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Plant population dynamics and species turnover on small islands near Karpathos (South Aegean, Greece)

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Abstract

The vascular flora of small offshore islets around Karpathos (Dodecanesos, Greece) has been surveyed and monitored during six consecutive years. The present study focuses on four islets that are inhabited by the 'islet specialist' *Silene holzmannii* (Caryophyllaceae), a species that has a widely scattered distribution in the Aegean where it exclusively occurs on very small islands. Repeated census of its populations, partly following controlled extirpation, reveals extreme variation in number of individuals. Sowing experiments involving various species demonstrate the low probability of successful new colonizations. Differences in the amount of apparent turnover of species as well as the occurrence of both stable micro-populations and mass-populations are discussed.

Nomenclature: Barclay (1986), Greuter *et al.* (1983, 1984, 1986) and Tutin *et al.* (1964–1980): Flora Europaea.

Introduction

Rechinger (1951: 201) was the first to recognize the floristic peculiarity that is a general feature of small islands in the Aegean Sea. He found that some plant species exclusively occur on such islets and are never found in similar habitats on larger islands. Besides these 'islet specialists' proper, Rechinger (1951: 167) also noticed that a number of so-called chasmophytes, i.e., taxa that are strictly limited to crevices of limestone cliffs on larger islands in the Aegean area, are able to colonize other habitats when occurring on small islands. In the following the term 'islet chasmophytes' will be used for this kind of species.

Rechinger's observations were since confirmed by others who had explored some of the countless islets of the Aegean Sea (Runemark 1969; Greuter 1972; Gustafsson & Snogerup 1974; Greuter & Pieper 1975; Snogerup *et al.* 1980; and Snogerup & Snogerup 1987).

In the course of the preparation of a checklist of the Karpathos flora (Greuter *et al.* 1983) the offshore islets surrounding the main island of Karpathos were thoroughly investigated. Eleven of them were selected for a detailed study of the quantitative and qualitative composition of their flora and of their changes in time and space (Fig. 1). Most of them are small enough to enable a complete inventory of their flora. Only three have been used for grazing purposes during the span of observation, and most are inhabited by at least some islet specialists and/or islet chasmophytes (Tables 1 and 2).

In this paper floristic changes observed on four of these islets (Nos 2, 4, 6 and 8) are discussed in detail, with special emphasis on the population dynamics of the islet specialist *Silene holzmannii* (caryophyl-

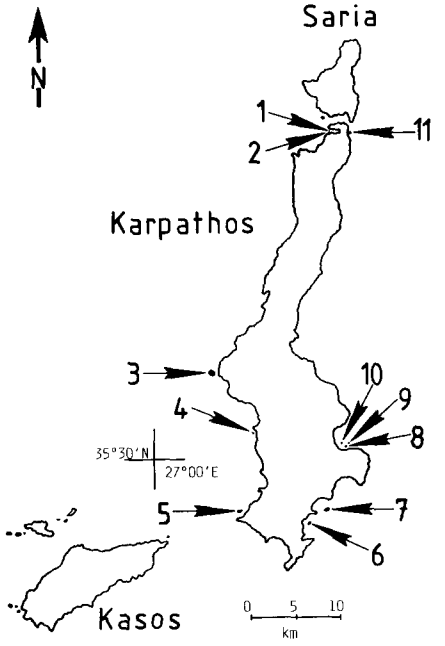


Fig. 1. Investigated islets near Karpathos (Dodecanesos, Greece). Numbers are used instead of names to designate the different islets. Generally known names exist for six islets only: No 3 = Sokastro, No 5 = Diakoptis, No 6 = Prasonisi, No 7 = Mira, No 9 = Despotiko, and No 11 = Ammoui.

Table 1. Plants confined to offshore islets in the Karpathos area ('islet specialists'). The numbers refer to the different islets as shown in Fig. 1.

	Plant name	Islets with positive records (disregarding sowing experiments)
	Salsola aegaea	6, 7, 9
Shrubs	*Suaeda vera*	3, 6
	Convolvulus oleifolius ssp. *scopulorum*	7, 8, 9
	Allium commutatum	6, 8, 9
Geophytes	*Asparagus stipularis*	3, 5, 6, 7, 8, 9
	Ornithogalum creticum	9
Biennials	*Lavatera arborea*	4, 7
	Silene holzmannii	2, 4, 6, 8
	Anthemis ammanthus ssp. *ammanthus*	3
	Anthemis ammanthus ssp. *paleacea*	7
Annuals	*Anthemis scopulorum*	2
	Hymenolobus procumbens ssp. *procumbens*	6, 7
	Trigonella rechingeri	2, 8, 10
	Orobanche sanguinea	8, 9

Table 2. Chasmophytic plant species confined to cliffs on Karpathos but growing outside of cliffs on small islands ('islet chasmophytes'). The numbers refer to the different islets as shown in Fig. 1.

	Plant name	Islets with positive records (disregarding sowing experiments)
	Achillea cretica	11
Shrubs	*Helichrysum orientale*	1
	Medicago arborea	4
Geophytes	*Allium bourgeaui* ssp. *bourgeaui*	4
Biennials	*Matthiola sinuata* ssp. *glandulosa*	4

laceae), a species that these four islets have in common and that has not so far been found elsewhere on or around Karpathos.

The area

Karpathos is the second largest island of the Dodecanesos. It is situated in the South Aegean Sea about halfway between Crete and Rhodes (coordinates see Fig. 1). The climate may be characterized as typically Mediterranean with a hot, dry summer and a cool, rainy winter. Normally rainfall is heaviest in January and February. The total amount of annual precipitation may vary considerably: Within a seven-year period (1971 to 1977) a maximum annual rainfall of 560 mm and a minimum of 230 mm were measured (Fischer 1980). There are only few days of calm weather in the course of the year. Strong winds are blowing almost permanently, mostly from the north-west but sometimes turning into warm southerly storms. Wind force frequently reaches values of 5–6 on the Beaufort scale (Fischer 1980).

The islets surrounding Karpathos mainly consist of calcareous rocks, sometimes overlain by sandstones (Christodoulou 1963). Rocky depressions are filled with clayey or sandy soil or with pebbles of varying size. Taking into consideration the present sea depths and the postulated values of eustatic lowering of the sea level during the past glaciations (Pfannenstiel 1951), as has been done by Greuter

(1970), one must conclude that all offshore islets of Karpathos have been fused to the main island up to the late Pleistocene. There is no evidence for post-glacial catastrophic events that might have impaired the islet floras. In particular, the influence of the eruption of the Santorin volcano (situated ca 180 km NW of Karpathos, eruption ca 1500 B.C.) on the eastern Mediterranean area should not be over-rated (Olausson 1971).

Some important features of the islets I 2, I 4, I 6 and I 8 are listed in Table 3. The total number of vascular plant species for each of the islets (according to the floristic surveys in 1987) may be seen from Fig. 2.

Table 3. Some important features of four islets off Karpathos that are inhabited by *Silene holzmannii*. The islet numbers refer to Fig. 1.

	I 2	I 4	I 6	I 8
Maximum elevation	6 m	8 m	18 m	12 m
Size	ca 9000 m^2	ca 2500 m^2	ca 9500 m^2	ca 2000 m^2
Smallest distance from the mainland	ca 35 m	ca 50 m	ca 150 m	ca 90 m
Distribution of vegetation	Mainly restricted to the easterly slopes of the top area (ca 1000 m^2)	Mainly restricted to the easterly slopes of the top area (ca 800 m^2)	About evenly distributed all over the islet	About evenly distributed all over the islet
Exposure to winds and breakers	Fully exposed to north-westerly winds and breakers	Partly sheltered from north-westerly winds and breakers	Fully exposed to most winds but sheltered from north-westerly breakers	Partly sheltered from most winds and breakers
Presence of man and disturbing animals	Not observed	Not observed	Inhabited by a large colony of silver gulls; occasional visits by bird-shooters	Inhabited by a single rat (1986, 1987); occasional visits by fishermen

Material and methods

Contributors to the field work for this study have been W. Greuter, D. Höner, R. Pleger, S. Potthoff and Th. Raus (all Berlin-West). The islets have been visited at regular intervals since 1982 (additional visits to I 1, I 2 and I 11 in 1981) generally in April or May (rarely in June). This is the best time to find most annuals alive and fully developed. With the exception of the year 1984, when the islets were visited only in September/October (no visits to I 1, I 2 and I 11), autumn-flowering geophytes may often have been overlooked, but in some cases bulbs have been dug out or withered remains have been identified.

In this paper, observed changes in the composition of the flora are based exclusively on the presence or absence of aerial organs and disregard underground parts, in particular the seed-bank in the soil. Therefore the term 'apparent turn-over' sensu Nilsson & Nilsson (1983) is appropriate, to indicate the total amount of observed introductions and extinctions. All visitors to the islets have been careful to

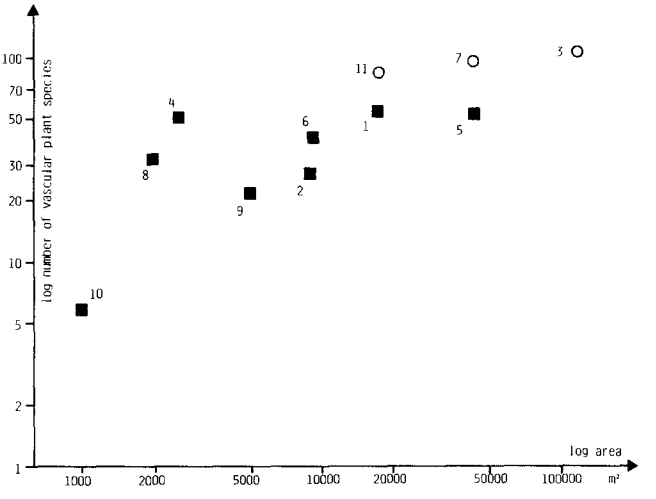


Fig. 2. Species-area relation of the investigated islets (according to the counts of 1987. The numbers refer to the different islets as shown in Fig. 1. Circles have been used for grazed islets, islets where no grazing has been observed are designated by black squares.

interfere as little as possible with the vegetation. Vouchers have been collected only to a very limited extent (all are deposited in the Herbarium of the Botanisches Museum Berlin-Dahlem-B). However, certain deliberate, controlled changes have been effected in order to test the probability of successful introductions of species. A total of 46 sowing experiments have been carried out on these four islets: Seeds or propagules of species that had been collected in the Karpathos area were sown and covered by soil in habitats suitable for germination on islets where these species did not occur previously. The list of these species comprises halophytes of the littoral zone, elements of the main vegetation type dominated by dwarf shrubs ('phrygana'), chasmophytic species and elements of the supralittoral zone (including islet specialists). Twenty-four different taxa have been tested using various amounts of seeds or propagules, from a single one up to unnaturally high quantities.

Whenever there was enough time available (which was usually the case) counts were made of the populations of the islet specialist *Silene holzmannii* (Caryophyllaceae). *Silene holzmannii* is a tall annual with somewhat weedy tendencies. It may occasionally reach a size of up to 50 cm and is particularly well suited for quantitative population studies since it may not easily be overlooked. Most of the capsules open very late and usually the dead remains of fruiting plants will remain upright for another year. More detailed information concerning the ecology of *Silene holzmannii* was presented by Greuter (1972). On I 4 an extirpation experiment was carried out in 1982, when all but three of the ca 250 individuals of the *Silene holzmannii* population were removed.

Results and discussion

Apparent turnover of species and sowing experiments

It has been emphasized before that the measure of apparent turnover only refers to observed floristic changes. Although we made every effort to achieve complete coverage by our floristic surveys, we cannot completely exclude that we might have overlooked one or the other of the present species in some cases so that the total number of recorded introductions is too low and/or the total number of recorded extinctions too high. Some of the islet specialists are minute indeed, such as *Hymenolobus procumbens* ssp. *procumbens*, a species that is so far only known from I 6, I 7 and a further islet near Kasos for the whole Karpathos island group (Karpathos, Kasos and Saria) but which, according to Greuter & Raus (1986: 105), 'may easily have been overlooked elsewhere due to its early flowering habit'. It was indeed found on sandy sea-shores on two places of the Nomos Argolis (Peloponnisos) and on the island of Gavdhos (S. of Crete) by Runemark (pers. comm.) but has not been observed on the numerous other islets in the Aegean investigated by Lund botanists, so that it is not an exclusive islet specialist throughout its Aegean range.

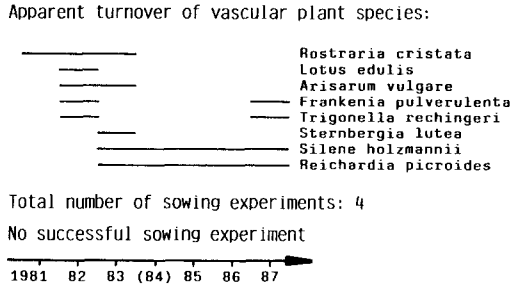
Figure 3 reveals that several species have been found to be temporarily missing on a given islet. Nearly all such cases concern micro-populations of annuals, so that three explanations are possible:

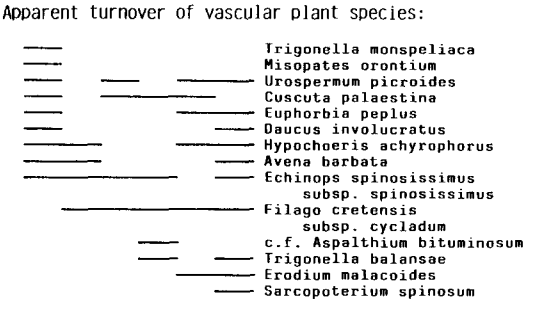
- extinction followed by introduction of the same species;
- successful survival of the species in the seed-bank of the soil, but without overground appearance in one or more of the vegetation periods;
- early or delayed germination (sprouting) of the species, so that it was overlooked or was indeed invisible at the time of the floristic survey (sampling error).

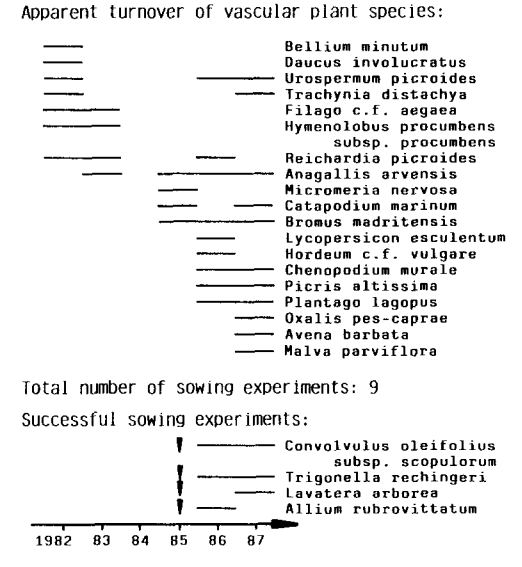
Considering the low success of sowing experiments that have been carried out on the islets (see below) the first explanation appears to be the least probable, whereas the assumption of 'pseudoturnover' sensu Lynch & Johnson (1974), as under the second and third explanation, is quite reasonable.

The apparent turnover rate so far observed on I 2 is very low as compared to those on the other islets within the same period of time. Two reasons may be responsible for this fact:

- No trace of permanent or frequent disturbances by man or animals (as has been the case on I 6 and I 8) has been found on I 2 and I 4. The pronounced effect of a silver gull colony on an islet flora is evidenced by the case of I 6 where a great number of introductions (mostly ruderals and







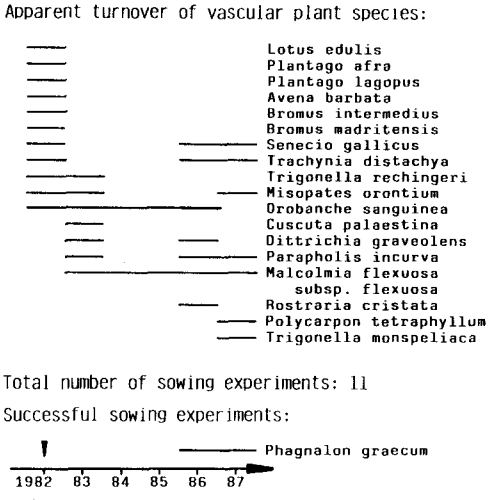


Fig. 3. Apparent turnover of plant species and introductions by sowing experiments on a) islet No 2, b) islet No 4, c) islet No 6 and d) islet No 8. Only species that have not been observed consistently have been listed. Presence in a given year is represented by a solid line, that is interrupted in years in which the species was not observed. (Note that the flora of islet No 2 has not been checked in 1984.) Successful sowing experiments are denoted by black arrowheads.

cultivated plants) has been recorded. Gillham (1961) emphasized the role of gulls in introducing seeds of alien annuals, and Abbott (1977) found significantly higher immigration rates of alien species on islets with gull rookeries. Raus (1986) exploring the flora of the volcanic island Nea Kaimeni in the Aegean also observed increased introductions of ruderals close to a gull colony.

– As has been noted above, I 2 is fully exposed to the prevailing north-westerly winds and to salt spray. A comparatively small number of species inhabits this islet (see Fig. 2), suggesting that only a few species well adapted to the extreme maritime conditions are actual or potential colonizers of such an islet. This explanation would account for the fact that most of the changes that have been observed on the other three islets concern ruderals or phrygana elements, i.e., species that are not or only imperfectly adapted to the conditions of coastal habitats. I 4, which is similarly undisturbed by man and animals, is partly sheltered from wind and waves, and indeed it has a more diverse flora and a higher rate of apparent turnover.

The results of the sowing experiments can be summarized as follows: When using a small amount of seeds or propagules (up to 9) no germination or sprouting could be observed in any case. But even using unnaturally high amounts of diaspores (up to a few hundred at one time and in a single place) success was far from overwhelming. The best success has been noted on I 6, which has a rather undersaturated flora in terms of species/area ratio, particularly considering its elevation and sheltered position. The two initially successful introductions of *Allium rubrovittatum* followed by extinction after one (I 6) or two years (I 4) reveal that germination or sprouting of an introduced species by no means guarantees a successful colonization in the long run (establishment). Actually, only those of our experimental introductions are at all likely to result in successful establishment that concern perennials, i.e., *Phagnalon graecum* (a dwarf shrub of rocky places and cliffs) on I 8 and the islet specialist *Convolvulus oleifolius* ssp. *scopulorum* on I 4 and I 6.

Dynamics of the populations of Silene holzmannii

The results are summarized in Fig. 4. On I 2 *Silene holzmannii* was unknown prior to 1983 when five individuals were counted. Experimental studies have shown that the capsules of *Silene holzmannii* are buoyant for up to several weeks and that the germination rate decreases only slowly under salt-water treatment, which is suggestive of possible long-range dispersal by sea currents (Greuter 1972; Potthoff in prep.). However, sea spray is unlikely to reach the site where this species has first been noticed on I 2, so that we now believe that birds were most likely the vectors for this introduction. Abbott & Black (1980) have pointed out that islands with sand and gravel beaches (lacking on the islets off Karpathos) are the ones that are likely to be reached by propagules over the sea. The *Silene holzmannii* population on I 2 grew steadily until 1986 when an explosive increase took place. Extraordinary propagation rates could also be observed on I 4 and I 6 – but not on I 8 – where a rat bit off nearly all the capsules of this species thereby reducing the population from 42 individuals (1985) to a single one (1987). The rapid decline on I 8 shows an extreme vulnerability of *Silene holzmannii* with respect to grazing. The parallel increases of the populations observed on the other three islets, situated at considerable distances from each other and covered by quite different vegetation types, have obviously been the consequence of unusually favourable weather conditions. Native inhabitants of Karpathos have told that autumn and early winter (1986/87) had been abnormally calm and dry. Another islet specialist that similarly profited from the unusual weather conditions is the shrub by *Convolvulus oleifolius* ssp. *scopulorum* of which more than 10000 seedlings per islet have been found in 1987 (I 8 and I 9).

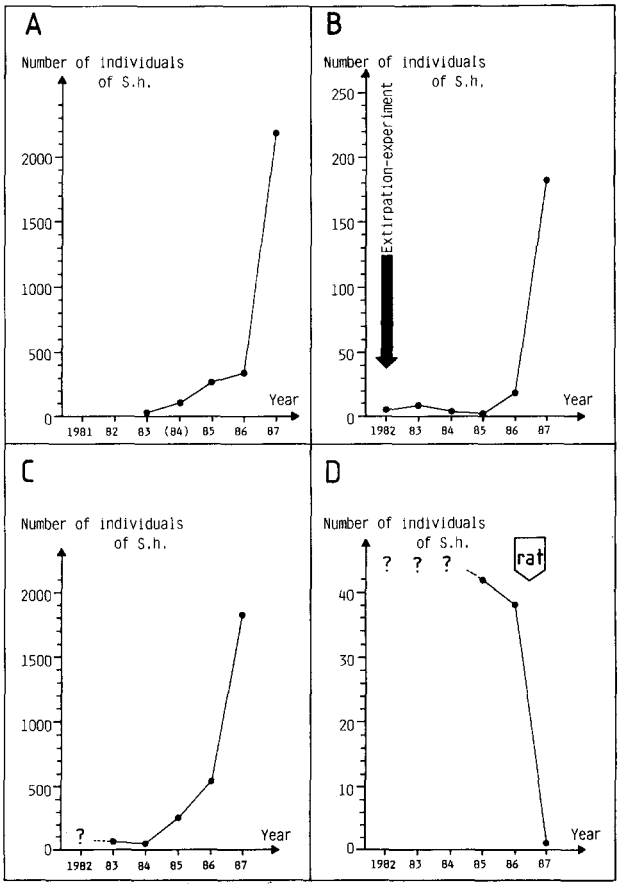


Fig. 4. Population dynamics of *Silene holzmannii* (S. h.) on a) islet No 2, b) islet No 4, c) islet No 6 and d) islet No 8. Note: On islet No 2 the population size for 1984 was determined by counting the withered fruiting inflorescenses in 1985.

The experimental extirpation of *Silene holzman-*

nii on I 4 first resulted in an astonishingly stable micro-population that did not exceed seven individuals over a period of four subsequent years. Due to high germination rates and lack of dormancy (Greuter 1972; Potthoff in prep.) the seed reserve in the soil must be virtually nil, a fact that might easily result in the extinction of the species in the event of its being decimated by, e.g., grazing.

Micro-populations and mass-populations

As in the case of *Silene holzmannii* on I 4, micro-populations of several species have been observed to maintain virtual stability in number and distributional pattern through several years. Often such micro-populations are found in isolated depressions of the rock filled with clayey soil or in the wind-screen provided by big stones. Such clay pans are of considerable interest in that they constitute in a way islets on the islet, their surroundings of bare rock obviously functioning as a kind of isolation barrier. In these sheltered places propagules of species already present on the spot accumulate, whereby an invasion by other species becomes more difficult. These micro-habitats present obvious analogies with cliff habitats found on the main island of Karpathos, and it is not too surprising to find that a number of islet chasmophytes form sizeable populations on some of the small islands (Table 2).

The principle of the first colonizing species being favoured regardless of their competitive properties has been called 'contingent exclusion' by Shmida & Ellner (1984: 42). This principle probably accounts for the stability of isolated micro-populations as well as for the build-up and maintenance of mass-populations that often dominate the vegetation of small islands. Examples of mass-populations on islets off Karpathos are provided by the two genera *Allium* and *Anthemis*. Three species of *Allium* tend to form mass-populations, viz., *Allium rubrovittatum* (an element of rocky, open places) on I 2, *Allium commutatum* (an islet specialist) on I 6, I 8 and I 9, and *Allium bourgeaui* ssp. *bourgeaui* (an islet chasmophyte) on I 4. Four taxa of *Anthemis* show the same strategy, viz., *Anthemis ammanthus* ssp. *ammanthus* (an islet specialist) on I 3, *Anthemis ammanthus ssp. paleacea* (an islet specialist) on I 7, *Anthemis rigida* (a common supralittoral element) on I 4 and *Anthemis scopulorum* (an islet specialist) on I 2. In none of these cases we have ever noticed a natural co-occurrence of two or more species of the same genus, nor has the establishment of additional taxa of the same genus by experimental sowing been successful so far. Even distances of a few metres separating an islet from the main island obviously constitute effective barriers to colonization. A big proportion of the islet specialists and islet chasmophytes has been found to form stable mass-populations on the offshore islets around Karpathos. Similar observations were made by Lund botanists on islets of the Central Aegean over a period of more than 14 years (Snogerup & Snogerup 1987).

Concluding remarks

The distributional limitation of certain species to small islands is a phenomenon that has been first reported from the Aegean area, where it is widespread and characteristic. However, islet specialists have meanwhile been shown to occur elsewhere. Abbott & Black (1980) recorded *Hymenolobus procumbens* and *Lavatera arborea* on small islands near Perth (Western Australia), Stearn (1984: 178) observed mass-populations of *Allium commutatum* that covered more than 50% of the ground on three Pityusic islets (Spain), and Lanza & Poggesi (1986) exploring 96 different islets off Corsica in the Mediterranean Sea found *Hymenolobus procumbens* on three islets, *Allium commutatum* on 28, and *Lavatera arborea* on 37 islets.

Some of such species are endemic to small areas, such as *Euphorbia margalidiana* (Kuhbier 1978) and *Daphne rodriguezii* (Lucas & Synge 1978: 525) in the Balearic islands (Spain), or *Silene velutina* (Lanza & Poggesi 1986), *Buphthalmum inuloides* (Valsecchi 1977) and *Asperula deficiens* (Diana-Corrias 1980) around Corsica and Sardinia (France/Italy). Similarly, a great number of Aegean islet specialists as well as elements of the characteristic cliff flora are endemic to this area, and they are supposed to be remnants of a competitively weak flora that oc-

curred around the Sea of Crete in the Pliocene (Runemark 1969). The ecological factors that characterize the cliff habitat, viz., absence of a well-developed soil layer, severe drought and extreme daily temperature ranges (Snogerup 1971) also influence the open vegetation of islets. Reduction or absence of grazing is another important factor that is common to vertical cliffs and the smallest islands. However, the obviously most important common feature of islets and cliffs is the low level of interspecific competition. According to Carlström (1986: 87) the same is true for open serpentine communities on Rhodes (Greece) and on the Marmaris peninsula (Turkey), where she found a number of usually strictly chasmophytic plants to occur outside of cliffs. One of the reasons why competition on small islands plays a minor role might be the low flux of foreign propagules that is a consequence of the surface compartmentation on the islets (already mentioned before); another reason is the under-saturation of the flora. Whitehead & Jones (1969) explain the notoriously low species numbers on small islands by the restricted pool of species that may find suitable habitats on them, and, in addition, small plant populations (such as are expected to occur frequently on islets) are exposed to a great risk of random elimination (Runemark 1969). Recurrent environmental changes will select for species with a broad ecological amplitude that are able to conquer new space quickly if the conditions are favourable. This has been evidenced for the islet specialist *Silene holzmannii*, and might quite likely also be the case for other small-island species.

Acknowledgements

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