICA	8721	82	43	S =	15	16	22	33	24	20
				s̄ =	6	7	8	12	10.5	9
				N =	16	18	19	24	22	19
SICILY	25709	89	52	S =	18	21	25	34	31	24
				s̄ =	6	6.5	7.8	11.5	11	9.5
				N =	18	19	20	27	26	20
CRETE	8222	67	36	S =	12	18	22	27	13	11
				s̄ =	4.5	5	7	7.5	7	6
				N =	13	15	20	22	18	15
CYPRUS	9250	63	34	S =	10	12	13	20	15	17
				s̄ =	5	5.5	5.5	9	7.5	8
				N =	13	14	17	24	18	16

habitat-breadth estimate of the species. Starting from F_1 values of conditional means and standard deviations for each species, we built canonical graphics of habitat-breadth (Chessel *et al.*, 1982). Moreover, in order to compare the four gradients we performed an AFC analysis on a single species/habitat matrix obtained by merging the previous ones, consisting of species frequencies for the overall 24 habitats. Community structure was stated by correlating the log of the frequencies to the species rank. The kind of regression obtained, especially the slope, consents to set and compare the distribution model for species in each habitat. Values of slopes are good indices of evenness (cf.James and Rathbun, 1981); high frequencies in the first ranks are typical of ecological models with high dominance (e.g.: log-series and brocken-stick). Steep slopes indicate low evenness, while soft slopes should match a lognormal distribution and a higher evenness (cf. May, 1975). The succession rate was measured by plotting the regression of log of turnover (TR) against time, being $TR = H'\beta/t_1-t_0$ (Glowacinski and Jarvinen 1975). $H'\beta = 100\ [H'_{(1+2)}-0.5(H'_{(1)}+H'_{(2)})]$, being $H'_{(1+2)}$ the Shannon-Wiener diversity calculated from the combined data of frequencies of two sequential habitats and $H'_{(1)}$ and $H'_{(2)}$ diversity of the two habitats separately. t_1-t_0 is the time interval in years, estimated between a successional habitat and the following (cf. Lo Valvo and Massa, 1989).

RESULTS

Species breeding along the four gradients

Appendix 1 lists all the species detected during the censuses. Four species are present in all the habitats of the Corsican gradient (*Turdus merula*, *T. troglodytes*, *Serinus citrinella* and *Emberiza cirlus*), only two are found in Sicily (*T. troglodytes* and *Carduelis cannabina*), as in the Crete gradient (*Sylvia melanocephala* and *Carduelis cannabina*); a single species (*Oenanthe cypriaca*) is present along the whole Cyprus gradient. Seven species are exclusive of the Corsica gradient, 10 species of the Sicily, three and five respectively of the Crete and Cyprus gradients. Corsica and Sicily gradients share eight species, which are absent from Crete and Cyprus; conversely four species present along the Crete and Cyprus gradients are absent from Corsican and Sicilian habitats. Important differences are observable in the habitat partitioning by some species; for example *Sylvia melanocephala* shows an increasing habitat breadth respectively in Sicily, Corsica and Crete, in the latter also colonizing the mature habitats; its ecological substitute at Cyprus,

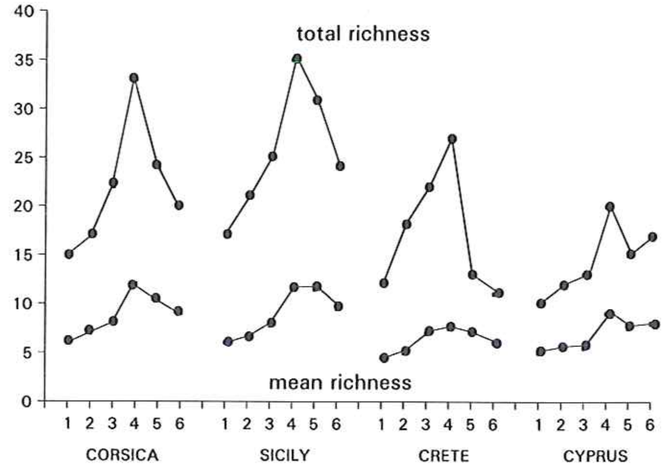

Fig. 2. Trend of total number (= total richness) and mean number (= mean richness) of bird species in the six habitats of the vegetational gradient in Corsica, Sicily, Crete and Cyprus.

S.melanothorax, is limited to the shrubby habitats, as well as *S. rueppelli* at Crete, where it shares the same space with *S. melanocephala*. *Carduelis cannabina* is a very euriecious species along the whole gradients of Sicily and Crete, but not in Cyprus and Corsica. Another finch, *Serinus citrinella*, is regularly present in the Corsican gradient, from CO1 to CO6, as already pointed out by Blondel *et al.* (1988). *Muscicapa striata* shows the maximum habitat breadth in Corsica, whereas it is sporadic in Sicily (SI6) and Crete (CR4). *Aegithalos caudatus* is a species typical of thickets and mature woods in Sicily, but is also widespread in the high matorral of Corsica.

Species richness and evenness

All the gradients share a similar trend of mean and total species richness (Table II, Fig. 2), with a peak in the shrubby habitats and a decrease in the mature ones (habitats 5 and 6). Since mean richness as obtained by the EFP method is thought to be a reliable index of the total abundance in the community (Blondel *et al.*, 1981), we could state that along insular gradients, shrubby habitats share both the highest bird species richness and density. On the whole, 76 species were detected, 52 of which along the Sicilian gradient, 43 in Corsica, 36 in Crete and 34 in Cyprus. These represent 61.8% of the overall terrestrial breeding birds in the four islands (n = 123) and c.55% (range: 53.7%-58.4%) of the birds breeding in each island (cf. Table II). Species number in each habitat is proportional to

Table III
Regression of species frequency model

habitat		CORSICA	SICILY	CRETE	CYPRUS
1	y =	1.119-0.044x r = -0.88	1.139-0.050x r = -0.98	2.082-0.121x r = -0.96	2.266-0.136x r = -0.96
2	y =	1.026-0.032x r = -0.95	1.102-0.049x r = -0.97	1.913-0.060x r = -0.98	1.980-0.064x r = -0.89
3	y =	0.957-0.031x r = -0.93	0.894-0.026x r = -0.97	1.902-0.045x r = -0.97	1.939-0.067x r = -0.94
4	y =	0.989-0.039x r = -0.96	0.899-0.030x r = -0.98	1.961-0.052x r = -0.97	1.902-0.047x r = -0.96
5	y =	0.999-0.036x r = -0.98	0.924-0.031x r = -0.97	2.288-0.107x r = -0.96	2.123-0.043x r = -0.91
6	y =	1.166-0.056x r = -0.97	1.019-0.038x r = -0.97	2.232-0111x r = -0.96	1.983-0.056x r = -0.97

the total number detected along the whole gradient and to global richness of each island, thus higher in Sicily and increasingly lower in Corsica, Crete and Cyprus. Values for mature habitats in Sicily and Corsica result notably higher than in Crete and Cyprus.
Regression between the log of species frequency and species rank (Table III) highlights that shrubby habitats generally yield a higher evenness than pioneer and mature habitats. Small differences are noticed in the values of slopes; namely, while the highest values for Corsica and Crete are found in habitat 2 and 3 (respectively CO2, CO3 and CR2, CR3, CR4), those for Sicily and Cyprus are more shifted toward mature habitats (respectively SI3, SI4, SI5 and CY4, CY5).

Habitat-breadth

The trend of mean habitat breadth is fairly parallel along the gradients of Corsica, Sicily and Cyprus (Fig. 3). CR1 is much higher than CO1, SI1 and CY1, and consequently the trend for Crete is different from those of the other islands. Correlation of habitat breadth along each gradient versus the other ones is good and significant, with the exception of pairs involving Crete (Tab. IV). All the gradients show a similar pattern in the canonical graphics of habitat breadth (Fig. 4), with the highest values in the intermediate habitats. Only that of Crete is truncated in mature habitats.

Species sedentariness

The percentage of sedentary species shows three different patterns (Fig. 5): 1) it lies more or less at high values over the different habitats (Corsica); 2) after a slow decrease in habitats 3 and 4, it increases in 5 and 6 (Cyprus); 3) it regularly increases from 1 to 6, ranging from lowest to highest values (Sicily and especially Crete). The latter is particularly different from the Cyprus one, yielding a noteworthy number of sedentary species in mature habitats, the counterpart habitats of Cyprus showing instead the lowest

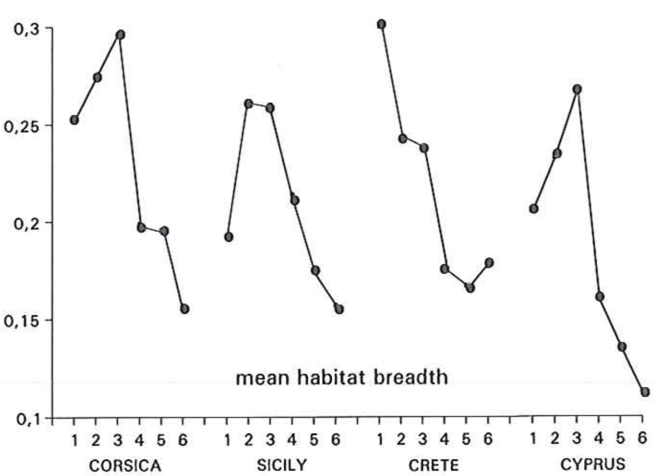

Fig. 3. Trend of mean values of habitat-breadth of breeding birds in the six habitats of the four insular gradients examined.

Table IV
Coefficient of linear correlation of the parameter values of each isle versus the other ones

	Total richness	Mean richness	Habitat breadth	Sedentariness	F1 values
CO/SI	0.96 **	0.97 ***	0.89 **	0.29 NS	0.98 ***
CO/CR	0.71 NS	0.87**	0.67 NS	0.21 NS	0.94 **
CO/CY	0.87 **	0.93 **	0.99 ****	0.49 NS	0.96 **
SI/CR	0.56 NS	0.84 *	0.40 NS	0.98 ***	0.96 **
SI/CY	0.85 *	0.91 **	0.90 **	0.03 NS	0.97 ***
CR/CY	0.44 NS	0.68 NS	0.70 NS	0.09 NS	0.94 **

**** P < 0.0001 *** P < 0.001 ** P < 0.02 * P < 0.05 NS = not significant

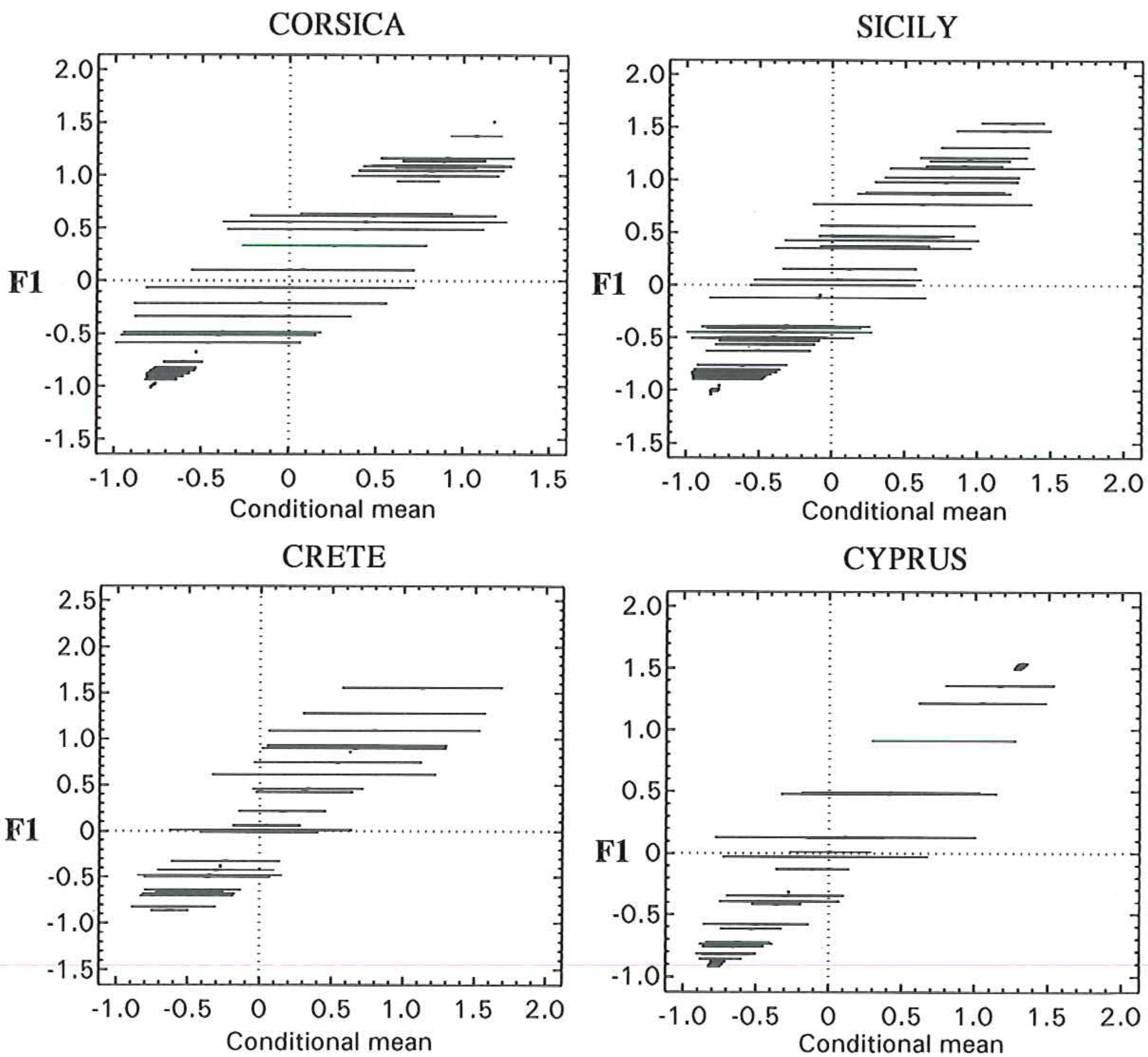

Fig. 4. Canonical graphics of habitat-breadth of breeding birds along the four mediterranean insular gradients; they were obtained by plotting conditional mean against F_1 values of species. Breadth of lines corresponds to values of conditional standard deviation. (cf. Chessel *et al.*, 1982).

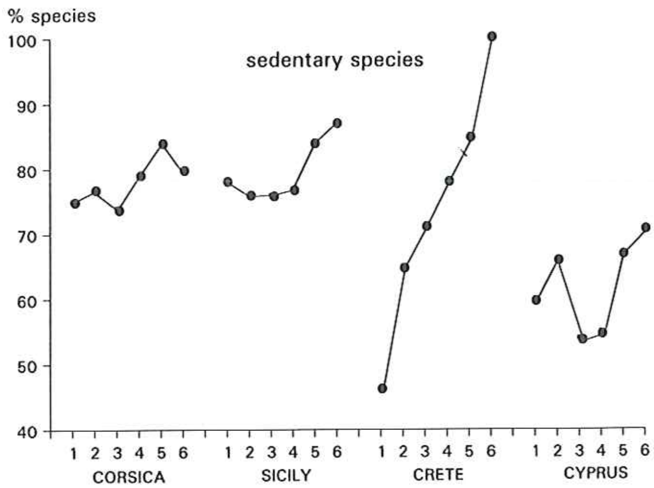

Fig. 5. Trend of percentage of sedentary species in the six habitats of the four mediterranean islands.

Tab. V
Diversity (H'β) and turnover (TR) between the following habitats of the four gradients

		HABITATS 1–2	2–3	3–4	4–5	5–6
Time interval (years)		5	10	18	20	50
CORSICA	H' β =	12.8	20.9	44.2	17.3	20.3
	TR =	2.57	2.09	2.4	0.87	0.41
SICILY	H' β =	25.9	20	30.1	28.1	9.9
	TR =	5.18	2	1.67	1.41	0.2
CRETE	H' β =	39.9	17.7	17.6	25.1	25.1
	TR =	8	1.77	0.98	1.25	0.5
CYPRUS	H' β =	8.9	45.1	30.4	39.2	23.5
	TR =	1.78	4.51	1.69	1.96	0.47

values. Correlation of sedentariness values for each island against those for the other islands is not significant, except for the Sicily-Crete pair (Table IV). Habitat breadth and sedentariness are inversely correlated, yet only values relative to the Crete gradient are statistically significant (SI: $r = -0.61$; P = NS; CO: $r = -0.39$; P = NS; CR: $r = -0.90$; $P = 0.01$; CY: $r = -0.06$; P = NS).

Succession rates

Table V reports the values of time interval, H'β and TR, as calculated for the four gradients. TR decreases regularly in Sicily and Corsica, while it shows a little increase between CR4 and CR5 and two peaks, one between CY1 and CY2 and another between CY4 and CY5, the highest values being in CO1, SI1, CR1 and CY2. Nevertheless all the data from the four gradients merge into a single pattern, when log TR values are plotted against time: the rate of succession decreases monotonously (Fig. 6), the slope of regression being steeper and steeper from Cyprus through Corsica, Crete and Sicily.

Correspondence analysis

The projection of point-species along the point-habitats on the F_1-F_2 plane shows a typically parabolic configuration (Fig. 7). F1 has the dominant value of variance; being related to the vegetational gradient, it exhibits an evident discriminant power between the set of the first three habitats (which always have positive values on F_1) and the last three (which instead have negative values). Values of the variance as explained by the factorial axes F_1-F_2-F_3 are very similar in the four gradients (Corsica: F_1=57.3%; F_2=16.9%; F_3=14%; total=88.2%; Sicily: F_1=56.6%; F_2=21.9%; F_3=11.3%; total=89.8%; Crete: F_1=50.4%; F_2=21.8%; F_3=13.8%; total=86.1%; Cyprus: F_1=50.6%; F_2=26.4%; F_3=12.1%; total=89.1%). Crete shows a more regular ordination of point-species, exhibiting similar distances among the point-habitats, and a pattern of a typical continuum. Point-species of Corsica and Sicily are more scattered and dis-

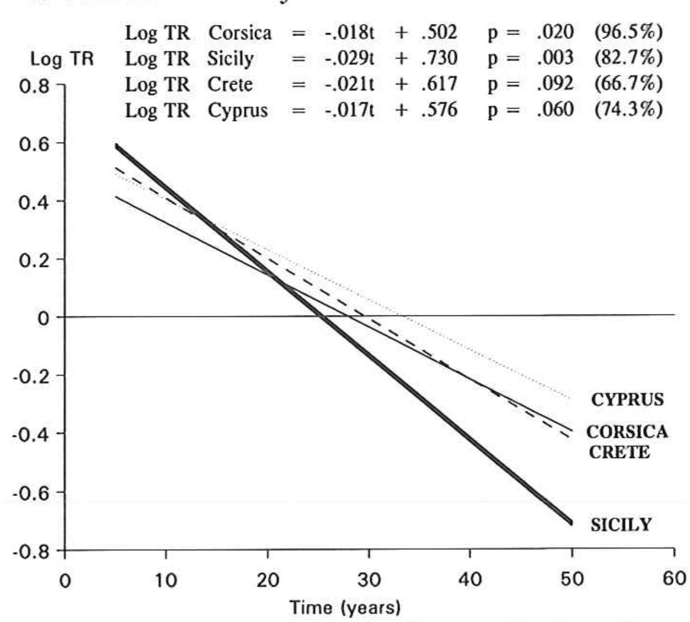

Fig. 6. Succession rate in the four gradients, calculated plotting the values of logTR against time in years. TR = $H'\beta/t_1$-t_0 (cf. Table V).

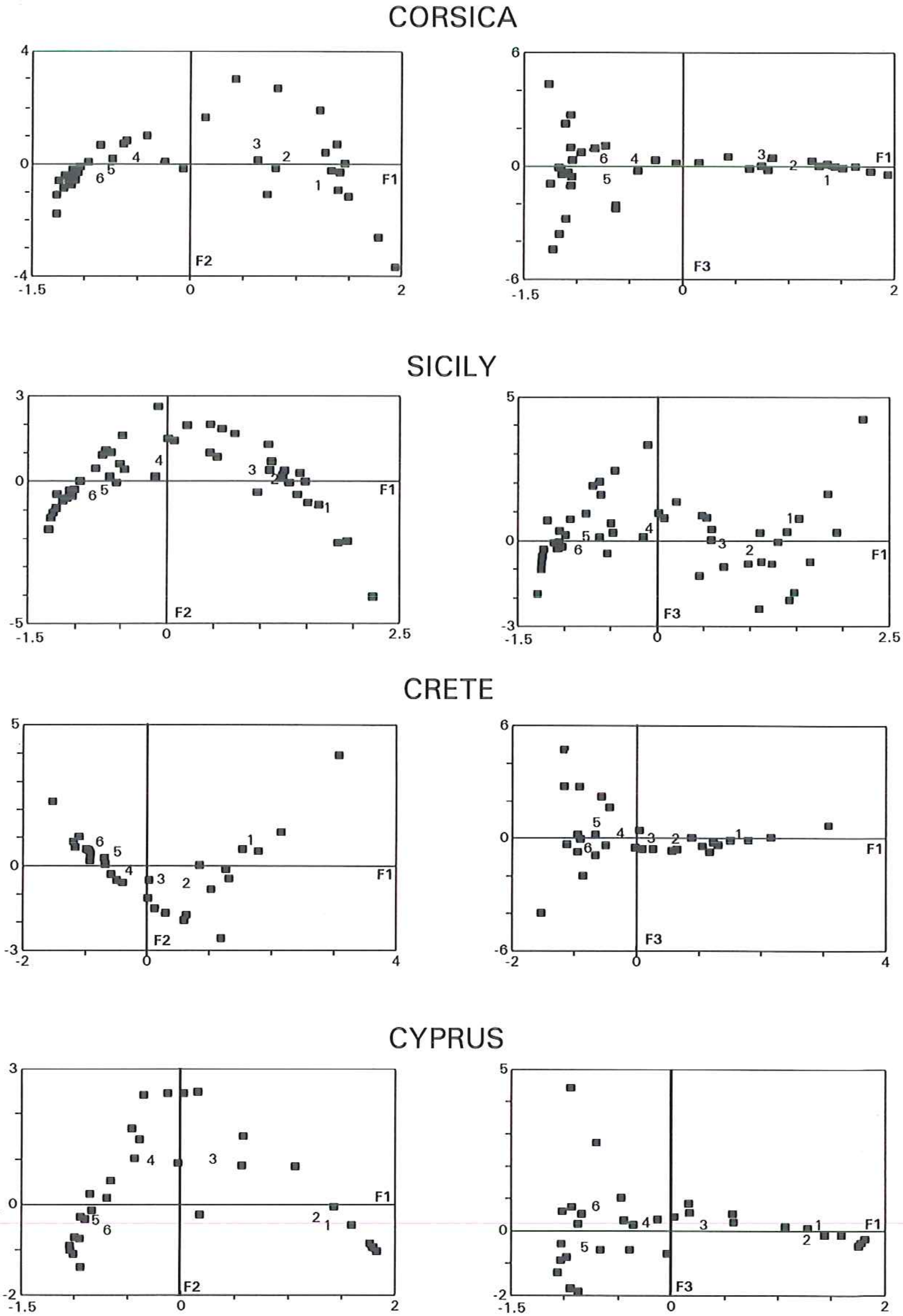

Fig. 7. Projection of the bird species (squares) and habitats (1 to 6) on the F_1-F_2 (left) and F_1-F_3 (right) planes of the correspondence analysis in the four insular gradients.

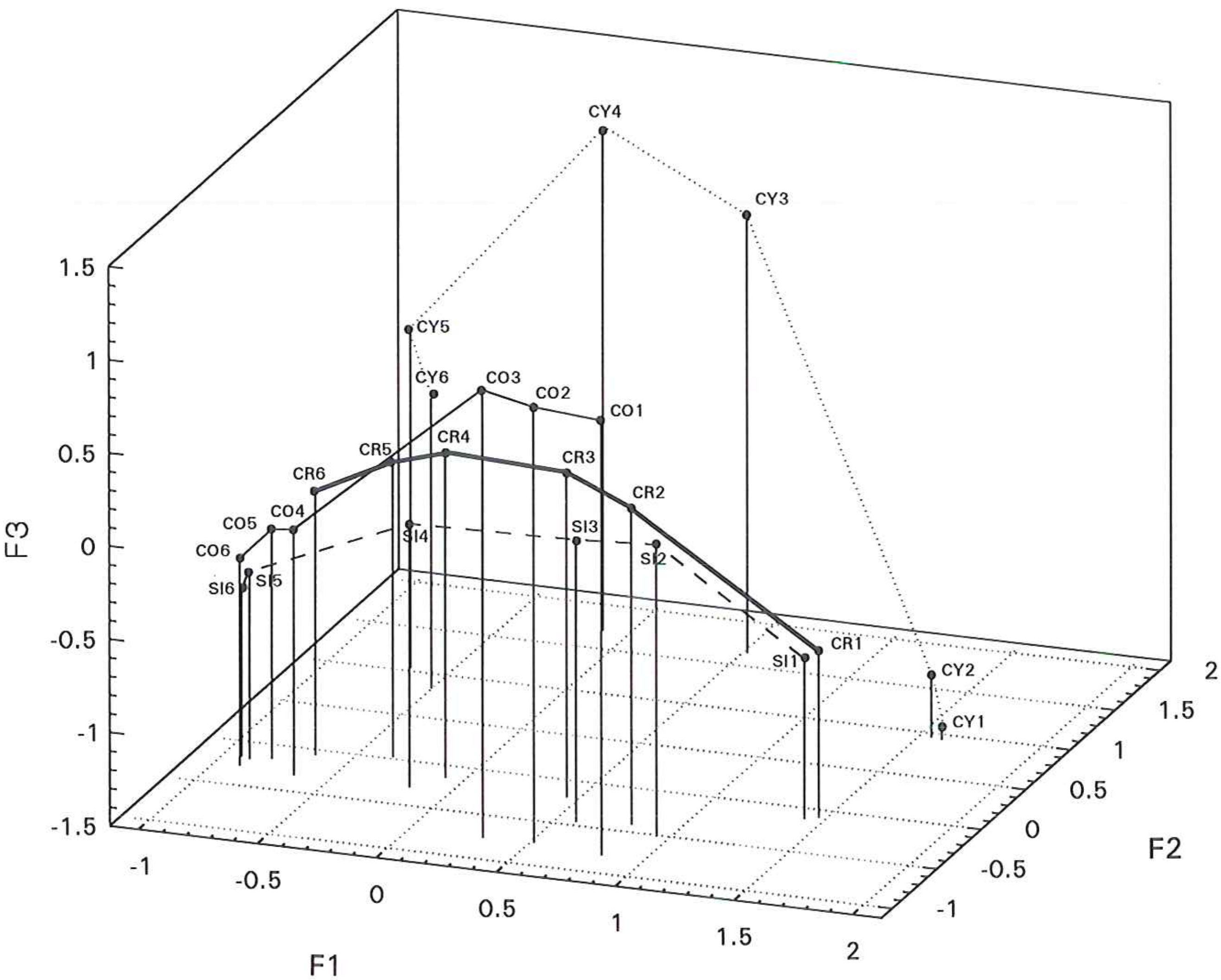

Fig. 8. Ordination on the F_1-F_2-F_3 planes of the six habitats, obtained by correspondence analysis of a cumulative matrix of the four insular gradients.

tributed, in such a way that it is evident a sharp passage between the habitats 1-2-3 and 4-5-6, probably due to a real dissimilarity between the two sets. Finally, the point-species of the Cyprus gradient are much confused and overlapped; in this case three sets of point-habitats are identifiable, namely 1-2, 3-4 and 5-6, dependent on a greater separation by relative bird communities. Distribution of point-species on F_1-F_3 plane is more or less sygmoidal-like in all the gradients.
The projection of 24 point-habitats of the F_1-F_2-F_3 planes (Fig. 8), drawn from a cumulative matrix of the four gradients, still shows the typical parabolic pattern of the gradients, which converge on the mature habitats, as already observed by Blondel *et al.* (1988: Fig. 5). The F_1-F_2-F_3 axes account only for 47% of the total variance (F_1=20.6%; F_2=15.1%; F_3=11.3%), being F_1 inertia scarcely dominant. As in the previous analysis, F_1 plane separates definitely 1-2-3 from 4-5-6 habitat-sets. Nevertheless, what seems more evident in Fig. 8 is the distance of the Cyprus gradient from the other three; in particular the point-species of this gradient seem well distinct on the F_1-F_3 plane, resulting in a separate pattern, with respect to the others.

DISCUSSION

Table IV summarizes correlations of the set of parameters of each island versus the other ones. Many differences between pairs of trends may be observed, in particular in those involving Crete; in spite of their geographical proximity, the Crete-Cyprus pair shows the least similar trends. Altogether, our results lead us to conclude that, even if by multivariate analysis we recognize a pattern of bird allocation rather similar for the four insular gradients, important divergences exist in some parameters of their avian communities. Incidentally, this suggests to be cautious in comparing islands/continent bird data, particularly for the eastern Mediterranean islands.

We try to compare breeding avian communities in similar habitats, as censused in a definite time in different geographical areas. Our censuses satisfy three of the four recommendations by Helle and Monkkonen (1985) for this type of analysis: 1) habitats were selected in such a way that the time interval between analogous of different gradients is of similar length; 2) avifauna was censused in different sites of the same habitat in order to quantify the intra-habitat variability; 3) the census method used was effective (cf. Blondel *et al.*, 1981; Martin, 1983; Bart and Klosiewski, 1989; Petty and Avery, 1990). However, our censuses fail to satisfy the fourth point, since our study takes into account only the breeding season, the influence of temporal variation of communities being unknown. Owing to the lack of winter climatic stress, Mediterranean ecosystems can supply vital resources to large numbers of wintering migrants (Telleria *et al.*, 1988), the majority of which take advantage, in shrubs, of the peaking fruit abundance, which occurs two months later than in Central Europe (Herrera, 1982; Jordano, 1985; Snow and Snow, 1988). The flow of wintering individuals in local populations could modify the community structure of an area and the resource exploitation within a limited time period. Temporal effects may shift communities along the equilibrium-non equilibrium continuum: thus long-term dynamics of communities in a single site might yield very different conclusions from short-term studies of similar communities in different sites scattered over a large area (Jarvinen and Haila, 1981; Wiens, 1984, 1989; Wiens *et al.*, 1986).

Nevertheless, our data on some of the islands were gathered during different years and it is possible that by looking at relative distribution patterns, the effect of annual differences may be minimized. Along two of the four gradients birds were censused during two successive years, respectively 1982-83 (Sicily) and 1983-84 (Crete). Results were divided into two sets and analysed separately, but we failed to find any significant difference between pairs of values (range of correlation between frequency values: 0.91-0.98 in the six habitats); besides, censuses along the Sicilian gradient were repeated in 1989-90, with no important differences being found with respect to those of 1982-83 (range of correlations: 0.92-0.96). Finally, our results for the Corsican gradient are satisfactorily in agreement with those provided by Blondel *et al.* (1988) for the same island; this encourages us to suppose that no significant short-time variation occurs within the bird communities along the gradients here investigated.

Some authors (Ferry *et al.*, 1976; Martin, 1982; Lo Valvo and Massa, 1989) have pointed out the immigration of species from mature habitats of Corsica and Sicily toward shrubby habitats, not balanced by the opposite movement, this accounting for the higher habitat breadth of shrubby species. Our results confirm a general shifting of species toward shrubby and pioneer habitats in insular gradients, so much that all the habitat breadth trends show the highest values in the first three or four habitats, especially in the low shrubby ones. Crete holds just 11 species in mature habitats, 100% of which are sedentary; they are all (with the exception of *Certhia brachydactyla*) able to colonize shrubby habitats, thus increasing habitat breadth values. As a matter of fact, 10 out of 11 species (91%) of CR6 also inhabit CR4 and CR5. This accounts for the significant inverse correlation found at Crete between sedentariness and habitat breadth, as well as the truncated pattern of canonical graphic of habitat breadth (Fig. 4). The trend of graphics for other gradients instead should depend on a lower percentage of species from mature habitats being able to colonize shrubby ones (namely 11/20 = 55% in Corsica, 9/24 = 37.5% in Sicily, and 5/17 = 29% at Cyprus).

Species of the four gradients do not show a habitat expansion related to their geographical isolation: Sicily, separated from the Italian continent by a sound of just 3 Kms, has indeed higher habitat breadth values than Crete and Cyprus, respectively 100 and 70 Kms away from Greece and Turkey. Corsica (80 Kms away from the closest continent) and Sicily show a moderate impoverishment in the mature habitats, while Crete and Cyprus show a dramatic species diminution in the same habitats. Division of ecological space in the four gradients should occur in a different way, and the sole geographical factors do not account for their insularity attributes. Bird turnover rate in the four gradients seems a good index of insularity: more sloped regressions should mean a more complete species turnover rate from habitat 1 to 6. Insular conditions generally have the attribute of an incomplete turnover, some species colonizing the whole gradient, namely habitats 1 to 6, and more species than in continental gradients being present from 1 to 5 or 2 to 6 (Blondel, 1986; Blondel *et al.*, 1988). It resulted more complete in Sicily (the least isolated island and of largest size), less at Crete, Corsica and Cyprus. The slope value recorded in the Sicilian turnover (0.29) lies within the minimum continental ones reported by Glowacinski and Jarvinen (1975).

Sicily revealed more similarities with bird communities of Corsican gradient than with Crete and Cyprus ones. Sicily and Corsica are much different in their paleogeographical, environmental and isolation aspects, and their convergence could be explained by botanical affinity. This is greater between the sets of the habitats of Corsica and Sicily than with those investigated at Crete and Cyprus (note that Sicily and Corsica vegetation alliance, *Q. ilicis*, is different from and less thermophilous than that of Crete and Cyprus, *Q. calliprini*: Le Houérou, 1980); there are also some differences in the botanical aspects of vegetational gradient of Crete and Cyprus, *Q. brachyphylla* being absent from mature habitats sampled at Cyprus. Consequently some differences in the community assemblage could depend just on the botanical differences in the gradients (cf. Rotenberry, 1985 vs. Cody, 1981).

Greater and older human impact on mature habitats of eastern Mediterranean islands, with respect to western ones could account for the higher bird poorness in mature habitats of Crete and Cyprus, with respect to those of Corsica and Sicily. Moreover eastern Mediterranean sclerophyll forest zone has a more xerothermic nature, merging in its drier borders with semiarid and less productive Irano-Turanian steppe formations (Naveh and Lieberman, 1984). Poorness of mature habitats of Crete and Cyprus might depend on their location at the most eastern part of the Mediterranean area, so much influenced by the climate of the Asian steppe areas, which in turn possibly affected the distinctiveness of bird allocation by their communities.

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		CORSICA	ah	SICILY	ah	CRETE	ah	CYPRUS	ah
Alectoris graeca	s			1 2	0.04				
Alectoris rufa	s	1 2 3 4	0.14						
Alectoris chukar	s					2 3 4	0.09	2 3 4 5	0.50
Francolinus francolinus	s							2 3	0.24
Coturnix coturnix	m	1 2	0.02	1	0.00	1	0.00	1 2	0.00
Columba palumbus	s	6	0.00	4 5 6	0.06	4 5 6	0.02	5 6	0.00
Streptopelia turtur	m	4 5	0.01	4 5	0.11	5	0.00	4 5 6	0.04
Cuculus canorus	m	4 5 6	0.01	4 5 6	0.06				
Coracias garrulus	m							4	0.00
Upupa epops	m	4 6	0.02	4 5 6	0.08			4 6	0.04
Picoides major	s	4 5 6	0.01	5 6	0.00				
Jynx torquilla	m	6	0.00						
Melanocorypha calandra	s			1	0.00			1 2	0.00
Calandrella brachydactyla	m			1	0.00	1	0.00	1 2	0.00
Galerida cristata	s			1 2 3	0.10	1 2 3 4	0.41	1 2	0.00
Lullula arborea	s	1 2 3 4	0.14	1 2 3 4	0.24	2 3 4	0.10	6	0.00
Alauda arvensis	m	2 3	0.01						
Anthus campestris	s	1 2 3	0.05	1 3	0.13	1 2 3 4	0.34		
Troglodytes troglodytes	s	1 2 3 4 5 6	0.60	1 2 3 4 5 6	0.56	2 3 4 5 6	0.25	5 6	0.00
Erithacus rubecula	s	4 5 6	0.01	4 5 6	0.08				
Luscinia megarhynchos	m	2 3 4	0.19	2 3 4 5	0.33			3 4	0.06
Phoenicurus ochruros	s			1 2 3 4	0.21				
Saxicola torquata	s	1 2 3 4	0.17	1 2 3 4	0.28	1 2 3 4	0.55		
Oenanthe oenanthe	m	1	0.00	1 2 3	0.08	1 2 3 4	0.15		
Oenanthe hispanica	m					1 2 3	0.31		
Oenanthe cypriaca	m	1 2 3 4 5 6	0.80						
Monticola solitarius	s			1 2 3	0.06	2	0.00		
Turdus merula	s	1 2 3 4 5 6	0.53	2 3 4 5 6	0.41	2 3 4 5 6	0.20		
Turdus viscivorus	s			5 6	0.00				
Cettia cetti	s	3 4	0.29	3 4	0.14	2 3 4	0.09		
Cisticola juncidis	s	1	0.00	2 3 4	0.09	1 3	0.42	1 2	0.00
Hippolais pallida	m					3 4 5	0.15	4 5 6	0.05
Sylvia sarda	s	1 2 3	0.05						
Sylvia undata	s	3 4	0.29	4	0.00				
Sylvia conspicillata	s			1 2 3 4	0.24	1 2 3	0.14		
Sylvia cantillans	m	3 4 5	0.32	2 3 4 5	0.34				
Sylvia melanocephala	s	2 3 4 5	0.42	2 3 4 5	0.22	1 2 3 4 5 6	0.41		
Sylvia melanothorax	m							3 4 5	0.16
Sylvia rueppelli	m					3 4	0.06		
Sylvia communis	m			3 4	0.15				
Sylvia atricapilla	s	4 5 6	0.01	3 4 5 6	0.31	4	0.00		
Phylloscopus collybita	s			5 6	0.00				
Regulus ignicapillus	s	4 5 6	0.01	5 6	0.00				
Muscicapa striata	m	3 4 5 6	0.39	6	0.00	4	0.00	4	0.00
Aegithalos caudatus	s	4 5 6	0.01	5	0.00				
Parus ater	s	4 5 6	0.01					5 6	0.00
Parus caeruleus	s	4 5 6	0.02	4 5 6	0.06	3 4 5 6	0.10		
Parus major	s	3 4 5 6	0.29	3 4 5 6	0.28	3 4 5 6	0.09	4 5 6	0.04
Sitta europaea	s			5 6	0.00				
Certhia familiaris	s	5 6	0.00						
Certhia brachydactyla	s			5 6	0.00	6	0.00	6	0.00
Lanius collurio	m	3 4	0.29						
Lanius senator	m			2 4	0.29	1 2 3 4	0.40		
Lanius nubicus	m							3 4 5 6	0.17
Garrulus glandarius	s	4 5 6	0.02	4 5 6	0.07			5 6	0.00
Pica pica	s			4 5 6	0.12				
Corvus corone	s	5	0.00	4 5 6	0.12	4 5 6	0.05	4 5	0.06
Passer italiae	s	4	0.00			4	0.00		
Passer domesticus	s							4 6	0.03
Passer hispaniolensis	s			4 5	0.10				
Passer montanus	s			4 5	0.11				
Petronia petronia	s			1 2 3	0.07				
Fringilla coelebs	s	4 5 6	0.02	4 5 6	0.06	3 4 5 6	0.11	4 5 6	0.02
Serinus serinus	s	4 5	0.01	3 4 5 6	0.34	4 5	0.03	4 5 6	0.02
Serinus citrinella	s	1 2 3 4 5 6	0.66						
Carduelis chloris	s	3 4 5	0.33	4 5 6	0.09	3 4 6	0.11	3 4 5 6	0.13
Carduelis carduelis	s	1 2 3 4 5	0.50	1 2 3 4 5	0.45	2 3 4 5	0.17	1 2 3 4 6	0.55
Carduelis cannabina	s	1 2 3 4	0.18	1 2 3 4 5 6	0.56	1 2 3 4 5 6	0.61	1 2 3 4	0.37
Emberiza cirlus	s	1 2 3 4 5 6	0.55	2 3 4 5 6	0.46	2 4	0.17		
Emberiza cia	s			2 3 4	0.13				
Emberiza melanocephala	m							3 4	0.08
Emberiza hortulana	m					2 3 4	0.11		
Emberiza caesia	m					2	0.00	3 4	0.07
Miliaria calandra	s	1 2 3 4	0.18	1 2 3 4	0.23	1	0.00	1 2 3	0.19

APPENDIX - List of species censused along the four gradients. Numbers reported in each line refer to habitat in which the species was detected. **s** = sedentary species; **m** = migrant breeding species; **ah** = mean value of habitat breadth.