



Turnover of plants on small islets of the eastern Aegean Sea within two decades

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ABSTRACT

Aim To estimate species turnover of plants on 32 small islands within a 20-year period and to assess possible changes in community composition and properties, such as species richness and factors affecting it, nestedness, species co-occurrence and overall community similarity. Additionally, to assess the possible effects of grazing, gull colonies and fire on turnover values.

Location Thirty-two islets in the eastern Aegean Sea (Greece).

Methods Complete sampling of plants was performed in 1974 and in 1990–94 (mostly in 1994, which was used as the reference year). Species turnover rates were estimated using both per island and per species approaches. Multiple regression was used to evaluate factors affecting species richness. Chi-square tests were applied to compare community composition among sampling periods. The effects of various factors on turnover rates and species richness were examined using one-way ANOVA and ANCOVA. Mann–Whitney tests were applied in order to check for differences between frequencies of occurrence of extinct, immigrant and persisting species. Community nestedness was calculated using BITMATNEST and the C-score index for co-occurrence was estimated using EcoSim7. Species similarities among islands in each of the 1974 and 1994 data sets were assessed using Jaccard's index and the two similarity matrices were compared using a Mantel test.

Results Of 391 species recorded on the islets, 334 were present in 1974, 301 in 1994 and 244 were common to both these periods. Species richness in the 1974 and 1994 data sets was significantly correlated with elevation and area, but not with distance from the nearest large island. Richness was positively affected by grazing, but not by fire or gull colonies. The slopes of species–area and species–elevation regressions were almost identical in 1974 and 1994. Mean relative turnover was 2.06 (species per islet) and 3.26 (islets per species). Turnover was not correlated with area, elevation or distance from the nearest large island. Nestedness and co-occurrence levels were very similar. Tables of islet by islet floral similarity (Jaccard's index) did not differ between the 1974 and 1994 data sets.

Main conclusions The turnover rates found are among the highest recorded for plants; at the same time the islet communities exhibit notable stability in overall properties. Our results provide evidence for rapid shifts in species number that may nonetheless be considered as equilibrial dynamics, as these islets are able to respond rapidly to environmental change and disturbance. Human activities, notably the application of grazing, have a significant complicating effect on community dynamics, enhancing observed turnover rates.

Keywords

Aegean, community dynamics, co-occurrence, extinction, Greece, immigrants, island biogeography, nestedness, species richness, species turnover.

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INTRODUCTION

The dynamics of insular floras and faunas has always been at the centre of biogeographical research, while the equilibrium theory of island biogeography (MacArthur & Wilson, 1967) has offered a robust theoretical background against which many studies have been conducted (see reviews in Lomolino *et al.*, 2005; Whittaker & Fernández-Palacios, 2007). Species turnover, that is the extinction of some species (in the sense of disappearance from a particular island) and their replacement by other species, is a central process of the MacArthur–Wilson theory (MacArthur & Wilson, 1967), according to which species richness on islands is the outcome of the balance between immigration and extinction rates. Many authors have attempted to document species turnover on real or ‘habitat’ islands (e.g. Diamond, 1969, 1971; Heatwole & Levins, 1973; Abbott, 1977; Brown & Kodric-Brown, 1977; Diamond & May, 1977; Abbott & Black, 1980; Nilsson & Nilsson, 1982; Flood & Heatwole, 1986; Brown & Dinsmore, 1988; Rogers & Morrison, 1994; Vidal *et al.*, 2000; Krieger *et al.*, 2003; Morrison, 2003; Cody, 2006; Foufopoulos & Mayer, 2007) or even through experimental manipulation (Simberloff & Wilson, 1969, 1970; Robinson & Quinn, 1988). Calculation of turnover depends on reliable species monitoring and on sampling intervals (Diamond & May, 1977; Whittaker *et al.*, 1989; Whittaker & Fernández-Palacios, 2007). Long-term studies have been reported by Diamond (1969), Abbott & Grant (1976), Abbott (1977), Abbott & Black (1980), McCoy (1982), Herwitz *et al.* (1996), Jerling (1998) and Cody (2006), but most studies are confined to a narrower time-scale, especially when the study area consists of islands that are hard to access. The estimated turnover rate is always an approximation of the real value due to the confounding effects of cryptoturnover (undetected turnover in between actual samplings; Simberloff, 1976) and pseudoturnover (species present but not detected during at least one sampling period; Lynch & Johnson, 1974; Abbott, 1983).

According to the equilibrium theory of island biogeography (MacArthur & Wilson, 1967), maximum turnover rates should be expected in small islands lying near to species source pools, while minimum turnover should be found in large and isolated islands. Obviously this is because small islands experience higher extinction rates and islands closer to species sources are subject to higher immigration rates.

Whittaker (2000) presented a conceptual scheme regarding extremes of species turnover according to different perceptions of insular dynamics, and argued for the recognition of both equilibrium and non-equilibrium island systems, suggesting that non-equilibrium dynamics may be more important than recognized in the MacArthur–Wilson theory. Scepticism on the estimation of turnover rate and the validity of equilibrium theory has been expressed by Gilbert (1980), while Heaney (2000) suggested that the existence of long-term equilibrium in remote island archipelagos is unlikely and proposed a tripartite model of island biogeography, taking into account evolutionary processes as well as immigration and extinction (see also

Losos & Schluter, 2000). These reservations notwithstanding, the study of community change in time remains an important tool towards understanding the processes structuring insular ecosystems.

Biotic communities exhibit several patterns emerging from processes of community assembly, such as nestedness (see Wright *et al.*, 1998) and species co-occurrence patterns (Gotelli, 2000). According to certain approaches, even species–area functions can be seen as process-driven patterns (e.g. Rosenzweig, 1995). The behaviour of such community-level patterns on islands experiencing turnover has not been worked out in detail yet. We would expect, though, that for islands near equilibrium, overall community structure should remain more or less stable over time while species turnover continues to occur.

Small islands (islets from now on) are of great value for such studies since immigration/extinction processes take place at a smaller temporal scale in comparison to larger islands. The deviation of many islets from ‘normal’ species–area patterns, whereby they show the so-called small island effect (Whitehead & Jones, 1969; Lomolino & Weiser, 2001; Triantis *et al.*, 2006) of a lack of a positive species–area relationship below a threshold island area, is directly related to increased extinction rates due to their vulnerability in extreme environmental perturbations and to the small, hence unstable, populations these islands can host (demographic stochasticity). Actually, MacArthur & Wilson (1967, p. 30) had suggested that extinction on such very small islands would be independent of area.

In this paper, we examine the plant communities of 32 small islets of the eastern Aegean (Greece) at the beginning and at the end of a 20-year period, in an attempt to document floristic and other structural changes concerning several aspects of plant community dynamics. How does the change in community composition (with respect to growth forms and salt tolerance) interplay with the overall community properties of insular biota? Our work addresses this question using methodological tools applied on these two levels of community organization (species composition and overall community properties), in an attempt to promote our understanding of the mechanisms involved in such temporal community dynamics. Community-level properties include, *inter alia*, species richness, nestedness and overall patterns of species co-occurrence, all of which may vary independently of community composition. A possible stability of community properties in the presence of high species turnover would provide strong evidence in favour of equilibrial dynamics (cf. Abbott, 1983).

Detailed and repeated published observations on the flora of Aegean islets are restricted to the studies by Snogerup & Snogerup (1987, 2004) and Höner & Greuter (1988). Similar studies on other Mediterranean islands have been carried out by Médail & Vidal (1998) and Vidal *et al.* (2000), who focused on the effect of gull colonies on the turnover of plant species. Lloret *et al.* (2005) studied species attributes and invasion success by alien plants on five large Mediterranean islands,

whereas García *et al.* (2002) studied the influence of gulls on chenopod shrub distribution in semi-arid Mediterranean islands. In a related framework, Lambdon & Hulme (2006) studied the interactions between invaders and congenics on the islands of the Mediterranean Basin, whereas Livanou-Tiniakou *et al.* (2003) and Bocchieri (1998) emphasized the remarkable changes in species composition on Mediterranean islands and islets through time. Finally, Panitsa *et al.* (1994, 2006), Panitsa & Tzanoudakis (2001), Snogerup & Snogerup (2004) and Bergmeier & Dimopoulos (2003) have identified grazing as an important factor shaping plant communities on Aegean islets. On this basis, we also explore the effects on floristic changes of grazing, the presence of gull colonies and fires.

The main questions addressed herein are: (1) what are the per species and per island turnover rates of plants on the small islets studied, (2) are the factors affecting species richness the same in the two sampling periods, (3) have the community-level properties changed in the 20-year period, (4) has the overall community composition changed in this period, and (5) what is the role of factors like grazing, fire and gull colonies in the plant community processes on these islets?

MATERIALS AND METHODS

Detailed censuses of plant taxa present on 32 islets (Fig. 1) lying around four larger inhabited islands of the eastern Aegean Sea (namely Agathonisi, Arkoi, Leros and Kalymnos) were performed in 1974 by the Swedish botanists Hans

Runemark and Roland von Bothmer (unpublished data), who kindly offered us their data set (see Acknowledgements). The same islets were again explored in detail by the authors (M.P. and D.T.) in the 1990s (visits to islets took place from 1990 to 1994, but most sampling was undertaken in 1994, which we use as the reference year from now on). Abbott (1983) considers the conduct of censuses by the same researchers crucial for studies of turnover in order to avoid pseudoturnover due to different sampling efforts. Nevertheless, given the very small total surface of each islet that makes possible a complete census by the researcher, in combination with the fact that both censuses were carried out by experienced botanists, we believe that pseudoturnover is not an important issue for our work. On the other hand, cryptoturnover cannot be excluded, as is the case in virtually every study of turnover on real islands. However, since the rates of turnover we detected (see Results) are already very high, the addition of cryptoturnover would serve to reinforce the conclusions of this study. Another possible cause of bias in turnover estimates comes from taxonomical changes between the two censuses ('taxonomical turnover'). Our results do not suffer from such a bias, since material collected by H. Runemark and R. von Bothmer has been thoroughly studied by one of the authors (M.P.) during a 1-month visit to Sweden, so that the taxonomical assignment of all species collected in both sampling periods has followed the same approach. Nomenclature follows Davis (1965–1985), Strid & Tan (1997, 2002) and Greuter *et al.* (1984, 1986, 1989), updated where necessary from more recent publications (Böhling & Scholz, 2003; Chilton & Turland, 2004).

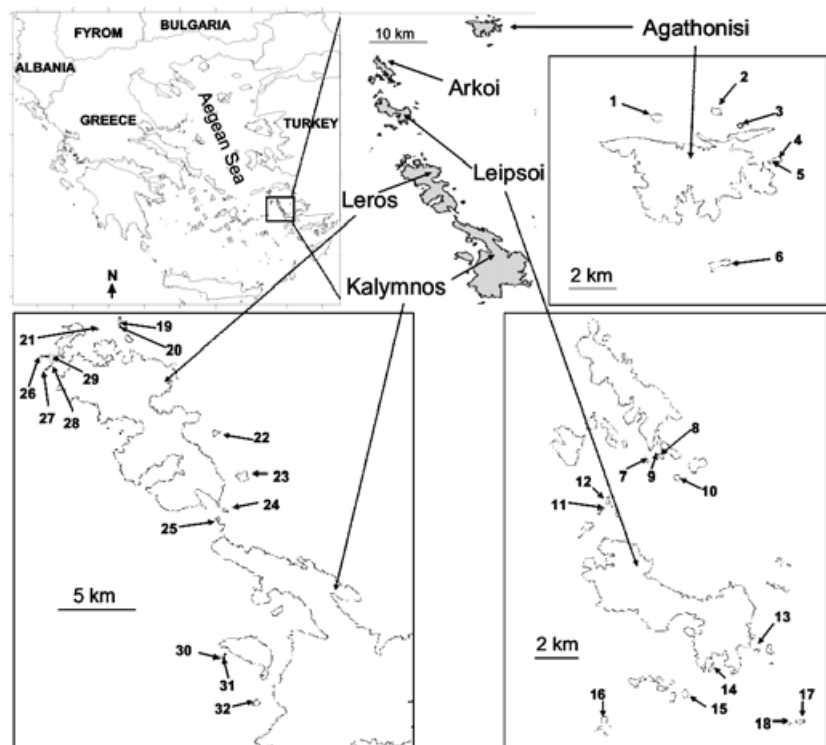


Figure 1 Map of the study area. Islets are indicated by arrows. Numbers are as in Table 1.

The area of the islets ranges from 0.002 to 0.23 km². In this part of the east Aegean area, sea depth does not exceed 100 m. Consequently, the islets were part of a continuous land mass encompassing most of the eastern Aegean islands and Asia Minor during Pleistocene glacial periods (Dermitzakis, 1990). More information regarding the flora, geology and climate of the area studied is given by Panitsa (1997) and Panitsa & Tzanoudakis (1997, 1998, 2001). Names, geographical coordinates, total surface area (*A*), species richness recorded by H. Runemark and R. von Bothmer (*S*₇₄), species richness recorded by us (*S*₉₄), shortest distance from the nearest large inhabited island (*D*), maximum elevation (*E*), application of grazing (GR), presence of breeding gull colonies (GU) and evidence of fire (F) for all islets are given in Table 1. The latter three variables have been coded in binary form (presence–absence), even though it is reasonable to assume that their intensity may vary from islet to islet, as well as in time.

Nevertheless, given the small size of the islets studied and the relatively short intercensus period (20 years), such variations would not affect our results to any significant degree. In fact, locals move grazing animals from islet to islet every few years, but not all islets are used (due to accessibility or proprietorship issues). In addition, the number of grazing animals is usually low (usually between 5 and 10), albeit with significant effects on vegetation due to the small size of the islets. Fire, too, when applied, affects a significant part of each islet, and the same is true for gull colonies, where present. Therefore, the effects of these factors are evident even if an islet had been grazed or burned a few years before the last census. Documentation of the relative intensity of these factors would be critical, of course, if the islets spanned a larger area range and if the study covered a larger time period. We use records of these factors made during the most recent survey in order to document effects during the time period between the surveys. It has to be

Table 1 Geographical data for the islets studied and values of species richness, turnover rates and application of grazing, breeding gull colonies and evidence for fire.

	Island name	<i>A</i> (km ²)	<i>E</i> (m)	<i>D</i> (km)	<i>S</i> ₇₄	<i>S</i> ₉₄	<i>S</i> _{pooled}	<i>I</i>	<i>E</i>	<i>S</i> ₂	<i>R</i> _t	Fire	Grazing	Gulls
1	Psathonisi	0.127	10	0.7	38	35	44	9	6	0.375	1.027	N	Y	Y
2	Stroggyli	0.096	20	1.1	58	40	63	23	5	0.700	1.428	N	Y	N
3	Prassonisi	0.011	2	1.3	10	11	14	3	4	0.175	1.667	N	N	N
4	Katsagani	0.090	30	0.2	64	42	72	30	8	0.950	1.792	N	Y	N
5	Katsaganaki	0.002	10	0.1	13	15	17	2	4	0.150	1.071	N	N	Y
6	Kounelonisi	0.230	50	1.7	53	45	59	14	6	0.500	1.020	N	Y	N
7	Minaronisi	0.021	20	0.4	40	26	46	20	6	0.650	1.970	N	Y	Y
8	Zouka (Megali)	0.028	20	0.4	59	65	96	21	27	1.200	1.935	Y	Y	N
9	Zouka (Mikri)	0.008	15	0.2	63	57	80	24	18	1.050	1.750	N	Y	N
10	Psathi	0.052	20	1.5	46	55	83	28	37	1.625	3.218	Y	Y	N
11	Kommeno nisi	0.028	10	1.2	24	28	33	5	9	0.350	1.346	N	N	Y
12	Spartonisi	0.025	15	1.3	25	31	38	8	14	0.550	1.964	N	Y	N
13	Kouloura	0.078	20	0.7	57	69	75	7	19	0.650	1.032	N	Y	N
14	Lyra	0.050	40	0.2	41	46	56	10	15	0.625	1.437	Y	Y	N
15	Psonos	0.071	30	1.3	47	59	93	35	47	2.050	3.868	Y	Y	N
16	Fragkonisi	0.225	75	4	53	87	103	16	50	1.650	2.357	Y	Y	N
17	Kalapodi megalo	0.039	25	3.2	42	40	55	15	13	0.700	1.707	Y	Y	Y
18	Kalapodi mikro	0.005	5	3.1	12	9	13	4	1	0.125	1.190	N	N	Y
19	Trypiti megali	0.072	30	1	38	59	78	19	40	1.475	3.041	N	Y	Y
20	Trypiti mikri	0.020	15	0.8	26	37	46	9	22	0.775	2.461	N	N	Y
21	Plakousa	0.050	10	0.6	17	13	26	13	9	0.550	3.667	N	N	Y
22	Agia Kyriaki 1	0.150	76	1.3	60	74	82	8	22	0.750	1.119	N	Y	N
23	Piganousa	0.350	139	0.7	100	89	130	41	31	1.800	1.905	Y	Y	N
24	Velona	0.070	15	0.3	62	57	90	33	28	1.525	2.563	N	Y	N
25	Glaronisi (north)	0.030	15	0.7	59	50	84	34	27	1.525	2.798	N	Y	Y
26	Faradonisi NW	0.040	10	1.3	30	31	41	10	11	0.525	1.721	N	N	Y
27	Faradonisi SW	0.020	10	0.9	19	15	25	10	6	0.400	2.353	N	N	Y
28	Faradonisi S	0.025	5	0.7	23	18	31	13	8	0.525	2.561	N	N	Y
29	Faradonisi megalo	0.160	55	0.8	59	45	81	44	24	1.700	3.269	Y	Y	Y
30	Apano nisi 1	0.079	30	0.4	69	51	84	33	15	1.200	2.000	N	Y	Y
31	Apano nisi 2	0.016	10	0.3	27	22	35	13	8	0.525	2.143	N	N	Y
32	Agia Kyriaki 2	0.150	60	1	49	53	76	23	27	1.250	2.451	N	Y	N

A, area; *E*, elevation; *D*, distance from nearest large island; *S*, species richness (in 1974, 1994 and both censuses pooled); *I*, number of species present only in last census; *E*, number of species present only in first census; *S*₂, absolute turnover per time; *R*_t, relative turnover rate (see text for formulae). N = no; Y = yes.

noted, also, that grazing and fire are usually interrelated (shepherds apply fire to provide newly grown vegetation for their animals), but their effects on species composition are not identical, especially in cases where no grazing had been applied after the last fire. For this reason, we consider the two variables separately. Local plant communities presumably bear the heritage of the combined long-term effects of both these factors, but the changes found in the census period of our study should reveal some responses to their separate effects.

In Table S1 in Supplementary Material we give a detailed list of all species found, together with data concerning the growth form of each plant species according to Raunkiaer's (1934) classification (therophytes, geophytes, hemicryptophytes, chamaephytes and phanerophytes) and whether it is a halophyte or not. Subspecies are also included in the lists, but since islets host only one subspecies of each species, richness values are not affected; for convenience, we use the term 'species richness' throughout the paper.

We explored the effects of the geographical factors on species richness (log-transformed values) recorded in the two periods using multiple and stepwise regression.

The effects of grazing, gulls and fire on turnover rates and species richness were examined using one-way ANOVA and ANCOVA, using area, elevation and distance as covariates. Mann-Whitney tests were applied in order to check for differences between frequencies of occurrence of extinct, immigrant and persisting species.

Standard chi-square tests (with Yate's correction for 2×2 matrices) were applied in order to check for differences in community constitution between the two sampling periods concerning growth forms for the total plant list and for each individual islet.

Turnover rates were calculated on a per islet and per species basis. Absolute (S_2 ; Herwitz *et al.*, 1996) and relative (Rt ; Diamond, 1969; Schoener, 1983; Morrison, 1997, 2003) turnover rates were calculated using the following formulae:

$$S_2 = (I + E)/2t$$

$$Rt = [(I + E)/t(S_{74} + S_{94})] \times 100$$

where t is the time period between censuses. For the per islet calculation, E stands for species present only in 1974 ('extinct') and I for species present only in 1994 ('immigrants'). For the per species calculation, E and I stand for number of islets where each species was present only in 1974 and only in 1994, respectively, whereas S_{74} and S_{94} stand for total incidences of each species in 1974 and 1994, respectively.

Community nestedness in both sampling periods was calculated using BINMATNEST software (Rodríguez-Gironés & Santamaría, 2006), which reduces the problems of matrix size dependence that are known to affect other metrics. This method exploits genetic algorithms to provide a metric of nestedness 'temperature' scaled from 0 (absolute nestedness) to 1 (completely unordered matrix) and a null model-based significance level. The null model 3 (no exact control of row and column sum totals) was used, as suggested by Rodríguez-

Gironés & Santamaría (2006). According to a recent evaluation of nestedness metrics (Ulrich & Gotelli, 2007), the better-performing metrics are the 'discrepancy index' suggested by Brualdi & Sanderson (1999) and the 'index of unexpected presences' proposed by Cutler (1991). Nevertheless, the modified 'temperature' calculation algorithm of BINMATNEST is supposed to have overcome the problems previously identified in 'temperature' algorithms. Unfortunately, it appears to have been published too recently to have been included in Ulrich & Gotelli's (2007) evaluation. Also, the two other metrics mentioned above do not provide a matrix-independent index that could be used for a direct comparison of two different matrices, whereas the 'temperature' provided by BINMATNEST can be used for such a comparison.

Species co-occurrence patterns at the community level were examined using the C -score index (Stone & Roberts, 1990) as provided in EcoSim7 software (Gotelli & Entsminger, 2004), using the fixed sum of rows and columns constraint for the construction of 5000 null matrices by the sequential swap algorithm, as suggested by the authors and Gotelli (2000). We also applied the independent swap algorithm for comparative purposes, but we did not find any important effect on the results. There was only a negligible increase in variance that did not affect significance levels or the values of the C -score indices; therefore, we do not present these results.

Floral similarity among islets was calculated using Jaccard's index. NTSYSpc 2.1 (Rohlf, 2000) was used for the application of a Mantel test in order to compare islet similarity matrices between the 1974 and 1994 data sets (9999 permutations). We used the 95% significance level for all analyses.

RESULTS

The grand total number of species recorded was 391. A total of 301 species were present in 1994 and 334 in 1974 (see Table S1). The total number of species present only in 1994 (I) was 57, while 90 were present only in 1974 (E); 244 species were common to both sampling periods (C).

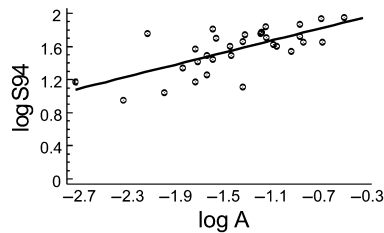
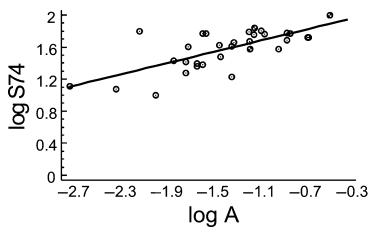
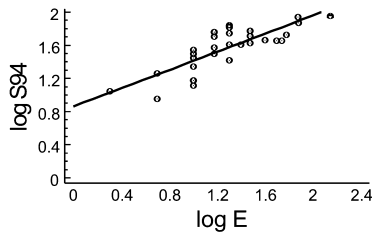
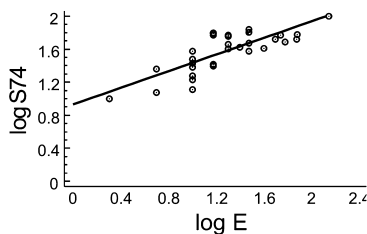
Only one independent variable (elevation) entered into the stepwise regression model explaining species richness in both sampling periods (Table 2). Significant collinearity has been documented between elevation and area, both of which are also highly correlated with species richness in both sampling periods ($r = 0.75$, $P < 0.001$). According to Shaw (2003), collinearity does not affect the significance of the multiple regression model. In addition, separate linear regressions of species richness with each factor and partial correlations supported the prevalence of elevation. Therefore, we regard elevation as the most important predictor of species richness. This primary effect of elevation is also apparent in the results of ANCOVA for the various subdivisions of the data set (see below).

Species-area and species-elevation relationships gave almost identical slopes for the 1974 and 1994 data sets (Fig. 2).

There were significant differences in size and elevation between islets grouped according to presence of grazing, gulls

Table 2 Results of stepwise regression (final model) using species richness (*S*) as the dependent variable and islet area (*A*), maximum elevation (*E*) and minimum distance from nearest large island (*D*) as independent variables for the two sampling periods. All values were log-transformed. Forward and backward selection gave identical results.

Sampling period	Model	<i>F</i>	<i>P</i>	<i>R</i> ² (adjusted)
1994	$\log S = 0.86 + 0.55 \log E$	55.06	<0.001	63.55
1974	$\log S = 0.93 + 0.50 \log E$	48.78	<0.001	60.65

(a) $\log S = 2.05 + 0.35 \log A$, $R^2 = 51.0$, $P < 0.001$ **(b)** $\log S = 2.06 + 0.36 \log A$, $R^2 = 47.5$, $P < 0.001$ **(c)** $\log S = 0.93 + 0.50 \log E$, $R^2 = 61.9$, $P < 0.001$ **(d)** $\log S = 0.86 + 0.55 \log E$, $R^2 = 64.7$, $P < 0.001$ **Figure 2** Species–area (a, b) and species–elevation (c, d) relationships of the 32 islets studied, for 1974 (a, c) and 1994 (b, d). *A*, area; *E*, elevation; *S*, species richness.**Table 3** Differences in size and elevation between islets affected by grazing, gulls and fire (one-way ANOVA).

	Area				Elevation			
	Mean	SD	<i>F</i>	<i>P</i>	Mean	SD	<i>F</i>	<i>P</i>
Grazing								
Yes	0.10	0.01	8.51	<0.01	36.82	5.35	8.60	<0.01
No	0.02	0.02			8.70	7.95		
Gulls								
Yes	0.04	0.02	5.20	<0.05	16.87	6.52	5.85	<0.05
No	0.10	0.02			39.19	6.52		
Fire								
Yes	0.12	0.03	4.08	=0.05	50.50	8.90	8.49	<0.01
No	0.06	0.01			20.54	5.14		

and evidence of fire (Table 3). Grazing and fire generally affected larger and higher islets, whereas breeding gulls occurred mostly in smaller and lower ones. Since these effects would confound the effects of grazing, gulls and fire on species richness, we used the residuals of the linear regression between species richness and elevation (log-transformed values) in the ANOVA. Only grazing affected species richness (positively) in both sampling periods (Table 4). Similar results were obtained by ANCOVA using elevation, area and distance as covariates (results not shown).

Table 4 Effects of grazing, breeding gull colonies and fire on species richness (residuals of species–elevation relationships) for the two sampling periods (one-way ANOVA). Similar results were obtained by using residuals of the species–area relationships.

	1974				1994			
	Mean	SD	<i>F</i>	<i>P</i>	Mean	SD	<i>F</i>	<i>P</i>
Grazing								
Yes	0.05	0.03	8.02	<0.01	0.04	0.03	5.88	<0.05
No	−0.10	0.04			−0.09	0.04		
Gulls			1.37	n.s.			3.88	n.s.
Fire			0.03	n.s.			0.24	n.s.

The proportions of particular growth forms and of halophytes/non-halophytes did not differ between 1974 and 1994, and the same was true for islets divided according to presence/absence of grazing, breeding gull colonies and evidence of fire (Table 5). On a per islet basis, significant differences in growth form constitution were detected in only 3 of the 32 islets (namely, Zouka Megali, Psonos and Plakousa). It has to be noted, though, that the absolute difference between extinct and immigrant species (33) is in large measure accounted for by therophytes (15) and geophytes (13). The numbers of extinct and immigrant species were highly correlated with respective species richness per island in 1974

Table 5 Percentage representation of growth forms and ecological categories on all islets, and islets divided according to several factors during the two sampling periods, with respective chi-square tests (with Yate's transformation for 2×2 tables).

	All		Grazing N		Grazing Y		Gulls N		Gulls Y		Fire N		Fire Y	
	1974	1994	1974	1994	1974	1994	1974	1994	1974	1994	1974	1994	1974	1994
Ch	9.9	11.0	21.6	24.7	9.8	11.0	10.2	11.2	12.6	14.4	10.4	11.9	11.3	12.1
G	14.1	11.3	15.5	7.1	13.8	11.6	12.7	10.4	16.1	13.9	15.4	13.1	12.6	8.2
H	14.7	14.3	17.5	14.1	14.1	13.7	13.8	13.5	14.3	13.3	15.4	14.3	13.9	12.6
Ph	6.3	7.3	9.3	9.4	6.1	7.2	6.7	6.2	7.2	8.9	7.5	8.6	4.8	4.3
Th	55.1	56.1	36.1	44.7	56.1	56.5	56.5	58.8	49.8	49.4	51.4	52.0	57.4	62.8
	$\chi^2 = 1.43$, n.s.		$\chi^2 = 4.13$, n.s.		$\chi^2 = 1.04$, n.s.		$\chi^2 = 0.94$, n.s.		$\chi^2 = 1.04$, n.s.		$\chi^2 = 1.03$, n.s.		$\chi^2 = 2.78$, n.s.	
HI	7.5	7.6	16.5	18.8	7.4	7.5	7.4	8.1	9.9	7.1	8.6	8.2	7.0	9.2
Nh	92.5	92.4	84.5	81.2	92.6	92.5	92.6	91.9	90.1	88.9	91.4	91.8	93.0	90.8
	$\chi^2 = 0.00$, n.s.		$\chi^2 = 0.06$, n.s.		$\chi^2 = 0.00$, n.s.		$\chi^2 = 0.02$, n.s.		$\chi^2 = 0.06$, n.s.		$\chi^2 = 0.00$, n.s.		$\chi^2 = 0.46$, n.s.	

N, no; Y, yes; Ch, chamaephytes; G, geophytes; H, hemicryptophytes; Ph, phanerophytes; Th, therophytes; HI, halophytes; Nh, non-halophytes; n.s., not significant.

Table 6 Effects of grazing, breeding gull colonies and fire on per island turnover rates for the two sampling periods (one-way ANOVA). Since S2 is a linear function of species richness, the significant effects (bold) are artefacts (see text).

	Rt				S2			
	Mean	SD	F	P	Mean	SD	F	P
Grazing								
Yes	2.07	0.17	0.04	n.s.	1.11	0.09	18.37	<0.001
No	2.02	0.25			0.41	0.14		
Gulls								
Yes	2.14	0.20	0.40	n.s.	0.72	0.13	3.54	n.s.
No	1.97	0.20			1.06	0.13		
Fire								
Yes	2.46	0.27	3.06	n.s.	1.42	0.16	14.65	<0.001
No	1.92	0.15			0.72	0.09		

and 1994, respectively (E -S74: $r = 0.75$, $P < 0.001$; I -S94: $r = 0.78$, $P < 0.001$). On the other hand, the ratios of extinct and immigrant species to respective species richness in 1974 and 1994 were not correlated with islet area, elevation or distance from nearest large island.

Turnover rates per islet are given in Table 1. Mean absolute turnover rate (S2) was 0.89 species per year and mean relative turnover rate (Rt) was 2.06 species per year (for $t = 20$ this gives 41.2% mean species change). Relative turnover rate did not show any correlation with area, elevation, distance from nearest large island or species richness.

Per islet turnover rates were not generally affected by grazing, gulls or fire (Table 6). Only the absolute turnover rate (S2) showed a significant (positive) effect of grazing and fire. Nevertheless, this index was linearly correlated with species richness ($r = 0.69$, $P < 0.001$ for 1974, and $r = 0.75$, $P < 0.001$ for 1994), so the apparent effects of these factors can be interpreted as artefacts of their effects on species richness (the

raw values of which were positively affected by both grazing and fire, and negatively by gulls – but see the previous paragraph). In fact, ANCOVA of S2 with grazing as factor and species richness as covariate confirmed this interpretation (for S74 $F = 6.71$, $P < 0.02$ and for S94 $F = 13.03$, $P < 0.002$, no significant effect of grazing in either case).

Relative turnover rates per species (see Table S1) varied from 0 to 5 with a mean of 3.26 islets per year. It is noteworthy that maximum turnover was exhibited not only by extinct and immigrant species, but also by several 'persisting' species that were present in completely different islets during the second census. Only 26 species (6.5%) had a turnover rate of 0. On the other hand, the total number of species with the maximum possible turnover rate was 185 (47.3%), 147 of which were immigrants and extinct and 38 (9.7%) species with completely different occurrences in 1994 than in 1974.

Per species turnover rates were significantly affected by growth form (ANOVA $F = 8.54$, $P < 0.001$), with geophytes (mean = 3.96) and therophytes (mean = 3.42) exhibiting higher values, while phanerophytes (mean = 1.93) and chamaephytes (mean = 2.34) exhibited lower values. Hemicryptophytes exhibited intermediate values (mean = 3.08). Halophytes did not differ from non-halophytes (ANOVA $F = 2.86$, $P > 0.05$). Similar trends were found also in the comparison between zero- and maximum-turnover species (with or without I and E).

Turnover per species was significantly affected by frequency of occurrence for both immigrant and extinct species (Table 7). Most species that went extinct or immigrated were present on one islet only in 1974 or 1994, respectively.

Even though the per islet net change of species richness ($I-E$) ranges from -22 to $+34$, the mean net change across the whole system did not differ significantly from 0 (t -test: $t = -0.146$, $P > 0.05$, mean value = -0.31). A decrease in species numbers was found in 17 islets and an increase in the other 15.

Nestedness values (Table 8) were very similar between the two sampling periods, although in the more recent census

Table 7 Frequencies of species occurrences in the two sampling periods. All Mann–Whitney tests comparing constant and turned-over species were significant ($P < 0.05$). Frequencies of occurrence did not differ between the two sampling periods ($P > 0.05$).

	Persisting species		Extinct and/or immigrant species		
	f_{74}	f_{94}	$f_{(Ext)}$	$f_{(Imm)}$	$f_{(All)}$
1	0.205	0.270	0.611	0.719	0.653
2	0.156	0.127	0.267	0.193	0.238
3	0.119	0.139	0.067	0.053	0.061
4	0.074	0.074	0.056	0.018	0.041
5	0.111	0.049	–	–	–
6	0.070	0.045	–	0.018	0.007
7	0.041	0.029	–	–	–
8	0.020	0.025	–	–	–
9	0.045	0.049	–	–	–
10	0.033	0.037	–	–	–
11	0.025	0.016	–	–	–
12	0.029	0.029	–	–	–
13	0.025	0.029	–	–	–
14	0.008	0.016	–	–	–
15	0.012	0.012	–	–	–
16	0.004	0.012	–	–	–
17	0.008	0.008	–	–	–
18	0.004	0.004	–	–	–
19	0.004	0.008	–	–	–
20	–	0.008	–	–	–
21	0.004	0.004	–	–	–
22	0.004	–	–	–	–
24	–	0.004	–	–	–
26	–	0.004	–	–	–

f_{74} , f_{94} , frequencies of persisting species in 1974 and 1994, respectively; $f_{(Ext)}$, frequency of extinct species; $f_{(Imm)}$, frequency of immigrant species; $f_{(All)}$, combined frequency.

Table 8 Results of community nestedness and species co-occurrence analyses for the two sampling periods.

Analysis	1974	1994
Nestedness		
T	15.59	14.75
P	<0.001	<0.001
Co-occurrence		
C observed	8.886	9.043
C simulated	8.740	8.856
Variance	0.0001	0.0007
P	<0.001	<0.001

T , matrix temperature; C , C -score (a standardized measurement of ‘checkerboard’ units, i.e. mutually exclusive species pairs in pairs of islets). In both analyses 1000 simulated matrices were used. The C -scores indicate a competitive structure within both matrices.

there was a small increase of nestedness (lower temperature) that could be attributed to the somewhat smaller number of species.

The C -scores for species co-occurrences were also very similar between sampling periods (Table 8). Both values indicate ‘competitive’ community structure, in the sense that mutually exclusive occurrences (‘checkerboard units’) are exhibited by more species pairs than expected by chance.

The matrices of islet similarity for the two sampling periods, based on Jaccard’s index, were significantly correlated (normalized Mantel test statistic $z = 0.72$, $t = 11.60$, $P < 0.001$).

DISCUSSION

The islet communities studied have suffered a 10% loss of plant species during the 20 years from 1974 to 1994. Furthermore, the patterns of occurrence have changed for a high proportion of species (93%), with 48% having being subjected to maximum turnover and 20% found only in one census. Therefore, the more recent communities contained 80% of the species present two decades previously, while 27% of the species present in 1974 went extinct from the system of islets. The fact that the vast majority of immigrant and extinct species occurred on one islet only, combined with the generally low values of all species occurrences (90% of the species occur on less than a third of the islets), indicate the dynamic character of the flora of these islets. Morrison (2003) reports a similar pattern for small Bahamian islands. This is also in agreement with Vidal *et al.* (1998), who noted that below a certain threshold area, islets are subject to an important variability of their environmental conditions, which is able to destroy their phytocenosis. The same authors also remarked that more than half of the plant species found in 1996 on Jarron Island (Riou Archipelago, south-eastern France) were not present on this island 36 years earlier.

Species richness was better explained by elevation, which is usually considered a proxy of habitat heterogeneity. However, the relative importance of area and elevation is hard to disentangle for this system, due to the very high correlation of the two factors. At the same time, species richness was affected by the application of grazing, a practice that is also more common on larger and more elevated islets (on which the animals can find more food and shelter). Elevation is also a control on the effects of sea-spray, so that more elevated islets can have protected sites that can host species intolerant of salt. It should be noted that species richness did not depend on distance from the nearest large island. This may be due to the fact that these islets are not isolated enough, so there is not enough variation in distances for an effect to be found. Triantis *et al.* (2005), studying a less dispersive taxon (land snails) on a similar nearby island group, attributed the lack of an effect of isolation on species richness to the fact that these islets still ‘behave’ as part of a uniform landmass, so that their fauna is not established through immigration from nearby species pools but through relaxation. Given the amount of turnover found herein, such an explanation is not likely for plants.

The high correlation of species richness with area and elevation does not support the existence of a small island effect,

a result in accordance with our previous analysis of plants on 86 small islets of the Aegean (Panitsa *et al.*, 2006).

The values of per islet relative turnover rate, ranging from 1.020 to 3.868% of species per year, are among the largest reported in literature for plants (see Schoener, 1983; Herwitz *et al.*, 1996; Vidal *et al.*, 2000; Krieger *et al.*, 2003; Morrison, 2003; Cody, 2006). Taking into account the small surface and very short distance of the islets from their presumed species pools (nearest large islands), this finding conforms to the predictions of MacArthur & Wilson's (1967) model. On the other hand, similarly small and near islands have also been censused in other studies, where turnover rates were lower. For example, Morrison (2003) found turnover rates between 0.22% and 0.76% species per year for small islands at Exuma Cays and near Andros (Bahamas), while Vidal *et al.* (2000) reported a maximum value of 1.187% species per year in a series of small islands in the Bay of Marseille (Mediterranean). Therefore, additional factors, such as human activities enhancing turnover, should be considered in our case. Furthermore, it should be noticed that per species turnover rates are also among the largest reported for plants. Using again the aforementioned examples, Morrison (2003) reports values ranging from 0.79 to 2.32% islets per year, while Vidal *et al.* (2000) reports a maximum of 2.703% islets per year, while the mean value in our case is 3.26% islets per year. In addition, only a small percentage (6.5%) of our species showed zero turnover, again contrasting with both of these studies.

Recently, Fofopoulos & Mayer (2007) have presented data on turnover rates of passerine birds on five Aegean islands. Besides the vast differences between birds and plants in most aspects related to the processes under investigation, we should note that these authors found increased annual turnover rate in the smallest island included in their study (Dilos, still much larger than all our islands) and, in fact, its value (1.08 species per year) is within the range found in the present work. It would be interesting to know the respective values for islets of similar size to those of our study, in order to see if birds exhibit even higher turnover values than plants.

Cody (2006), studying a very different island system and using a different methodological approach, has documented comparable values of per island species turnover within a 22-year period and a similar percentage of 'resident' species (compared after proper calculations from published values). The islands he studied (in Barkley Sound, Vancouver Island, Canada), although similar in size to those of the present study, have an even stronger continental character than ours since they are located inside one of the bays of the large Vancouver Island, while most of the islands in our study lie in the open sea (compare our Fig. 1 with Fig. 2.1 in Cody, 2006). His detailed observations and analyses show that plant species turnover is a highly variable phenomenon, depending on both the biological properties of each species and the local topographic and ecological conditions of the islands. Nevertheless, even when we take into account the complexity of the phenomenon, the turnover rates documented in our analysis are still notably high.

The very large turnover values reported herein should be considered with some caution due to a possible 'pseudoturnover' effect caused by the inconspicuous presence of plants in the form of seed banks and/or subterranean bulbs that remain dormant for relatively long periods of time. As a consequence, some of the species designated as 'immigrants' could in fact have been present in the seed bank or bulb bank in 1974 and the same may apply to those designated 'extinct' in 1994. This type of 'pseudoturnover' affects all studies of plants, so the published turnover rates remain comparable.

The fact that turnover was not related to area, elevation or distance from the nearest large island could be attributed to the generally small distances of most islets from their respective putative sources, and to the relatively narrow range of areas and elevations of these islets. Snogerup & Snogerup (2004) have also suggested that, for plants, turnover is independent of distance because diaspore establishment faces similar difficulties regardless of the distance that the immigrants have to cross. Nevertheless, such an approach does not take into account possible differences in dispersal rates due to distance effects, that would lead to different probabilities of colonization and rates of arrival to an islet. In the case of our data set, we believe that the independence of turnover rates from topographic factors is mainly due to the small geographical scale of the system.

Despite this high turnover, though, the plant communities seem to have retained very similar general properties during the 20-year period of the study. This apparent stability is exhibited by the almost identical response of species richness to area and elevation in both sampling periods, and to the very similar values of nestedness and co-occurrence indices. Patterns of floral similarity among islets also support this observation. The similar constitution of plant communities with respect to growth forms can also be considered as evidence of structural stability, especially when we take into account that the relative growth form representation has not changed in 29 of the 32 islets.

Even though the documentation of turnover *per se* cannot be taken as proof of equilibrium theory (Abbott, 1983), the evidence of community stability *despite* high turnover is indicative of some kind of equilibrium dynamics. An important complicating factor is the continuous effects of humans for at least the last 3000 years. The most common activities on such small islets are the application of grazing by domestic sheep and goats and the periodical application of fire in order to facilitate grazing (see also Panitsa *et al.*, 1994; Panitsa & Tzanoudakis, 2001; Bergmeier & Dimopoulos, 2003). Indeed, grazing seems to increase species richness (see also Panitsa *et al.*, 2006). A plausible explanation for this is the creation of 'open' spaces ready to receive new immigrants in combination with zoochory. We could assume that reduced richness in the more recent sampling period might be related to the general on-going trend towards the abandonment of grazing practices as we come to the present, even though no differences in overall species loss between grazed and ungrazed islets could be detected during the period of our study. Nevertheless, the

excess species loss mostly comprises growth forms (therophytes and geophytes) that are positively affected by grazing (Snogerup & Snogerup, 1987; Bergmeier & Dimopoulos, 2003). Therefore, the larger relative turnover values of therophytes and geophytes are probably related to grazing practices. According to Vidal *et al.* (2000), therophyte species have a higher species turnover rate than other plant life-forms due to their variable population fluctuations, and this pattern occurs on different types of islands (Snogerup & Snogerup, 1987; Robinson *et al.*, 1994; Herwitz *et al.*, 1996). It is important to note that these growth forms have not increased their relative frequency in the period 1974–94 despite their higher turnover rate. This is obviously due to the fact that more such species have become extinct and also to the fact that they already comprise a very large part (70%) of all species present in local communities (therophytes alone make up 56%), whereas only 6% are phanerophytes, 10% chamaephytes and 14% hemicryptophytes. More than 30% of the therophytes are leguminous plants (15.1%) and grasses (15.5%), groups that are particularly affected by grazing (Bergmeier & Dimopoulos, 2003). In addition to grazing, therophytes constitute a large percentage of the species present on Mediterranean islands because of their overall adaptations to local conditions and their abilities to colonize new open habitats quickly, so that typically they represent a large number of the invasive plants, particularly in the Mediterranean Basin (Qu  zel *et al.*, 1990). The predominance of therophytes in the Aegean islands reflects the bioclimatological position of the area, with its intense thermo-Mediterranean character and long summer aridity (Livaniou-Tiniakou *et al.*, 2003; Panitsa *et al.*, 2003, 2004; Tzanoudakis *et al.*, 2006).

Consequently, we consider that grazing may be a factor keeping the system away from equilibrium, the removal of which leads to rapid system responses through the high turnover potential of plants. This hypothesis should be tested by longer-lasting monitoring of species dynamics on such islets.

On the other hand, the periodical application of fire (if not followed by grazing) does not seem to play any significant role in the dynamics of plant communities on these islets. This must be due also to the speed of change in these systems, which recover quickly after fire, since the vegetation of a burned islet recovers mostly from the seed bank (Snogerup & Snogerup, 1987). An important difference from grazing is that the latter is a continuous activity whereas fires are applied at intervals of several years. It has to be noted that even very few grazing animals can affect these islets significantly due to their very small total surface. According to Vidal *et al.* (2000), the presence of breeding gull colonies is another crucial factor for the dynamics of small Mediterranean islands. Nevertheless, we did not detect any effect of gulls on plant community structure or richness. In our previous work (Panitsa *et al.*, 2006) we also detected a significant effect of grazing (see also Bakker *et al.*, 2003) but no effect of gull colonies.

According to species co-occurrence analysis based on ‘checkerboard units’, the plant communities of these islets appear to be ‘competitively’ structured. Of course, ‘competitive

structure’ does not necessarily imply actual species competition, as it can result from structured environmental heterogeneity or other historical factors (Sfenthourakis *et al.*, 2006). Nevertheless, if we take into account the high turnover rates of most species, most of which occur on different islets at the start and end of the 1974–94 period, a plausible explanation for this competitive structure should be sought in actual competition for the very limited space and soil resources. In a simulation study, Seagle & Shugart (1985) found that competition is expected to increase turnover rates, so such processes would further enhance the dynamics on small islets. This interpretation is supported further by the effect of frequency of occurrence on per species turnover rates and by the fact that most turned-over species occur on one or a very few islets. According to H  ner & Greuter (1988), very low interspecific competition could be found between plants on the small islands they studied, mainly due to the low flux of foreign propagules and the commonly undersaturated floras. The very high turnover and the reduction of overall species number found in our study are in conflict with these presumed processes. Cody (2006) discussed a few (weak) cases of possible competition in species inhabiting edge habitats, which are analogous to the habitats that are common in small Mediterranean islands. So it seems, on the basis of existing literature, that we cannot preclude the possibility of competition among plant species. In any case, in the light of our results, the occurrence of negative interspecific interactions can be seen as a plausible factor enhancing turnover of plants on small islets.

In conclusion, we have found evidence for very fast floral changes on small Aegean islets that do not alter the overall structural properties of the floras. Such islet systems seem able to respond quickly to change by establishing communities of different composition but with similar structure. Turnover processes, though, are complicated by human activities, most importantly by the application of grazing. It would be very interesting to exclude such activities experimentally from a number of islets and monitor floral changes through time, in an attempt to estimate ‘natural’ turnover levels. The dynamics of these islets make them excellent cases for the study of many aspects of island biogeography.

ACKNOWLEDGEMENTS

We wish to express our deep gratitude to Professor H. Runemark (University of Lund, Sweden) for providing access to the 1974 data collected with Professor R. von Bothmer (Swedish University of Agricultural Sciences). Many thanks also to Sinos Giokas for stimulating discussions throughout the preparation of this paper. Kostas Triantis and an anonymous reviewer provided valuable comments on previous versions of this manuscript. The contribution of editorial comments was crucial. Fieldwork was partially financed by the Greek Secretariat of Research and Technology and the Greek Ministry of Environment, Regional Planning and Public Works. The Greek Navy provided crucial assistance in accessing several islets.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article online:

Table S1 List of species found on the 32 islets studied.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2699.2007.01846.x>

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Editor: José María Fernández-Palacios