Phytocoenologia	33 (2–3)	447–474	Berlin–Stuttgart, June 10, 2003

The vegetation of islets in the Aegean and the relation between the occurrence of islet specialists, island size, and grazing

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with 6 figures and 8 tables

Abstract. The phenomenon of 'islet specialists' has received much attention in plant geographical literature on the Aegean. Islet specialists occur chiefly on small uninhabited islands about 0.1 to few hundred hectares small. A list of islet specialists is presented, and their distribution in the Aegean is outlined. For 56 islets, the relation between the occurrence and proportion of islet specialists and parameters such as island area, altitude, and grazing is calculated. The species-area relation increases with grazing, and the proportion of islet specialists decreases. The high species numbers of grazed islets are chiefly due to annual species of phrygana habitats. The species composition of 30 South Aegean islets, which were ordinated by Correspondence analysis and Canonical correspondence analysis, suggests that grazing is more relevant to explaining the variance of the data than island size. Islet floras are neither uniform nor randomly composed, but reflect environmental (limited area) or geographical variation (wider area). A classification of 111 relevés with islet specialists from 26 small islands throughout the Aegean (except the Kiklades) revealed 10 plant communities, which are briefly outlined in terms of species composition, ecology and distribution. The most prominent vegetation is that of coastal rocks (Crithmo-Staticetea) and halo-nitrophilous scrub (Pegano-Salsoletea). In the Aegean, the Pegano-Salsoletea vegetation seems to be more diverse and variable on islets than along other coasts. For most units, formal description as associations was considered premature, but the syntaxonomy is discussed and some nomenclaturally insufficient names from literature are validated or corrected.

Keywords: Aegean; coastal vegetation; Crithmo-Staticetea; endemism; grazing; Greece; island flora; Pegano-Salsoletea; Saginetea maritimae.

1. Introduction

The smallest of islands deserve high priority in nature conservation efforts in the Mediterranean (Greuter 2001). The vulnerability of islets is due to the limited resilience of the fragile ecosystems, which are always at risk of external impact. Half of the few documented extinctions of Mediterranean island endemics are related to minute islands (Greuter 1995). If under human pressure, especially through grazing by domestic animals, the vegetation structure of grazed islets differs strikingly when compared to untouched islets (Sfougaris & Papageorgiou 1999). The small ungrazed islands are in fact one of the very few ecosystems in the Mediterranean without,

DOI: 10.1127/0340-269X/2003/0033-0447 0340-269X/03/0033-0447 $ 7.00

or almost so, human interference. 'Islet specialists', i.e. plant species which are exclusive to small islands (or more frequently occur here than on large islands or mainlands), are known from various archipelagos in the Mediterranean and elsewhere in the world. The phenomenon was first described from the Aegean, where the islet specialists constitute a characteristic phytogeographical element (Rechinger & Rechinger-Moser 1951: 201). The Aegean Sea is extraordinarily rich in islands of different magnitudes, from very small to medium-sized. A varying set of islet specialists, together with geographically and ecologically less restricted species, makes each islet unique in species composition and appearance. Individual and often peculiar species combinations are encountered, which are a consequence of reduced competition among species, founder and isolation effects, and random eliminations by reproductive drift (Runemark 1969). As islets are sharply delimited and relatively isolated ecosystems, they are highly significant as 'natural laboratories' (Greuter 1995), perfectly suited to scientific research in plant population biology, in particular for monitoring of processes such as dispersal, establishment and extinction.

The Aegean islands are chiefly of continental, non-volcanic origin. The geological and geographical history of the Aegean and its effects on plant geography were outlined by Greuter (1970, 1972). The plant geographical subdivision (Fig. 1) founded by Rechinger (1943, 1950) was basically confirmed by subsequent plant geographical investigations (Greuter 1972, Runemark 1972, Strid 1996). The peculiar species composition of minute Aegean islands, the 'islet phenomenon', has been in the focus of floristic, biosystematic and plant geographical research by teams from Lund (Runemark 1969, von Bothmer 1974) and Berlin (Höner & Greuter 1988, Raus 1990, Höner 1991). Their findings may be summarized as follows:

- relatively low species numbers (Höner 1991, Greuter 1995);
- presence of islet specialists (Rechinger & Rechinger-Moser 1951, Runemark 1969, Höner & Greuter 1988, Raus 1990, Höner 1991);
- random effects in the composition of local floras (Runemark 1969);
- relative stability of islet floras (Snogerup & Snogerup 1987, Höner 1991);
- adaptive features of species to cope with salt spray and poorly developed, more or less saline soils;
- specialized reproductive and dispersal mechanisms (von Bothmer 1974);
- random oscillations in the frequencies of individuals in subsequent generations ('reproductive drift', Runemark 1969), as an explanation for the erratic pattern of endemics as well as presence-absence phenomena of non-endemic species on islands;
- 'non-adaptive radiation' as a principle in the evolution of small populations (Runemark 1970; Strid 1970; Snogerup 1967).

Owing to the difficult, and sometimes risky, access by boat, floristic inventories of Aegean islets are still scarce, at least in relation to the great number of islets existing (e.g., Gustafsson &Snogerup 1974, Greuter & Pieper 1975, Snogerup & Snogerup 1987, Raus 1990, Christodoulakis

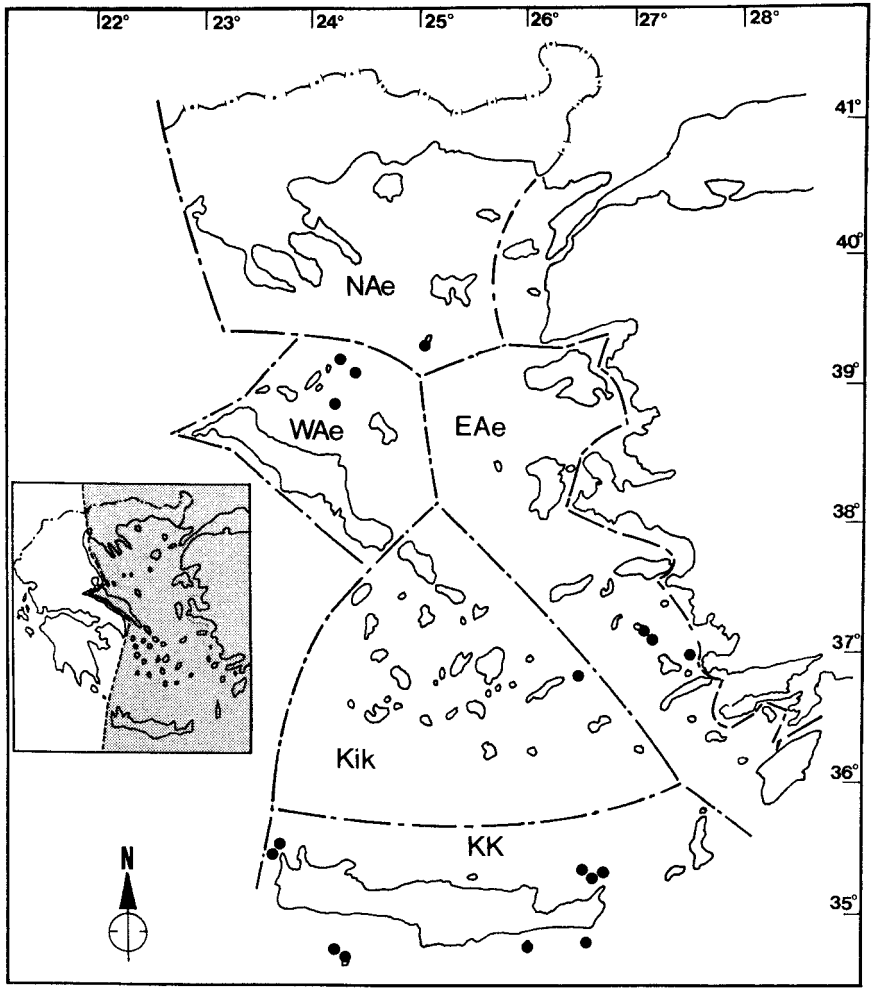


Fig. 1. The Aegean and its plant geographical subdivision according to RECHINGER (1943) and subsequent authors. NAe, North Aegean; WAe, West Aegean; EAe, East Aegean; Kik, Kiklades; KK, Kriti (Crete) and Karpathos. The dots indicate small islands with relevé plots used in the present paper.

et al. 1991, HÖNER 1991, PANITSA et al. 1994, PANITSA 1997, PANITSA & TZANOUDAKIS 1998, BERGMEIER & DIMOPOULOS 2001, BERGMEIER et al. 2001). Previous investigations, however, have largely ignored patterns of vegetation, and knowledge on niche preferences of islet specialists is scarce. Human interference, in particular grazing, has generally been recognized as affecting islet ecosystems in the Aegean (HÖNER 1991, SFOUGARIS & PAPAGEORGIOU 1999, GREUTER 2001), but has not been specified as to de-

gree and consequences of this influence. These topics are addressed here, following three approaches, floristics, ordination, and phytosociological classification, thus providing a background for answering the following questions:

- Is the species-area relation of small Aegean islets influenced by grazing?
- Is the proportion of islet specialists in island floras restricted by grazing?
- What is the influence of the environment on the composition of islet floras and the presence of islet specialists?
- Do islet specialists have similar habitat requirements, or do they occur in different plant communities?
- What do the plant communities in which the islet specialists occur indicate about their habitat?
- Can the peculiar flora of small islands be understood by corresponding peculiar features of the islets?

2. Materials and methods

A list of Aegean islet specialists was compiled from the relevant plant geographical literature. The nomenclature of taxa follows Flora Europaea (Tutin et al. 1968–1993) and Flora of Turkey (Davis 1965–1988), except for *Asparagus horridus* (Jahn & Schönfelder 1995), *Prospero autumnale* and *Charybdis maritima* (Speta 2000, 2001), *Atriplex mollis* (Greuter & Raus 1999), and *Hornungia procumbens* (Appel & Al-Shehbaz 1997). The number and proportion of islet specialists in island floras was investigated using a data set of 56 small islands which differ in surface area (0.04–462 ha), total species number (3–275), abiotic environmental conditions and human impact. The sources of data are our investigations (26 islets; Table 1), Raus (1990; 15 islets) and Höner (1991; 15). Some of the islands had been populated in former times and show signs of old fields abandoned since decades. Several islands were occasionally or regularly grazed by sheep or goats, seasonally restricted to a short time in spring, owing to the lack of freshwater. This is still common practice on many islands. Rabbits were found to be introduced to some of the islets. Eutrophication was encountered locally on islands with gull colonies (*Larus cachinnans*).

The variation among the species combinations of islets along environmental and diversity gradients was explored using floristic inventories provided by Raus (1990) and Höner (1991). A total of 30 islets from the Karpathos archipelago was used, thereby largely excluding plant geographical variation. The size of the islets used for the ordination ranges from 0.02 to 23.6 ha, and the species numbers from 1 to 131. In the data set taken from Raus (1990), islets with no vascular plant species were omitted, and the island of Armathia was disregarded as it deviates much in surface area and species number. The geographical position of the islets, as well as various other geographical, biological and ecological parameters are given in Raus (1990: 20f.) and Höner (1991: 52ff., 76ff.). The islets were ordinated on the basis of their floristic composition. The main variation in species

Table 1. Geographical, floristic and ecological parameters of small Aegean islands with relevé documentation or own floristic investigations used for the present paper. The coordinates refer to the center of the island. Taxon numbers include species and additional subspecies. Region: see Fig. 1 for abbreviations of plant geographical regions. Fields: abandoned (+) or presently cultivated (!) fields seen. Grazing: regularly +, previously (+).

Island	Coordinates Long. E	Latit. N	Region	Area (ha)	Altitude (m)	Number of taxa	Number of islet specialists	Islet Specialist Ratio	Fields	Grazing	Number of relevés	Floristic information
Ajioi Apostoloi	25°00′20″	39°34′00″	NAe	1.75	5	14	3	21.4	–	+	3	Dimopoulos et al., ined.
Velia or Roumbos	25°03′45″	39°32′25″	NAe	0.45	21	6	3	50	–	–	2	Dimopoulos et al., ined.
W Mavra	26°22′03″	36°59′50″	EAe	13.2	20	32	2	6.3	–	–	2	Panitsa 1997
E Mavra	26°22′50″	36°59′50″	EAe	14.8	20	38	3	7.9	–	–	2	Panitsa 1997
Mikro Kalapodi	26°48′30″	37°15′20″	EAe	0.5	5	12	3	25	–	–	1	Panitsa 1997
E Imia	27°09′00″	37°03′02″	EAe	1.7	20	17	3	17.6	+	(+)	1	Panitsa 1997
Prassonisi	27°04′55″	37°02′55″	EAe	1.2	15	32	2	6.3	–	(+)	2	Panitsa 1997
Pitta	27°04′00″	37°03′10″	EAe	2.4	20	22	3	13.6	–	–	2	Panitsa 1997
Kassidis	24°05′30″	39°06′20″	WAe	0.75	5	6	1	16.7	–	–	2	Dimopoulos et al., ined. Gustafsson & Snogerup 1974
Strongylo I[1]	24°05′15″	39°05′00″	WAe	1.5	30	18	4	22.2	–	–	6	Gustafsson & Snogerup 1974
Islet close to Yioura (Ormos Pnigmenou)	24°11′15″	39°23′50″	WAe	0.9	30	12	2	16.7	–	–	1	Dimopoulos et al., ined.
Korakas	24°03′45″	39°02′05″	WAe	11	23	78	4	5.1	–	–	3	Gustafsson & Snogerup 1974
Melissa	24°05′30″	39°17′40″	WAe	0.5	25	4	3	75	–	–	1	Snogerup et al. 1991
Lachanou	24°05′50″	39°06′20″	WAe	3.75	22	43	2	4.7	–	–	3	Gustafsson & Snogerup 1974
Strongylo II[1]	24°07′40″	39°21′05″	WAe	1.25	26	36	1	2.8	–	–	1	Dimopoulos et al., ined.
Gavdos	24°05′00″	34°51′00″	KK	c.3000	368	469	2	–	+!	+	4	Bergmeier et al. 1997
Gavdopoula	24°00′00″	34°55′40″	KK	262	113	134	1	0.7	–	+	6	Bergmeier, ined.
Chrisi	25°42′30″	34°52′20″	KK	462	27	275	3	1.1	+	(+)	10	Bergmeier et al. 2001
Mikronisi	25°44′40″	34°52′35″	KK	12	16	71	3	4.2	–	–	0	Bergmeier et al. 2001
Koufonisi	26°08′20″	34°56′10″	KK	392	64	273	3	1.1	+	(+)	22	Bergmeier et al. 2001
Makrouli	26°07′45″	34°57′15″	KK	6	7	115	5	4.3	–	(+)	8	Bergmeier et al. 2001
Strongili	26°08′00″	34°57′40″	KK	12	19	110	4	3.6	–	(+)	7	Bergmeier et al. 2001
Trachilos	26°08′00″	34°55′10″	KK	11	43	96	4	4.2	–	–	0	Bergmeier et al. 2001
Elassa	26°20′20″	34°16′30″	KK	200	72	111	3	2.7	+	+	8	Bergmeier et al. 2001
Paximada	26°10′20″	35°22′40″	KK	30	136	72	10	13.9	–	–	6	Bergmeier & Dimopoulos 2001
Janisada	26°10′30″	35°19′40″	KK	208	150	213	8	3.8	+	(+)	1	Bergmeier & Dimopoulos 2001
Dragonada	26°10′30″	35°20′50″	KK	284	125	235	7	3.0	+	(+)	3	Bergmeier & Dimopoulos 2001
Agria Gramvousa	23°35′10″	35°38′20″	KK	81	100	94	2	2.1	–	+	4	Christodoulakis et al. 1991

[1] Strongylo I is close to Skantzoura, Strongylo II is between Yioura and Kira Panagia.

composition was correlated to island size, altitude, number of species, grazing intensity, and number and proportion of islet specialists.

Indirect ordination (Correspondence analysis, CA) was used to show the principal patterns in the species data. The relations of the unconstrained axes and the environmental and diversity parameters were calculated subsequently in order to interpret the ordination. Default options (biplot scaling, no transformation, no downweighting), and inter-species distance scaling were applied. Gradients in the data matrix and the role of islet specialists and other species groups have been visualized by ordination diagrams. Pearson's correlation coefficient was used for calculating regression values between independent geographical variables (size, altitude) and the number and proportion of islet specialists for all islets as well as various partial data sets. Direct gradient analysis (Canonical correspondence analysis, CCA) was also performed using the environmental variables altitude, area size, and grazing intensity. The latter two were treated alternately as covariables in order to understand the influence of these parameters on species composition. The significance between the environmental variables and the species composition was tested using Monte Carlo permutation. The ordinations were performed using CANOCO 4 (ter Braak & Šmilauer 1998).

A classification was carried out on 111 relevés from uninhabited islands in various parts of the Aegean (Table 1, Fig. 1). Although commonly present to various extent on all but the smallest islands, non-halophytic phrygana vegetation is not treated here as it approaches the ecological conditions of larger islands. Preference was given to relevés which include at least one islet specialist. Except for a few samples from Panitsa (1997), most relevés have not been published so far. For cover-abundance estimates, the 7-point Braun-Blanquet scale applied in all plots. The relevés were collated to a database managed by TURBOVEG (Hennekens & Schaminée 2001), and classified and edited using the MEGATAB tool which incorporates TWINSPAN (Hill 1979). Misclassified relevés were reshuffled in order to improve interpretability. No attempt was made to formally describe syntaxa because our material from a rather special environment can hardly serve as a syntaxonomic standard for the entire Aegean coastal vegetation. Due to the lack of more extensive relevé material of rocky coastal vegetation from other parts of the Aegean, knowledge on the geographical and ecological variation is scanty.

3. Results

3.1. Floristic analyses

A list of Aegean islet specialists is presented in Table 2. In a few cases, it is a matter of discussion whether to recognize or not certain taxa as islet specialists. We disregarded *Convolvulus oleifolius* var. *scopulorum* and *Matthiola sinuata* subsp. *glandulosa* for taxonomic reasons; and *Achillea cretica*, *Dactylis glomerata* subsp. *hackelii*, *Elymus rechingeri*, *Helichrysum orientale*, *Ornithogalum creticum* and *Sagina maritima* are distributed on larger

Table 2. Aegean islet specialists. Families: *All* - Alliaceae, *Asp* - Asparagaceae, *Ast* - Asteraceae, *Bra* - Brassicaceae, *Car* - Caryophyllaceae, *Che* - Chenopodiaceae, *Fab* - Fabaceae, *Hya* - Hyacinthaceae, *Mal* - Malvaceae, *Oro* - Orobanchaceae, *Plu* - Plumbaginaceae. Life forms: P - perennial herb; G - bulbous or rhizomatous geophyte; S - shrub or subshrub; T - short-lived herb (annual or biennial).

Species	Family	Life form	Aegean endemic	Widely distributed	Number of plots with the species	Remarks
Achillea aegyptiaca	*Ast*	P	x		0	islet specialist and confined to the SE Kiklades according to Rechinger & Rechinger-Moser (1951: 201, as '*A. aegyptiaca* ssp. *Tournefortii*')
Allium commutatum	*All*	G	x		15	recognized as islet specialist by Höner & Greuter (1988: 130) and Raus (1990: 34); distribution map by von Bothmer (1974: 25)
Anthemis ammanthus	*Ast*	T	x		10	includes 2 subspecies, both of which considered islet specialists by Höner & Greuter (1988), but the exclusivity is not absolute (Raus 1990); distribution map in Höner (1991: 60)
Anthemis glaberrima	*Ast*	T	x		4	local endemic of the islands Agria and Imeri Gramvousa off NW Kriti (Christodoulakis et al. 1991)
Anthemis scopulorum	*Ast*	T	x		3	recognized as islet specialist by Rechinger & Rechinger-Moser (1951: 201), Höner & Greuter (1988: 130)
Anthemis werneri	*Ast*	T	x		8	following Georgiou (1991, with distribution map) including *A. flexicaulis*; at best a weak relationship to small islands may be established
Arenaria aegaea	*Car*	T	x		2	recognized as islet specialist by Rechinger & Rechinger-Moser (1951: 201), Höner & Greuter (1988: 130), Raus (1990); distribution map in Strid & Tan (1997: map 308)
Asparagus horridus	*Asp*	G		x	29	recognized as islet specialist by Höner & Greuter (1988: 130) and Raus (1990: 35)
Atriplex recurva	*Che*	S	x		8	found in coastal sites of large islands but with a marked preference to small ones (see also Rechinger 1950: 255); distribution map in Strid & Tan (1997: map 232)
Cistanche phelypaea	*Oro*	G		x	3	parasitizing chiefly on *Atriplex halimus*; in the Aegean restricted to few small islands in the Cretan area (Raus 1990, Bergmeier et al. 2001)
Filago cretensis ssp. *cycladum*	*Ast*	T	x		2	distribution map in Wagenitz (1970: 121); since then the presumed affinity to islets of this subspecies was largely confirmed
Fibigia lunarioides	*Bra*	S	x		2	this chasmophyte was recognized as islet specialist by Rechinger & Rechinger-Moser (1951: 201)
Hornungia procumbens	*Bra*	T		x	8	recognized as islet specialist by Höner & Greuter (1988: 130) and Raus (1990: 35f.); nomenclature according to Appel & Al-Shehbaz (1997)
Lavatera arborea	*Mal*	T		x	16	recognized as facultative islet specialist by Runemark (1969), Höner & Greuter (1988: 130) and Raus (1990: 36)
Limonium doerfleri	*Plu*	P	x		0	recognized as islet specialist by Rechinger & Rechinger-Moser (1951: 201) and Raus (1990: 36); distribution map in Rechinger (1950: map 32)
Limonium sitiacum	*Plu*	P	x		6	recognized as islet specialist by Raus (1990: 36); distribution map in Mayer (1995: 78)
Medicago arborea	*Fab*	S		x	11	frequently planted; native populations in the Aegean mostly on cliffs of small islands; given as islet chasmophyte by Höner & Greuter (1988: 130)
Muscari dionysicum	*Hya*	G	x		5	restricted to few islands north of Kriti (Rechinger 1950: map 33; Rechinger & Rechinger-Moser 1951: 201)
Orobanche sanguinea	*Oro*	T		x	0	recognized as islet specialist by Höner & Greuter (1988: 130) and Raus (1990: 36)
Salsola aegaea	*Che*	S	x		24	mentioned as islet specialist by Rechinger (1950: 255), Höner & Greuter (1988: 130) and Raus (1990: 37); distribution map in Strid & Kit Tan (1997: map 253)
Salsola carpatha	*Che*	S	x		2	largely confined to cliffs on small islands in the NE Cretan area and adjacent Kiklades; distribution map in Strid & Kit Tan (1997: map 252)
Silene holzmannii	*Car*	T	x		1	recorded as islet specialist by Runemark (1969), Höner & Greuter (1988: 130) and Raus (1990: 37); distribution map in Strid & Kit Tan (1997: map 589)
Suaeda vera	*Che*	S		x	7	recorded as islet specialist by Runemark (1969), Höner & Greuter (1988: 130) and Raus (1990: 37); distribution map in Strid & Kit Tan (1997: map 246)
Trigonella rechingeri	*Fab*	T	x		2	recorded as islet specialist by Rechinger & Rechinger-Moser (1951: 201), Höner & Greuter (1988: 130) and Raus (1990: 37); distribution map in Höner (1991: 66)

islands and mainlands as well. The affinity to small islands of the species (and in one case subspecies) considered in Table 2 was realized by Rechinger (1950, Rechinger & Rechinger-Moser 1951) and subsequent plant geographers in the Aegean. Islet specialists form a heterogeneous group with respect to plant systematics, life form, and distribution. While most of the species are endemics of the Aegean (or part thereof), others (e.g., *Asparagus horridus*, *Cistanche phelypaea*, *Hornungia procumbens*, *Suaeda vera*) have a wider distribution area but proved to be islet specialists in the Aegean. Apomictic species (*Limonium*) are represented but this genus is still insufficiently known in the area. The genus *Anthemis* adds to the list of islet specialists with four species representing different subgenera. *A. werneri* is a constituent of islands in the north and west Aegean; *A. ammanthus* (with two subspecies) in the south; *A. glaberrima* on islets off the north-west coast of Kriti; and *A. scopulorum* chiefly in the Kiklades (central Aegean). Specialization to islets is not very pronounced except for the latter two, of which *A. scopulorum* is a 'classic' islet specialist.

The islet element is irregularly distributed in the Aegean phytogeographical regions (Table 3; data from the Kiklades (Kik), a region rich in islets

Table 3. Distribution of islet specialists in the Aegean plant geographical regions, according to present relevés and literature. NAe, North Aegean; WAe, West Aegean; EAe, East Aegean; Kik, Kiklades; KK, Kriti (Crete) and Karpathos.

Species	NAe	WAe	EAe	Kik	KK
Achillea aegyptiaca				x	
Allium commutatum	x	x	x	x	x
Anthemis ammanthus				x	x
Anthemis glaberrima					x
Anthemis scopulorum			x	x	x
Anthemis werneri	x	x		x	
Arenaria aegaea			x	x	x
Asparagus horridus		x	x	x	x
Atriplex recurva	x	x		x	x
Cistanche phelypaea					x
Filago cretensis ssp. cycladum				x	x
Fibigia lunarioides			x	x	x
Hornungia procumbens					x
Lavatera arborea		x	x	x	x
Limonium doerfleri				x	x
Limonium sitiacum					x
Medicago arborea		x	x	x	x
Muscari dionysicum					x
Orobanche sanguinea			x	x	x
Salsola aegaea			x	x	x
Salsola carpatha				x	x
Silene holzmannii			x	x	x
Suaeda vera			(x)	x	x
Trigonella rechingeri		x	x	x	x

and islet specialists but not represented by relevés, are taken from literature). Not only regional endemics, but also widespread species of the islet element may be restricted in their regional distribution. *Hornungia procumbens* and *Cistanche phelypaea*, for instance, are exclusive to the southern islet element of Kriti and Karpathos (KK), whereas *Lavatera arborea* is a frequent constituent of islet floras but very scattered in the south Aegean. The majority of islet specialists occurs in the central (Kiklades) and southern part of the Aegean (Kriti and Karpathos), while the islet element is relatively poorly represented in the north and west.

Islands supporting islet specialists may be characterized by their small size being of a magnitude between less than 0.1 to 500 ha or rarely more. The number of islet specialists for the islands investigated varies between 1 and 10 per islet, while the islet specialist ratio (i. e., the proportion of islet specialists in the total species number) is between 0.75 % and 75 % (Table 1). Fig. 2 shows the relation between area size and species number for 56 islets. Grazed and ungrazed islands have been distinguished. Minute islands of less than 1 ha surface area are not grazed while, to various extent, grazing has been an obligatory factor for islands of more than 30 ha. Islets of 1 to 30 ha comprise grazed and ungrazed ones. If grazed, the number of species is generally higher than for ungrazed islets (Fig. 2). The islet specialist ratio varies much among the smaller islands (Fig. 3). It is highest for minute ungrazed islands, and it approaches zero for islands of several hundreds of hectars. For islets between 1 and 30 ha, the islet specialist ratio is

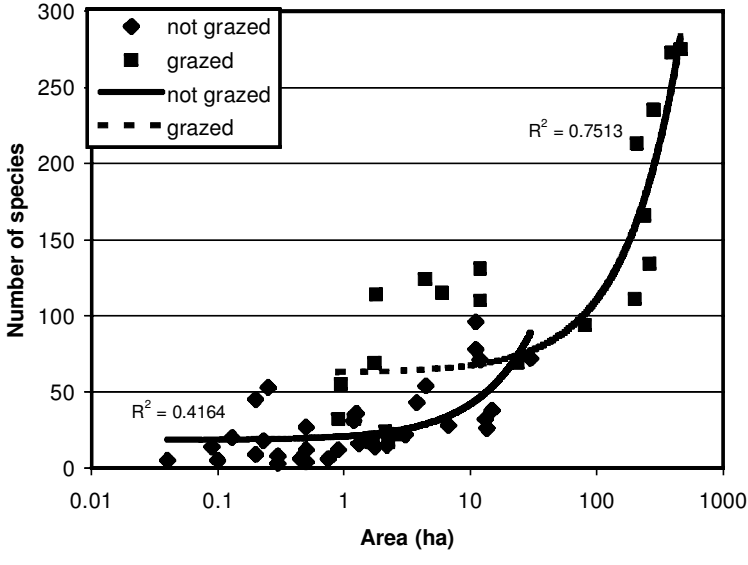


Fig. 2. The effect of grazing on species-area ratios of small Aegean islands (n = 56). The scaling of the horizontal axis (Area) is logarithmic, while the scaling of the regression curves is linear.

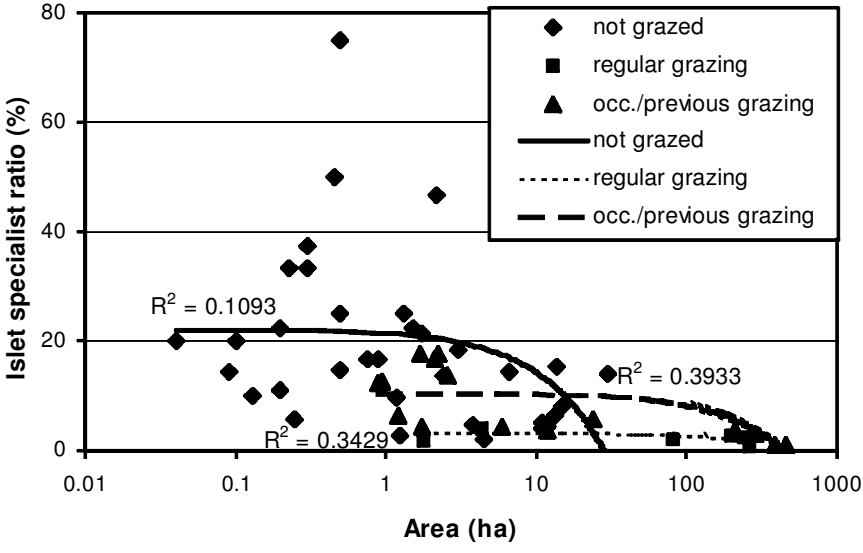


Fig. 3. The proportion of islet specialists in the floras of small Aegean islands (n = 56) under different grazing regimes. The scaling of the horizontal axis (Area) is logarithmic, while the scaling of the regression curves is linear.

generally higher for ungrazed islets, lower for regularly grazed ones, and intermediate for islets with grazing taking place occasionally or previously. The significance of the islets' size and topography for explaining the number of islet specialists decreases from ungrazed to regularly grazed islets while, for the islet specialist ratio, the explanatory value increases along increasing grazing intensity (Table 4).

3.2. Ordination analyses

The variation in species combinations of 30 islets of the Karpathos archipelago is shown by the CA diagrams (Fig. 4). Relatively species-rich islets are assembled in the left part of the diagram (low axis 1 values), and the islets grouped on the lower right are particularly low, small, and poor in species. An islet named Phira or 'Isola Monte' which consists of little more than a rising cliff forms an outlier on the upper right (Fig. 4A). Axis 1 is negatively correlated with species numbers, grazing intensity and altitude, while the islet specialist ratio is positively correlated (Table 5). The area size is well correlated with axis 3 (Fig. 4B). Grazing intensity explains more of the variance of the islet floras than does area size (Table 5). The proportion of islet specialists (Fig. 4B, right) and the occurrences of phrygana annuals (Fig. 4B, left) are indicated per island by the circle size in the inset diagrams. Phrygana annuals are almost restricted to grazed islets, and they are partic-

Table 4. Regression values (Pearson's correlation coefficient R and coefficient of determination R^2) of the environmental and diversity parameters for all islets investigated, and for a geographically restricted and three management-related partial data sets. Significance (P) at the 0.001 level: **, at 0.05 level: *, not significant: ns. Significance is also indicated by bold figures.

Variables		all islets (n = 56)			Karpathos archipelago (n = 30)			no grazing (n = 33)			previous or occasional grazing (n = 15)			regular grazing (n = 8)		
dependent	independent	R	R^2	P	R	R^2	P	R	R^2	P	R	R^2	P	R	R^2	P
Number of	Nr of species	**0.306**	**0.094**	*	**0.380**	**0.145**	*	0.345	0.119	ns	0.328	0.107	ns	0.210	0.044	ns
islet	Area	0.102	0.010	ns	0.268	0.072	ns	**0.529**	**0.280**	**	0.137	0.019	ns	0.389	0.152	ns
specialists	Altitude	**0.453**	**0.205**	**	0.331	0.110	ns	**0.681**	**0.464**	**	**0.649**	**0.422**	*	0.263	0.069	ns
Islet specialist	Area	**0.334**	**0.111**	*	0.226	0.051	ns	0.330	0.109	ns	**0.627**	**0.393**	*	**0.648**	**0.420**	*
ratio	Altitude	0.270	0.073	ns	0.132	0.018	ns	0.031	0.001	ns	0.338	0.114	ns	**0.671**	**0.450**	*

Table 5. Correlation matrix of the Correspondence analysis displayed in Fig. 4 using the species composition of 30 islets of the Karpathos archipelago. High (positive or negative) correlations are underlined.

	Axis 1	Axis 2	Axis 3	Axis 4	Altitude	Area	Nr Islet Specialists	Grazing intensity	Islet Specialist Ratio
Number of species	−0.899	0.161	0.158	0.218	0.763	0.313	0.264	0.898	−0.690
Islet Specialist Ratio	0.784	−0.373	−0.052	0.113	−0.367	−0.234	0.236	−0.544	1
Grazing intensity	−0.805	0.099	0.109	0.170	0.736	0.265	0.282	1	
Number islet specialists	−0.081	−0.177	0.256	0.489	0.271	0.255	1		
Area	−0.183	0.149	0.860	−0.185	0.495	1			
Altitude	−0.529	0.166	0.342	0.083	1				

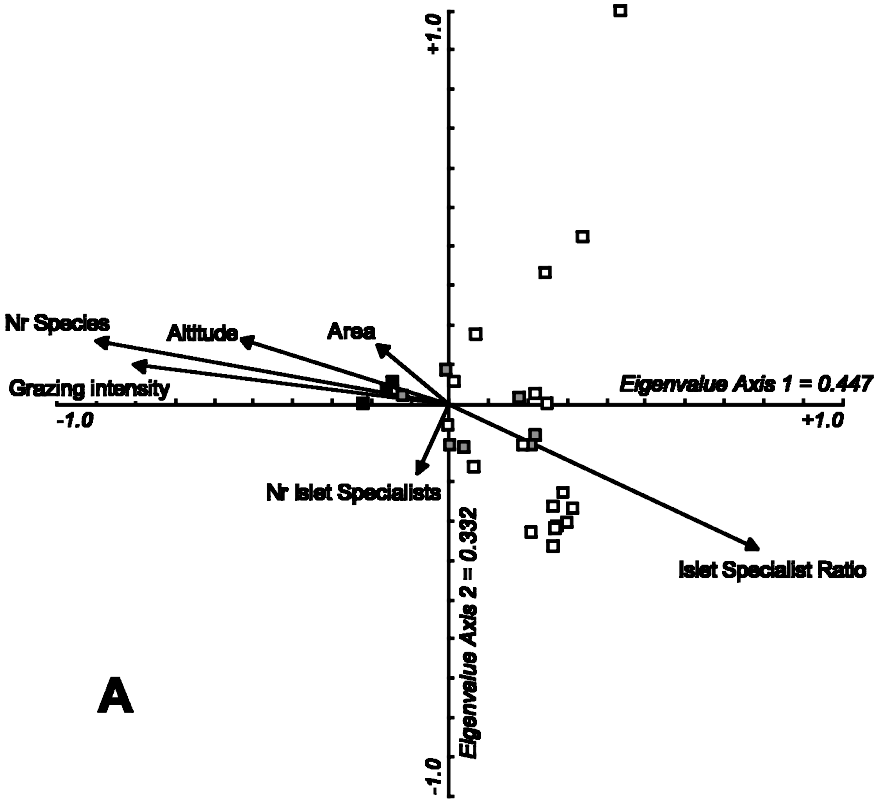
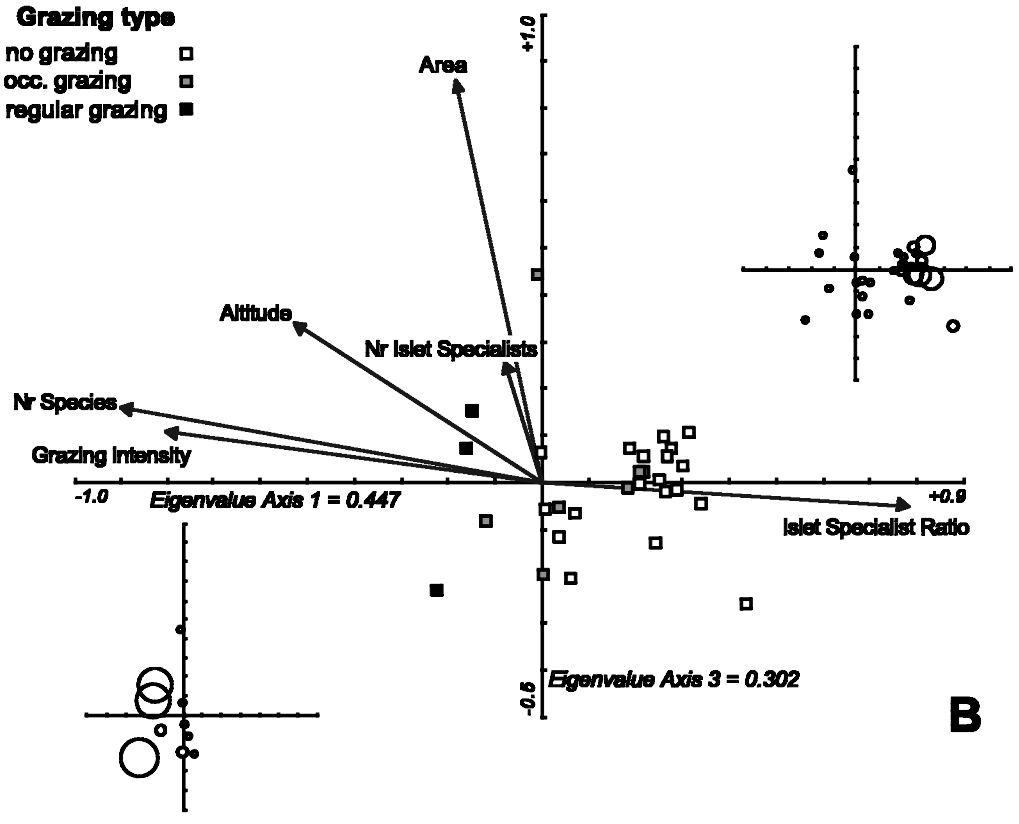


Fig. 4. CA diagrams (A – axes 1 and 2; B – axes 1 and 3) displaying the variance in the floristic composition of 30 islets of different grazing type in the Karpathos archipelago (source data from RAUS 1990 and HÖNER 1991). The islet scores are represented by squares, and the ordination axes are unconstrained by the environmental and diversity variables. The inset diagrams in B show the proportion of islet specialists (right) and the occurrences of phrygana annuals (left) per islet.

ularly abundant in the regularly grazed ones. Clearly, much of the high species numbers on grazed islets are due to phrygana annuals.

The variance along axis 2 (Fig. 4A) is poorly explained by the given variables, and species-environment correlations are consequently low for axis 2 (Tables 5 and 6). What axis 2 reflects becomes more transparent through the representation of habitat-related species groups on the islets (App. 1; Fig. 5). Chasmophytes of maritime cliffs are particularly well represented on islets in the upper part of the diagram. Halo-nitrophilous shrubs and islet specialists, on the other hand, are better represented on islets with low axis 2 values. Axis 2 is apparently best explained by a gradi-



ent of complex habitat qualities ranging from marly islets with a smooth relief to precipitous islets consisting of hard rock. For the given data set, the species groups comprising ephemeral halophytes and halo-nitrophilous shrubs, do not show restriction by grazing, while phrygana annuals and nitrophilous herbs show a clear preference to regularly grazed islets (Fig. 5). The floras of the small ungrazed islets assembling at high axis 1 values chiefly consist, to various proportions, of halonitrophilous shrubs, chasmophytes and islet specialists.

CCA results corroborate the high relevance of grazing for the understanding of species numbers and composition of islets. While each of the environmental variables adds significantly (at least at the 5 % significance level) to the total variance explained, the explanatory value of grazing intensity is higher than that of area size and altitude (Table 7). When excluding grazing intensity as an environmental variable, area size and altitude largely

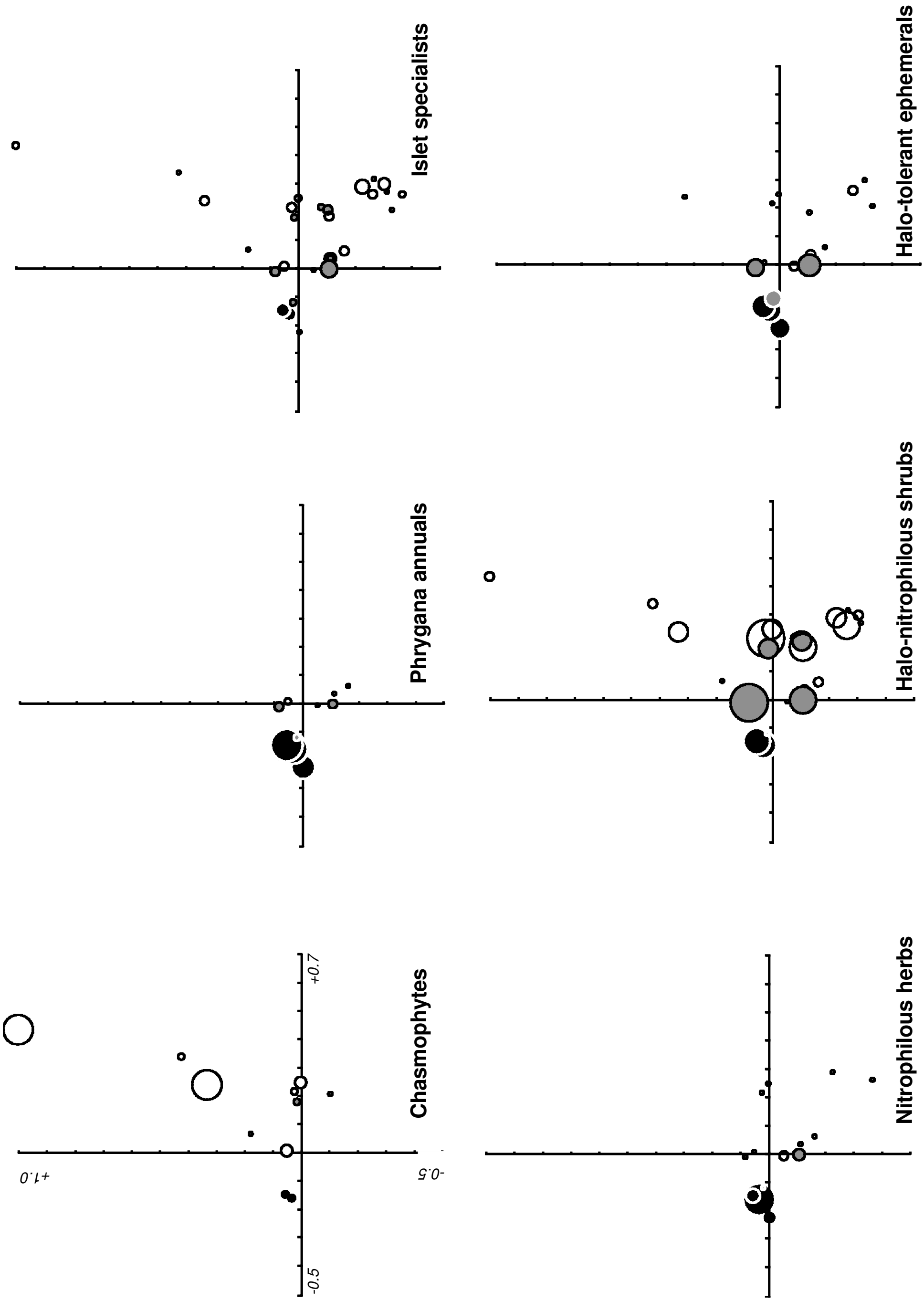

Islet specialists
Phrygana annuals
Chasmophytes
Halo-tolerant ephemerals
Halo-nitrophilous shrubs
Nitrophilous herbs
+0.7
-0.5
+1.0
-0.5

Fig. 5. Ordination diagrams (CA axes 1 and 2) of the species composition of 30 islets in the Karpathos archipelago. White circles indicate ungrazed, grey circles occasionally grazed, and black circles regularly grazed islets. The circle sizes indicate the number of occurrences per islet of species related to certain habitats (see App. 1).

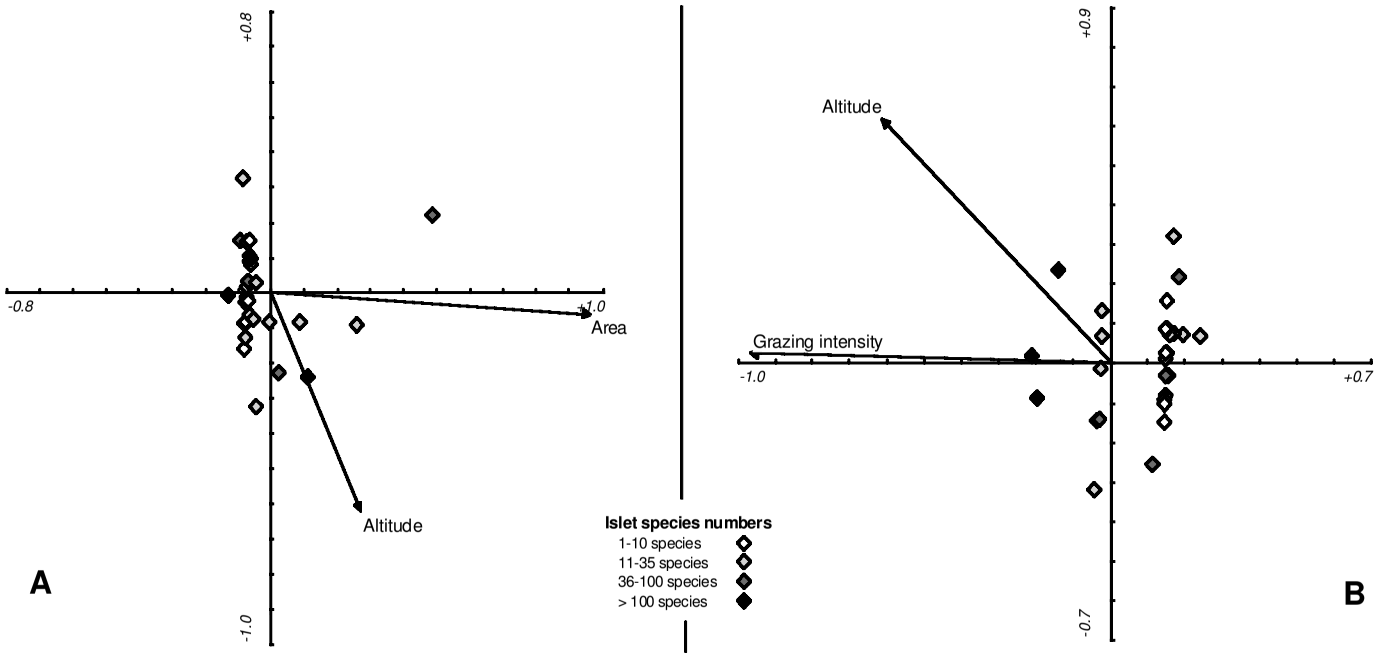


Fig. 6. Direct gradient analysis (CCA, axes 1 and 2) of the species composition of 30 islets in the Karpathos archipelago, grouped according to species numbers per island. Grazing intensity (A) and area size (B) are used as covariables, thus excluding the influence of each variable on the respective data set.

Table 6. Eigenvalues and species-environment correlations (SEC) of CA and CCA ordination axes, calculated on the basis of the floristic composition of 30 islets in the Karpathos archipelago. The total inertia is 4.234. CCA1 refers to the analysis with covariable 'Grazing intensity', CCA2 is with covariable 'Area'.

	Axis	1	2	3	4
CA	Eigenvalue	0.447	0.332	0.302	0.272
	SEC	0.947	0.446	0.878	0.634
CCA1	Eigenvalue	0.273	0.185	0.331	0.297
	SEC	0.970	0.963		
CCA2	Eigenvalue	0.348	0.186	0.331	0.297
	SEC	0.934	0.967		

Table 7. Monte Carlo permutation test results of significance between the environmental parameters and the species combinations of 30 islets in the Karpathos archipelago. Expl.Var. gives the additional variance each variable (in the given order) adds to the total variance explained by all variables (0.82). F, test statistic value; P, significance level.

	Expl.Var.	F	P
Grazing intensity	0.36	2.57	0.005
Area	0.27	2.05	0.005
Altitude	0.19	1.41	0.05

fail to explain the enormous variation in species numbers of the islets (Fig. 6A). When, however, area size was used as a covariable, the grazing intensity gradient (axis 1) explains much of the diversity pattern, with the highest species numbers neatly separated from the lowest (Fig. 6B).

3.3. Phytosociological classification

Characteristic features of the classified vegetation types are listed below. The order of communities follows the sequence of columns in the synoptic table (Table 8). Locations are given in *italics* if occurrences were assumed from general species distribution but are not substantiated by relevés. Phytogeographical regions are abbreviated as in Fig. 1 and Table 3.

Pistacia lentiscus-Periploca angustifolia community

Diagnostic and dominant species: *Pistacia lentiscus, Prasium majus, Periploca angustifolia*
Distribution: KK: Islands south of Kriti
Ecology: evergreen, wind-prone dense scrub of few decimetres height on dunes or calcareous coastal rock

Limoniastrum monopetalum community

Diagnostic and dominant species: *Limoniastrum monopetalum*
Distribution: KK: Islands south of eastern Kriti, *opposite coast of the main island*
Ecology: tall, dense, often vigorous, sometimes monodominant *Limoniastrum* stands on (periodically) wet saline sandy and/or gravelly coastal sites

Asparago stipularis-Atriplicetum halimi

Diagnostic and dominant species: *Atriplex halimus, Asparagus horridus, Lycium schweinfurthii, Cistanche phelypaea*
Distribution: KK: Islands south of eastern Kriti (Koufonisi, *Mikronisi*); *Karpathos and Kasos offshore islets*
Ecology: halo-nitrophilous scrub, on calcareous rock, flysch and sands; above the littoral belt, exposed to salt-spray; seldom further inland

Suaeda palaestina-Atriplex halimus community

Diagnostic and dominant species: *Suaeda palaestina, Atriplex halimus, Limonium graecum*, *Salsola aegaea, Lygeum spartum, Erodium crassifolium*
Distribution: KK: Koufonisi (south of eastern Kriti)
Ecology: xeric halophilous scrub on fixed dunes and calcareous marl

Atriplex halimus-Suaeda vera community

Diagnostic and dominant species: *Atriplex halimus, Asparagus horridus, Salsola aegaea, Reichardia orientalis, Suaeda vera, Muscari dionysicum, Anthemis ammanthus, Malcolmia flexuosa*
Distribution: KK: Dionysades: Paximada, Dragonada; *Trachilos* (south of eastern Kriti close to Koufonisi); *offshore islets in the Karpathos archipelago*; *Kik*: ?
Ecology: halo-nitrophilous vegetation of dwarf shrubs and herbs on calcareous rock and marl above the littoral belt; exposed to salt-spray

Anthemis ammanthus-Limonium sitiacum community

Diagnostic and dominant species: *Anthemis ammanthus, Senecio leucanthemifolius, Limonium sitiacum, Sedum litoreum, Frankenia hirsuta*
Distribution: KK: Dionysades: Janisada; Elassa (off north-east Kriti); *Dia*; *Karpathos archipelago: Kasos and offshore islets*
Ecology: Predominantly herbaceous epilitoral vegetation, calcareous flysch and limestone rock exposed to salt-spray

Table 8. Synoptic table of 111 relevé plots on small islands. Islet specialists are set bold and given even if rare; otherwise only species of diagnostic significance are shown. Constancy values in columns with 5 or more relevés are given in percent, in columns with 4 relevés as absolute number.

	Quercetea ilicis	Pegano-Salsoletea				Crithmo-Staticetea				Saginetea maritimae
Plant community	1	2	3	4	5	6	7	8	9	10
Number of relevés	10	10	14	13	9	7	27	5	4	12
Pistacia lentiscus	100	10	.	.	.	.	7	.	.	.
Prasium majus	70	10	21	8	33	.	.	.	.	.
Periploca angustifolia	60	30	.	.	.	.	.	.	.	.
Coridothymus capitatus	50	.	7	.	.	.	.	.	.	.
Atriplex mollis	30	.	.	.	.	.	.	.	.	.
Limoniastrum monopetalum	10	100	14	.	.	.	.	.	.	.
Arthrocnemum macrostachyum	.	40	7	15	22	.	19	.	2	.
Limonium graecum agg.	30	10	14	62	11	.	.	.	.	.
Asparagus horridus	40	.	86	31	89	14	.	.	.	.
Atriplex halimus	30	.	93	85	89	14	.	.	.	.
Salsola aegaea	30	.	36	54	56	.	15	.	.	.
Lycium schweinfurthii	.	.	79	15	.	.	.	.	.	.
Cistanche phelypaea	.	.	21	.	.	.	.	.	.	.
Suaeda palaestina	.	.	.	100	.	.	.	.	.	.
Lygeum spartum	.	.	7	69	.	.	.	.	.	.
Erodium crassifolium	.	.	.	54	.	.	.	.	.	.
Gynandriris monophylla	.	.	.	39	.	.	.	.	.	8
Plantago amplexicaulis	.	.	.	39	.	.	.	.	.	.
Reichardia orientalis	.	.	14	8	78	.	.	.	.	8
Suaeda vera	.	10	.	.	67	.	.	.	.	.
Muscari dionysicum	.	.	.	.	56	.	.	.	.	.
Bupleurum semicompositum	.	.	.	8	44	.	.	.	.	17
Silene sedoides	10	.	.	8	44	14	4	.	3	.
Medicago truncatula	.	.	.	.	44	.	4	.	.	.
Brassica cretica	.	.	.	.	44	.	11	.	.	.
Matthiola sinuata	.	.	.	.	44	.	.	40	.	.
Fibigia lunarioides	.	.	.	.	33	.	7	.	.	.
Limonium frederici	.	.	.	.	33	.	.	.	.	.
Trigonella rechingeri	.	.	.	.	22	.	.	.	.	.
Anthemis ammanthus	.	.	.	.	89	100	.	.	.	.
Senecio leucanthemifolius	.	.	.	.	33	100	11	.	.	8
Limonium sitiacum	.	.	.	.	.	86	.	.	.	.
Sedum litoreum	.	.	7	.	56	57	11	.	2	.
Frankenia hirsuta	.	.	.	.	33	57	22	20	1	8
Lotus cytisoides	10	.	.	.	33	14	37	.	.	.
Malcolmia flexuosa	.	.	7	.	100	.	63	40	3	8
Capparis orientalis	.	.	.	.	11	.	63	.	.	.
Lavatera arborea	.	.	.	.	.	.	59	.	.	.
Medicago arborea	.	.	.	.	.	.	41	.	.	.
Crithmum maritimum	.	.	.	.	.	29	41	.	.	.
Convolvulus oleifolius	20	.	.	.	.	.	33	20	.	.
Limonium narbonense	.	.	.	.	.	.	22	.	.	.

Table 8. (cont.)

Anthemis scopulorum	.	.	.	.	.	.	11	.	.	.
Allium commutatum	.	.	.	.	.	.	44	60	.	.
Anthemis werneri	.	.	.	.	.	.	11	100	.	.
Atriplex recurva	.	.	.	.	.	.	11	100	.	.
Trigonella balansae	.	.	.	.	.	.	.	80	1	.
Pancratium maritimum	10	.	.	8	.	.	.	40	.	.
Phleum arenarium	.	.	.	.	.	.	.	40	.	.
Elymus rechingeri	.	.	.	.	.	.	7	40	.	.
Muscari weissii	.	.	.	.	.	.	.	40	.	.
Beta maritima	.	.	.	.	.	.	.	40	.	.
Anthemis glaberrima	.	.	.	.	.	.	.	.	4	.
Inula crithmoides	.	.	.	.	.	.	.	.	4	.
Limonium spec.	.	.	.	.	.	.	.	.	2	.
Chlamydophora tridentata	.	10	7	46	.	.	.	.	.	83
Plantago weldenii	.	10	.	8	11	.	.	.	.	67
Hornungia procumbens	.	20	7	.	.	.	.	.	.	42
Bellium minutum	.	10	.	.	.	.	.	.	1	42
Filago aegaea	.	.	.	.	.	14	.	.	.	42
Phleum crypsoides	.	.	.	.	.	43	.	.	.	42
Limonium echioides	20	.	.	.	.	.	.	.	1	33
Sedum rubens	.	.	.	.	.	14	.	.	.	33
Erodium cicutarium	.	.	.	.	.	14	.	.	.	33
Sagina maritima	.	.	.	.	.	.	.	.	1	25
Catapodium marinum	.	.	.	8	.	.	4	.	2	25
Parapholis marginata	.	.	.	.	.	.	.	.	1	25
Filago cretensis ssp. cycladum	.	.	.	.	.	.	.	.	.	17
Parapholis incurva	.	.	.	8	.	.	7	.	.	17

Plant communities and origin of relevés (number of rels. in brackets):
1, *Pistacia lentiscus-Periploca angustifolia* comm.: KK: Gavdos (1), Gavdopoula (5), Chrisi (1), Makrouli (1), Strongili (2).
2, *Limoniastrum monopetalum* comm.: KK: Chrisi (9), Makrouli (1).
3, Asparago stipularis-Atriplicetum halimi: KK: Koufonisi (9), Makrouli (3), Strongili (2).
4, *Suaeda palaestina-Atriplex halimus* comm.: KK: Koufonisi (13).
5, *Atriplex halimus-Suaeda vera* comm.: KK: Paximada (6), Dragonada (3).
6, *Anthemis ammanthus-Limonium sitiacum* comm.: KK: Janisada (1), Elassa (6).
7, species combinations with *Lavatera arborea* and *Medicago arborea*: EAe: W Mavra (2), E Mavra (2), Mikro Kalapodi (1), E Imia (1), Prassonisi (2), Pitta (2); WAe: Kassidis (2), Strongylo I (6), unnamed islet close to Yioura (1), Strongylo II (1), Melissa (1), Korakas (3), Lachanou (3).
8, *Anthemis werneri-Atriplex recurva* comm.: NAe: Ajioi Apostoloi (3), Velia (2).
9, *Anthemis glaberrima-Inula crithmoides* comm.: KK: Agria Gramvousa (4).
10, *Chlamydophora tridentata* comm.: KK: Gavdos (3), Gavdopoula (1), Makrouli (3), Strongili (3), Elassa (2).

Lavatera arborea-Medicago arborea community

Diagnostic and dominant species: *Lavatera arborea, Medicago arborea, Capparis orientalis, Malcolmia flexuosa, Crithmum maritimum*
Distribution: WAe: Northern Sporades island complex (islets close to Skantzoura: Kassidis, Strongylo, Korakas, Lachanou, islet close to Kira Panagia: Melissa, islet close to Yioura: Strongylo, unnamed islet in Pnigmenos

bay); EAe: islets north-east of Kalymnos (East Imia, Prassonisi, Pitta), between Leros and Amorgos and more specifically between Kinaros and Levitha (E, W Mavra), south-east of Lipsi (Mikro Kalapodi); *Kik*: ?
Ecology: (sub)nitrophilous frutescent vegetation on moderately inclined islet rocks and steep islet cliffs

Anthemis werneri-Atriplex recurva community

Diagnostic and dominant species: *Anthemis werneri, Atriplex recurva, Trigonella balansae, Allium commutatum, Malcolmia flexuosa, Elymus rechingeri, Beta maritima*
Distribution: NAe: islets Velia (Roumbos) and Ajioi Apostoloi close to Aj. Evstratios; *WAe: Sporades, Skyros*
Ecology: subnitrophilous, perennial herbaceous vegetation on sandy or gravelly soil accumulated between coastal rock, exposed to salt-spray

Anthemis glaberrima-Inula crithmoides community

Diagnostic and dominant species: *Anthemis glaberrima, Inula crithmoides, Malcolmia flexuosa, Silene sedoides*
Distribution: KK: Agria Gramvousa, *Imeri Gramvousa* (?)
Ecology: coastal chasmophyte vegetation on step-crevices of limestone cliffs

Chlamydophora tridentata community

Diagnostic and dominant species: *Chlamydophora tridentata, Plantago weldenii, Bellium minutum, Hornungia procumbens, Filago aegaea, Phleum crypsoides, Limonium echioides*
Distribution: KK: Islands south and, without *Chlamydophora*, north-east of Kriti
Ecology: inconspicuous ephemeral halo-tolerant vegetation on sand, silt or fine gravel accumulated among coastal rock

4. Discussion and conclusions

4.1. Syntaxonomy

The plant communities on islets show affinities to different phytosociological classes (Table 8). As sand accumulation on small islands is generally poor, psammophilous vegetation (Cakiletea, Ammophiletea) is hardly represented, and therefore it is not treated in this paper. If present (not on minute islands, and not in exposed situations), sclerophyllous *Pistacia* scrub is found to be more wind-prone than anywhere else. It indicates the ecological limits of the Quercetea ilicis, and the Pistacio-Rhamnetalia. Due to the presence of *Periploca angustifolia* and other (sub)halo-tolerant species of south Mediterranean distribution, the classification of the *Pistacia*

scrub into the Periplocion angustifoliae is justified. The latter alliance was described by Rivas-Martínez (1975) to comprise the most xerophytic Pistacio-Rhamnetalia vegetation, chiefly that of North Africa and south-eastern Spain. Recently Brullo & Guarino (2000) have classified the *Pistacia-Juniperus* scrub of the south Aegean island of Chrisi within this alliance as well.

Halo-nitrophilous scrub with *Atriplex halimus* is among the most significant features in the Aegean islet vegetation, particularly in the south of the area. Other frutescent *Chenopodiaceae* such as *Salsola aegaea, S. carpatha, Atriplex mollis, Suaeda palaestina* and *S. vera* may locally be associated with *Atriplex halimus* or even become predominant. *Asparagus horridus*, *Limonium graecum* and *Lycium schweinfurthii* are more or less frequent constituents in this vegetation as well. The Pegano-Salsoletea to which the various species combinations found on south Aegean islets should be classified, is well-known on islands and mainland coasts in the West and Central Mediterranean (e.g., Brullo et al. 1985, Peinado et al. 1988, Rivas-Martínez et al. 1999). In the East Mediterranean only very scanty evidence on Pegano-Salsoletea vegetation was brought from Cyprus (Géhu et al. 1990), Karpathos (Géhu et al. 1992) and Chrisi (Brullo & Guarino 2000). The class is probably more widespread in the Aegean than the few plots recorded so far might suggest, and it seems to be most representative and variable on small islands. Brullo & Guarino (2000) described a Pegano-Salsoletea association from Chrisi dominated by *Limoniastrum monopetalum* accompanied by *Asparagus horridus* and *Lycium schweinfurthii*. In our relevés from the same area, the *Limoniastrum* stands are not always associated with the Pegano-Salsoletea species. Stands with *Atriplex halimus* and *Asparagus horridus* in the Aegean are almost identical with the Asparago stipularis-Atriplicetum halimi described by Géhu et al. (1990) from northern Cyprus. The other Pegano-Salsoletea communities on small Aegean islands are less similar to any described vegetation type. They are probably best attributable to the Atriplici halimi-Suaedion verae described by Géhu et al. (1990), an alliance based on two associations from Cyprus. The latter name is validated here by completing the insufficient original diagnosis. The missing elements concern art. 8 of CPN (Weber et al. 2000): *Asparagus horridus* ('*A. stipularis*'), *Atriplex halimus* and *Lycium schweinfurthii* ('*L. ferocissimum*') are indicated here as diagnostic species of the alliance; and Géhu et al. (1990: 225, table 11, rel. 5) is designated lectotypus for the association Asparago stipularis-Atriplicetum halimi, which is the nomenclatural type chosen by Géhu et al. (1990) for the Atriplici halimi-Suaedion verae. Géhu et al. (1990: 210, 218) designated erroneously rel. no. 6 in table 11 as type; however, such a number does not exist in his table 11 which comprises only the relevés numbered 1–5.

Plant communities of coastal rocks under salt-spray influence (Crithmo-Staticetea) are well represented in the vegetation of islets. The proportion of shrubs is commonly lower, that of herbs mostly higher than

in the Pegano-Salsoletea. We are far from overlooking the full syntaxonomic range of the class in the Aegean, and the variation known from islet plots does not permit formal syntaxonomy beyond the order level. Therefore, at present state of knowledge, we refrain from formal description of vegetation types.

The Saginetea maritimae and the Frankenietalia pulverulentae are poorly known in the Eastern Mediterranean and have often been overlooked by students of the coastal vegetation. Characteristic herbaceous species combinations on Aegean islets were found on sandy or silty soils. There is considerable salt input by sea-spray, but freshwater conditions may temporarily prevail in winter due to increased rainfall. The Frankenietalia communities are probably widespread in the Aegean, and the *Chlamydophora* community is likely to be the most thermophilous among those. It has only been found on the small islands south of Kriti, but it does not apparently depend on specific islet environments. A similar species combination was mentioned from Cyprus (Holmboe 1914: 210). The halotolerant, slightly succulent asteraceous annual *Chlamydophora tridentata* belongs to the North African phytogeographical element. The *Chlamydophora* community should be classified within the Limonion avei which was proposed to comprise the Central and Eastern Mediterranean Frankenietalia vegetation (Brullo 1988a: 48). The alliance name is corrected here to the Limonion echioidis, according to art. 43 of CPN (Weber et al. 2000). In contrast to Brullo (1988b), no records of *Limonium avei* are known from the Aegean, nor apparently from elsewhere in the Eastern Mediterranean (Erben, in litt.). All material seen belongs to *Limonium echioides* (Bergmeier et al. 1997: 334).

Syntaxa and communities treated in the present paper are listed in the conspectus below:

Quercetea ilicis Br.-Bl. ex de Bolòs 1950
  Pistacio lentisci-Rhamnetalia alaterni Rivas-Martinez 1975
    Periplocion angustifoliae Rivas-Martinez 1975
      Pistacia lentiscus-Periploca angustifolia community

Pegano harmalae-Salsoletea vermiculatae Br.-Bl. & de Bolòs 1958
  Salsolo vermiculatae-Peganetalia harmalae Br.-Bl. & de Bolòs 1955
    Atriplici halimi-Suaedion verae Géhu et al. ex Bergmeier & Dimopoulos hoc loco
      Asparago stipularis-Atriplicetum halimi Géhu et al. ex Bergmeier & Dimopoulos hoc loco
      Limoniastrum monopetalum community
Suaeda palaestina-Atriplex halimus community
Atriplex halimus-Suaeda vera community

Crithmo-Staticetea Br.-Bl. in Br.-Bl. et al. 1952
  Crithmo-Staticetalia Molinier 1934
    ?

Anthemis ammanthus-Limonium sitiacum community
Lavatera arborea-Medicago arborea community
Anthemis werneri-Atriplex recurva community
Anthemis glaberrima-Inula crithmoides community

Saginetea maritimae Westhoff et al. 1962
Frankenietalia pulverulentae Rivas-Mart. ex Castroviejo et Porta 1976
Limonion echioidis Brullo 1988 nom. corr. hoc loco ('Limonion avei')
Chlamydophora tridentata community

4.2. Habitat preferences of islet specialists

Our studies suggest that islet specialists form an ecologically heterogeneous group. The classification approach finds islet specialists in various Pegano-Salsoletea and Crithmo-Staticetea communities. These classes may jointly be considered phytosociological equivalents to the epilitoral zone (or 'sublitoral', 'supralitoral', 'paenelitoral' in the terms of Runemark 1969, Höner & Greuter 1988, and Höner 1991, respectively). The Crithmo-Staticetea communities distinguished in the present paper, each with its own set of islet specialists, rather reflect a geographical pattern. However, a more fine-scaled analysis of islets can be expected to reveal more detailed spatial patterns and habitat preferences of islet specialists. On small islands, *Medicago arborea* forms part of a characteristic chasmophytic vegetation of maritime cliffs (Rechinger & Rechinger-Moser 1951, Runemark 1969, Höner 1991). Such vegetation is poorly documented so far, and almost no relevés exist from islets. The same is true for *Allium*-dominated islets, many of which carry the Greek name 'Prasonisi' ('Island of Leeks').

Most prominent in Aegean islet vegetation are the plant communities of coastal rocks (Crithmo-Staticetea), and halo-nitrophilous scrub (Pegano-Salsoletea). The significance of the latter, if compared to large islands and mainland coasts in the wider area, is a peculiar feature of islets and is probably associated with nutrient input ('guano-trophication') caused by excrements of nesting or resting sea-fowl and migrating birds. While the halophilous Crithmo-Staticetea vegetation forms a more or less narrow belt along the coasts of mainlands and larger islands, the belt may be considerably wider on islets (Höner 1991). This and the consequently marginal role of phrygana vegetation is due to the prevailing influence of salt-spray which is commonly blown all over the small islands during the frequent storms. In semi-arid climates, such as that of the Aegean, salt accumulates in soils and selects for the halo-tolerant Crithmo-Staticetea vegetation. Höner (1991: 145) explains the phenomenon to be related to the much reduced 'pressure' of diaspores of phrygana species on islets, compared to the amounts encountered on the coasts of larger islands.

4.3. Islet floras, islet specialists and the influence of grazing

For islets of 1 to 30 ha surface area, two general conclusions may be drawn from our data: The species-area relation increases with grazing, and the proportion of islet specialists decreases. The unusually high number of species on grazed islets results chiefly from annuals which are otherwise abundant in the principal rangeland vegetation of the big islands and mainlands, the phrygana. High species numbers on islands or, more precisely, high numbers of annuals suggest human interference (Höner 1991, Panitsa et al. 1994, Panitsa & Tzanoudakis 1998, pers. obs.). It is safe to assume that the seasonal browsers on the islets, the goats, introduce diaspores. Since the diaspores of many annuals are armed with hooked or barbed spines or other appendages, they qualify for being transported via goatskin. The absence of islet specialists on big islands and mainlands, and their relatively low proportions on regularly grazed small islands, is probably due to two reasons:

- islet specialists are susceptible to direct mechanical damage through browsing (as exemplified by Höner 1991 in the case of *Silene holzmannii*),
- introduced species (by goats) shift the competitive balance of the species to the cost of islet specialists.

The influence of grazing on the floristic composition of islets and the occurrence of islet specialists cannot quite as well be predicted for the smallest islands (< 1 ha) and for those of more than 30 ha. The former have never been grazed (and in the first place do not produce enough fodder to make grazing economically reasonable), and among the latter, unfortunately, untouched islands which would be required for comparison are lacking. We may assume that grazing enhanced the rate of introduction of species to such islands, and that it caused extinctions of susceptible species. What we do not know is how long it will take to turn such effects after grazing has come to an end. On the Dionisades islets (200–300 ha), not anymore grazed since more than 20 years now, we observed species susceptible to grazing, such as the islet specialists *Medicago arborea* and *Fibigia lunarioides*, spreading from inaccessible cliffs to even grounds (Bergmeier & Dimopoulos 2001).

Aegean islets and its floras suffer from grazing, and a consequence of what we know should be to leave more of them ungrazed and untouched in any respect. Insight into the necessities of effective nature conservation for these fascinating ecosystems should be disseminated particularly among fishermen and other residents of the larger islands of the Aegean.

Acknowledgements. We thank Laco Mucina and an anonymous reviewer for constructive comments and suggestions on a first version of the manuscript. The field research was funded by the Greek Ministry of Environment, Regional Planning and Public Works (YPEXODE), in the framework of the Greek Natura 2000 Habitat Types Mapping and Documentation Project. Logistic support from the Athens University team (Department of Biology, Section of Botany) is gratefully acknowledged.

References

Appel, O. & Al-Shehbaz, I. A. (1997): Generic limits and taxonomy of Hornungia, Pritzelago, and Hymenolobus (Brassicaceae). – Novon **7**: 338–340.

Bergmeier, E. & Dimopoulos, P. (2001): Chances and limits of floristic island inventories – the Dionysades group (South Aegean, Greece) re-visited. – Phyton (Horn, Austria) **41**: 277–293.

Bergmeier, E., Jahn, R. & Jagel, A. (1997): Flora and vegetation of Gávdos (Greece), the southernmost European island. I. Vascular flora and chorological relations. – Candollea **52**: 305–358.

Bergmeier, E., Kypriotakis, Z., Jahn, R., Böhling, N., Dimopoulos, P., Raus, Th. & Tzanoudakis, D. (2001): Flora and phytogeographical significance of the islands Chrisi, Koufonisi and nearby islets (South Aegean, Greece). – Willdenowia **31**: 329–356.

Bothmer, R. von (1974): Studies in the Aegean flora. XXI. Biosystematic studies in the Allium ampeloprasum complex. – Opera Bot. **34**: 1–104.

Brullo, S. (1988a): Le associazione della classe Frankenietea pulverulentae nel Mediterraneo centrale. – Acta Bot. Barcinon. **37**: 45–57.

– (1988b): Miscellaneous notes on the genus Limonium (Plumbaginaceae). – Willdenowia **17**: 1–18.

Brullo, S. & Guarino, R. (2000): Contribution to the knowledge of flora and vegetation of Khrisi islet (Crete, SE Mediterranean sea). – Fl. Medit. **10**: 265–282.

Brullo, S., Guglielmo, A. & Pavone, P. (1985): La Classe Pegano-Salsoletea in Sicilia. – Boll. Acc. Gioenia Sci. Nat. **18**: 247–254.

Christodoulakis, D., Economidou, E. & Georgiadis, Th. (1991): Geobotanische Studie der Grabusen-Inseln (Südägäis, Griechenland). – Bot. Helv. **101**: 53–67.

Davis, P. H. (ed.) (1965–1985): Flora of Turkey and the East Aegean Islands. Vols. **1**–**9**. – Edinburgh University Press, Edinburgh.

Géhu, J.-M., Costa, M. & Uslu, T. (1990): Analyse phytosociologique de la végétation littorale des côtes de la partie turque de l'île de Chypre dans un souci conservatoire. – Doc. Phytosociol. **12**: 203–234.

Géhu, J.-M., Apostolides, N., Géhu-Franck, J. & Arnold, K. (1992): Premières données sur la végétation littorale des îles de Rodhos et de Karpathos (Grèce). – Coll. Phytosociol. **19** ('1989'): 545–582.

Georgiou, O. (1991): Anthemis werneri (Asteraceae), an endemic species of the Aegean islands (Greece). – Bot. Chron. **10**: 741–747.

Greuter, W. (1970): Zur Paläogeographie und Florengeschichte der südlichen Ägäis. – Feddes Repert. **81**: 233–242.

– (1972): Betrachtungen zur Pflanzengeographie der Südägäis. – In: Strid, A. (ed.): Evolution in the Aegean. – Opera Bot. **30**: 49–64.

– (1995): Origin and peculiarities of Mediterranean island floras. – Ecol. Medit. **21**(1/2): 1–10.

– (2001): Diversity of Mediterranean island floras. – Bocconea **13**: 55–64.

Greuter, W. & Pieper, H. (1975): Notiz zur Flora und Biogeographie der landfernen südägäischen Klippe Avgo. – Candollea **30**: 7–11.

Greuter, W. & Raus, Th. (eds.) (1999): Med-Checklist Notulae, 18. – Willdenowia **29**: 51–67.

Gustafsson, M. & Snogerup, S. (1974): Studies in the Aegean flora. XXII. The flora of the island of Skantzoura. – Bot. Not. **127**: 364–372.

Hennekens, S. M. & Schaminée, J. H. J. (2001): TURBOVEG, a comprehensive data base management system for vegetation data. – J. Veg. Sci. **12**: 589–591.

Hill, M. O. (1979): TWINSPAN. A FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. – Ecology and Systematics, Cornell University, Ithaca, NY.

Holmboe, J. (1914): Studies on the vegetation of Cyprus, based upon researches during the spring and summer 1905. – Bergens Museums Skrifter, N. R. **1**(2): vi + 342.

Höner, D. (1991): Mehrjährige Beobachtungen kleiner Vegetationsflächen im Raume von Karpathos (Nomos Dhodhekanisou, Griechenland). Ein Beitrag zur Klärung des "Kleininselphänomens". – Diss. Bot. **173**: [5] + III + 185, attachments.

Höner, D. & Greuter, W. (1988): Plant population dynamics and species turnover on small islands near Karpathos (South Aegean, Greece). – Vegetatio **77**: 129–137.

Jahn, R. & Schönfelder, P. (1995): Exkursionsflora für Kreta. – Ulmer, Stuttgart.

Mayer, A. (1995): Comparative study of the coastal vegetation of Sardinia (Italy) and Crete (Greece) with respect to the effects of human influence. – IHW-Verlag, Eching bei München.

Panitsa, M. (1997): Symbole ste gnose tes hloridas kai tes blasteses ton nesidon tou Anatolikou Aigaiou. [Contribution to the knowledge of the flora and vegetation of the east Aegean islets (Greece).] – PhD thesis, University of Patras, Patras.

Panitsa, M. & Tzanoudakis, D. (1998): Contribution to the study of the Greek flora: Flora and vegetation of the E Aegean islands Agathonisi and Pharmakonisi. – Willdenowia **28**: 95–116.

Panitsa, M., Dimopoulos, P., Iatrou, G. & Tzanoudakis, D. (1994): Contribution to the study of the Greek flora: Flora and vegetation of the Enousses (Oinousses) islands (E. Aegean area). – Flora **189**: 69–78.

Peinado, M., Martínez Parras, J. M., Bartolomé, C. & Alcaraz, F. (1988): Sintesis sintaxonomica de la Clase Pegano-Salsoletea en España. – Doc. Phytosociol. **11**: 283–301.

Raus, Th. (1990): Die Flora von Armathia und der Kleininseln um Kasos (Dodekanes, Griechenland). – Bot. Chron. ('1989') **9**: 19–39

Rechinger, K. H. (1943): Flora Aegaea. Flora der Inseln und Halbinseln des ägäischen Meeres. – Akad. Wiss. Wien, Math.-Naturwiss. Kl., Denkschr. **105**(1): xx + 924 + maps.

– (1950): Grundzüge der Pflanzenverbreitung in der Ägäis I–III. – Vegetatio **2**: 55–119, 239–308, 365–386.

Rechinger, K. H. & Rechinger-Moser, F. (1951): Phytogeographia Aegaea. – Akad. Wiss. Wien, Math.-Naturwiss. Kl., Denkschr. **105**(2.2): 1–208 + tables.

Rivas-Martínez, S. (1975): La vegetación de la clase Quercetea ilicis en España y Portugal. – Anal. Inst. Bot. A. J. Cavanilles **31**: 205–259.

Rivas-Martínez, S., Fernández-González, F. & Loidi, J. (1999): Check-list of plant communities of Iberian Peninsula, Balearic and Canary Islands to suballiance level. – Itin. Geobot. **13**: 353–451.

Runemark, H. (1969): Reproductive drift, a neglected principle in reproductive biology. – Bot. Not. **122**: 90–129.

– (1970): The role of small populations for the differentiation in plants. – Taxon **19**: 196–201.

– (1972): The phytogeography of the central Aegean. – Opera Bot. **30**: 20–28.

Sfougaris, A. I. & Papageorgiou, N. K. (1999): Effects of different management practices on vegetation structure of some Greek island ecosystems. – In: Papanastasis, V. P., Frame, J. & Nastis, A. S. (eds.): Grasslands and woody plants in Europe. Proceedings of the International Occasional Symposium of the European Grassland Federation, Thessaloniki, Greece, May 27–29, 1999, pp. 413–417. – Thessaloniki.

Snogerup, S. (1967): Studies in the Aegean flora. IX. Erysimum sect. Cheiranthus. B. Variation and evolution in the small-population system. – Opera Bot. **14**: 1–86.

Snogerup, S. & Snogerup, B. (1987): Repeated floristical observations on islets in the Aegean. – Plant Syst. Evol. **155**: 143–164.
Snogerup, S., Snogerup, B., Phitos D., Kamari G., & Anagnostopoulos A. (1991): Flora and vegetation of Kira Panagia, N Sporades, Greece. – Bot. Chron. **10**: 547–566.
Speta, F. (2000): Beitrag zur Kenntnis der Gattung Prospero Salisb. (Hyacinthaceae) auf der griechischen Insel Kreta. – Linzer Biol. Beitr. **32**: 1323–1326.
– (2001): Die Echte und die Falsche Meerzwiebel: Charybdis Speta und Stellarioides Medicus (Hyacinthaceae), mit Neubeschreibungen und Neukombinationen im Anhang. – Stapfia **75**: 139–176.
Strid, A. (1970): Studies in the Aegean flora XVI. Biosystematics of the Nigella arvensis complex with special reference to the problem of non-adaptive radiation. – Opera Bot. **28**: 1–169.
– (1996): Phytogeographia Aegaea and the Flora Hellenica Database. – Ann. Naturhist. Mus. Wien **98 B Suppl.**: 279–289.
Strid, A. & Kit Tan (eds.) (1997): Flora Hellenica, **1**. – Koeltz, Königstein.
ter Braak, C. J. F. & Šmilauer, P. (1998): CANOCO Reference Manual and User's Guide to Canoco for Windows: Software for Canonical Community Ordination (version 4). – Microcomputer Power, Ithaca, NY, USA.
Tutin, T. G. et al. (eds.) (1968–1980, 1993): Flora Europaea. Vols. **2**–**5**, Vol. **1** (2nd ed.). – Cambridge University Press, Cambridge.
Wagenitz, G. (1970): Die Gattung Filago L. s.l. (Compositae-Inuleae) in der Ägäis. – Willdenowia **6**: 115–138.
Weber, H. E., Moravec, J. & Theurillat, J.-P. (2000): International Code of Phytosociological Nomenclature. 3rd edition. – J. Veg. Sci. **11**: 739–768.

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Appendix 1

Habitat-related species groups which have been used for the interpretation of the CA pattern of 30 islet floras in the Karpathos archipelago (see Fig. 5).

A. Chasmophytes:
- *Allium bourgeaui* subsp. *bourgeaui*
- *Brassica cretica* subsp. *cretica*
- *Capparis orientalis*
- *Euphorbia dendroides*
- *Matthiola sinuata*
- *Medicago arborea*
- *Scariola acanthifolia*

B. Phrygana annuals:
- *Anagallis arvensis*
- *Tractylis cancellata*
- *Vena barbata*
- *Brachypodium distachyon*
- *Bromus fasciculatus*
- *Bromus intermedius*
- *Bromus haussknechtii*
- *Catapodium rigidum*
- *Daucus involucratus*
- *Erodium malacoides*
- *Euphorbia peplus*
- *Lagoecia cuminoides*
- *Lotus edulis*
- *Lotus peregrinus*
- *Medicago coronata*
- *Medicago disciformis*
- *Picris altissima*
- *Plantago lagopus*
- *Psilurus incurvus*
- *Trifolium campestre*
- *Trifolium scabrum*

C. Islet specialists:
- *Allium commutatum*
- *Anthemis ammanthus* subsp. *ammanthus*
- *Arenaria aegaea*
- *Asparagus horridus*
- *Filago cretensis* subsp. *cycladum*
- *Hornungia procumbens*
- *Lavatera arborea*
- *Medicago arborea*
- *Orobanche sanguinea*
- *Salsola aegaea*
- *Salsola carpatha*
- *Silene holzmannii*
- *Suaeda vera*
- *Trigonella rechingeri*

D. Nitrophilous herbs:
- *Chenopodium murale*
- *Convolvulus althaeoides*
- *Fumaria macrocarpa*
- *Geranium rotundifolium*
- *Lavatera arborea*
- *Mercurialis annua*
- *Malva parviflora*
- *Malva sylvestris*
- *Oxalis pes-caprae*
- *Reseda alba*
- *Sonchus oleraceus*

E. Halo-nitrophilous shrubs:
- *Asparagus horridus*
- *Atriplex halimus*
- *Lycium schweinfurthii*
- *Salsola aegaea*
- *Suaeda vera*

F. Halo-tolerant ephemerals:
- *Bellium minutum*
- *Catapodium marinum*
- *Filago cretensis* subsp. *cycladum*
- *Hornungia procumbens*
- *Limonium echioides*
- *Parapholis incurva*
- *Parapholis marginata*
- *Phleum crypsoides*
- *Plantago weldenii*
- *Sagina maritima*