Testing for nestedness in the terrestrial isopods and snails of Kyklades islands (Aegean archipelago, Greece)

Spyros Sfenthourakis, Sinos Giokas and Moysis Mylonas

Most insular communities exhibit nestedness, with the species assemblages of the more depauperate islands constituting subsets of those of the richer. Several methods for the estimation and evaluation of nestedness have been developed during the last fifteen years. In this paper we use two of the more recent and elaborate methods, namely the "temperature" method of Atmar and Patterson and the "departures" method of Lomolino, in order to investigate patterns of nestedness in the distribution of two well studied and specious animal groups, terrestrial isopods and land snails, in the Kyklades archipelago (Aegean Sea, Greece) that lies between two continental regions. Significant nestedness is present in both species assemblages and, surprisingly, each method gives almost identical levels of nestedness for the two animal groups. Isolation has been found to be more important in producing nestedness in both groups than area, which does not seem to be an important explanatory factor. However, the role of isolation in this case is better understood under an historical perspective, taking into account the complex palaeogeography of the region and the differential departmentalisation of distinct island groups. Additionally, certain metrics of habitat diversity that were included in the analysis were the best explanatory factors of nestedness, indicating a more complex causal pattern that also involves extinction. Since the two methods used are based on different assumptions and have different scopes, their results do not converge. The "temperature" method finds the maximum possible nestedness in an island sorting which does not necessarily lead to plausible biogeographical explanations, while the "departures" method, although more useful in detecting causality, fails to fully evaluate levels of nestedness. Nevertheless, both methods are valuable tools in the exploration of interesting distributional patterns, when this effort is accompanied by a good understanding of historical, ecological and idiosyncratic properties of each particular data set.

S. Sfenthourakis (sfendo@biology.db.uoa.gr) and S. Giokas, Zoological Museum, Dept of Biology, Univ. of Athens, GR-15784 Athens, Greece. – M. Mylonas, Dept of Biology, Univ. of Crete, P.O. Box 1470, GR-71110, Greece.

The distribution of organisms is not random. The fauna of a particular area of a certain size is generally characterised by spatially structured subsets. When such an area consists of disjunct habitable units, such as islands in an archipelago, it is reasonable to assume that these subsets consist of overlapping assemblages. Inevitably, these assemblages are expected to exhibit some degree of nestedness, since the latter is defined with reference to the total fauna of the area as a whole. It would be surprising to find assemblages of totally different species composition on each island of a natural archipelago. Where species richness is positively related to island size, the species assemblages of the more depauperate islands (smaller) usually constitute subsets of those of the richer (larger). Therefore, the existence of some degree of nestedness is generally a trivial fact for insular biotas. On the other hand, the levels and patterns of nestedness are of considerable importance for biogeography (Simberloff and Martin 1991, Hecnar and M'Closkey 1997).

During the past two decades there has been a continuously rising interest in the measurement and interpretation of nestedness patterns (Schoener and Schoener 1983, Simberloff and Levin 1985, Patterson and Atmar 1986, Patterson 1987, 1990, Cutler 1991, Patterson and Brown 1991, Simberloff and Martin 1991, Wright and Reeves 1992, Atmar and Patterson 1993, Kadmon 1995, Lomolino 1996, Worthen et al. 1996, Hecnar and M'Closkey 1997, Lomolino and Davis 1997, Wright et al. 1998). Several methods for measuring or approximating nestedness have been proposed, such as the Mann-Whitney U-statistic for testing the orderness of species distribution (Schoener and Schoener 1983, Simberloff and Levin 1985), the index N of Patterson and Atmar (1986) and the respecive algorithms RANDOM0 and RANDOM1, the standardized index C (Wright and Reeves 1992), the "temperature" method of Atmar and Patterson (1993, 1995) and the "departures" method of Lomolino (1996). Among these, the last two methods offer the most direct and justified quantifications of nestedness, without recourse to questionable null models for estimating metrics. Both methods use Monte Carlo simulations for estimating significance of nestedness. Nevertheless, there are significant differences between them, since they have been developed for different purposes. The temperature method estimates the highest possible nestedness in a given matrix by reorganising its topology in a way that minimises the "unexpectedness" of species occurrences, expressed by their topological deviations from the perfectly nested pattern. The method of Lomolino, assuming that isolation and island size are proxies for immigration and extinction respectively, estimates the unexpected presences (changes from 0 to 1) of species in matrices with constrained row (island) sorting, according to these factors. Consequently, while the temperature method is useful for the quantification of nestedness in an absolute mathematical way, the "departures method" of Lomolino is oriented in investigating particular biogeographical processes.

Absolute nestedness is an unrealistic situation for large species assemblages. Factors such as endemism, idiosyncratic histories of species and islands, habitat heterogeneity and stochastic processes reduce nestedness in real biotas. In order to investigate the patterns of nestedness in a real composite case, we tested the performance of these two methods when applied to the distribution of two speciose animal groups in a continental archipelago with complex palaeogeography and topography. We selected 14 of the Kyklades islands (Aegean archipelago, Greece) for which we have a very good knowledge of their terrestrial isopod and land snail fauna. The Aegean archipelago lies between two continental areas (Greek mainland and Asia Minor) and has been formed by the fragmentation of a continuous landmass that connected the two mainlands during the Miocene. It subsequently suffered many episodes of partial re-connections and disjunctions, both among island groups and between islands and mainland, especially during the glacial periods of Pleistocene (see Fig. 2). Terrestrial isopods and land snails are represented by numerous species on the 14 islands (57 and 87, respectively), are not good dispersers, have similar but not identical ecological properties, and have been intensively studied in this area (Mylonas 1982, Sfenthourakis 1994, 1996a, b, Giokas 1996).

In this study we estimate and compare the levels of nestedness present in these data sets (plus two subsets excluding endemic species and species with unique presence on one island), as calculated by the two methods. Then we elucidate the effect of several factors on the patterns of nestedness. These factors include isolation, measured by several estimations of distance from the two adjacent continental regions, island size, habitat diversity and favourable substrate. We also check the relation of the temperature method with the departures method of Lomolino, by using the results of the former as input to the latter.

Methods

Metrics

In order to check for nestedness we used the method of Atmar and Patterson (1993) for calculating the "temperature" (T) of each matrix. T is a measure of matrix entropy. The lower it is, the higher the nestedness of the matrix (in a range between 0–100). The method is described in detail in that paper, and it suffices here to say that the algorithm used shuffles the columns (species) and rows (islands) – without altering, of course, the incidences of species per island – in a way that maximum nestedness is achieved. In doing this, species with extended distribution are moved to the left of the new matrix, while islands with more omnipresent species are placed in the top rows, allowing thus a further evaluation of the results in terms of individual cases. This method has been computerised by Atmar and Patterson (1995), and has been made available on the world-wide-web. As a measure for the statistical significance of the temperature of each matrix, the method gives a probability of getting a smaller temperature from random permutations of the matrix (keeping incidences unaltered). For reasons of computing time we used the default number of 50 permutations. This number might appear small, but the resulting probabilities are of a level that renders unquestionable the significance of the results (see Table 2). Nevertheless, we ran one matrix (isopods without endemics) for 1000 permutations. The result was almost identical, as expected: for $T = 32.24$, $p(T < 32.24) = 1.61e{-}12$, average $T = 61.27$ $(SD = 4.22)$.

Another measure of nestedness is the percent of perfect nestedness (PN) calculated by the algorithm proposed by Lomolino (1996), and included in his software NEST.BAS. This method evaluates the relative merits of factors, such as area and isolation, as causal factors of nestedness. It is well described by Lomolino (1996) so here we only provide a brief definition of the terms (some abbreviations are ours): $D =$ departures from perfect nestedness, that is the number of times a presence follows an absence of each species when the matrix is read from top to bottom row. In each case the order of rows in the matrix is defined by an extrinsic factor (e.g. declining island area or increasing distance from mainland). $P =$ proportion of 1000 random matrix permutations (with incidences kept unaltered) with departure values lower than or equal to D, i.e. a measure of the statistical significance of nestedness in each matrix. $\%PN =$ percent of perfect nestedness, i.e. the product of the formula $100 \times (Dm-D/Dm)$, where Dm is the mean number of departures in 1000 permutated matrices (with incidences kept unaltered) and can be used as a measure of nestedness (the higher it is, the higher the nestedness). In contrast to T, this measure of nestedness is constrained by the sequence of islands in the matrix. Consequently, it is a measure of nestedness under a certain hypothesis of spatial organisation, while T is neutral against any such arrangements. By this we do not mean that the latter is superior, only that the two measures are subject to different interpretations. $PaN =$ partial nestedness, i.e. the number of Ds in a matrix (e.g., with rows ordered

according to declining area) that can be attributed to the other factor (e.g., distance), as judged by the relative row positions of the islands involved in the other matrix (e.g. the smaller island is closer to the mainland). $Pp =$ the probability, resulting from a binomial test, that more than half of the Ds in each matrix satisfies the preceding conditions, here at a significance level of 95%.

Data sets

The Kyklades Islands are in the central Aegean Sea (Greece), between continental Greece and Asia Minor. They comprise 21 large islands ($A > 30$ km^2) and many smaller islets (Fig. 1).

Existing data on the fauna of the islands are confined to a few groups. Among these, the only dependable and "complete" data sets are those for land snails and terrestrial isopods. We chose 14 of the major islands for which there is information in both data sets. Small islands were not considered, in order to avoid the effects of different size classes of the species richness and trivial nestedness caused by the depauperate faunas of small islands.

For terrestrial isopods we used the data of Sfenthourakis (1994). The species per island matrix is given in the Appendix. The complete data set includes 57 species for the 14 islands examined. Of these, 9 are endemic to central Aegean islands, while 10 were present on only one island (= singletons, excluded in some analyses).
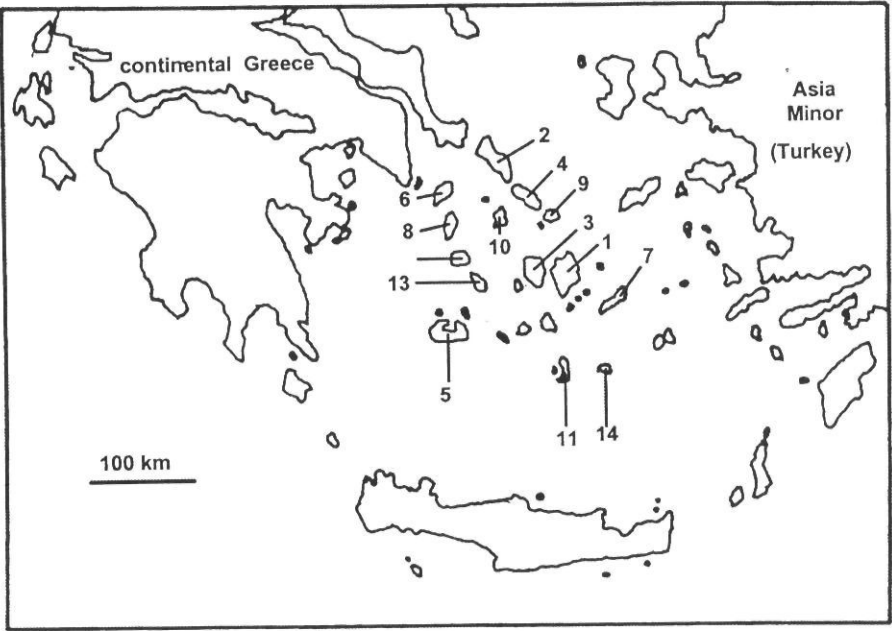

Fig. 1. The study area. Numbers indicate islands in descending order of area, as follows: 1: Naxos, 2: Andros, 3: Paros, 4: Tinos, 5: Milos, 6: Kea, 7: Amorgos, 8: Kythnos, 9: Mykonos, 10: Syros, 11: Thira, 12: Serifos, 13: Sifnos, 14: Anafi.

Table 1. Correlation between species richness, area, isolation, habitat diversity and limestone area for the 14 islands examined. z, c = slope and intercept of the linear regression, respectively.

Parameters	r	p<	z	c
log species/log area (isopods)	0.78	0.001	0.24	0.88
log species/log area (snails)	0.56	0.05	0.24	0.95
isolation/area	−0.26	ns		
residuals S-A/isolation (isopods)	0.06	ns		
residuals S-A/isolation (snails)	0.12	ns		
log species/log isolation (isopods)	−0.27	ns		
log species/log isolation (snails)	−0.11	ns		
species/habitats (isopods)	0.83	0.001		
log species/log limestone area (snails)	0.70	0.01		

The data for terrestrial molluscs were taken from Mylonas (1982) and were updated to meet current state of knowledge. The complete data set for the 14 islands is given in the Appendix. There are 87 species, 17 of which are endemic to the Kyklades and 25 occur on one island.

Since the Kyklades Islands are located between two continental areas, continental Greece and Asia Minor, in order to apply the "departures" method of Lomolino, we made separate tests for matrices ordered according to geographic distances from: continental Greece (DCG), continental Asia Minor (DAM), Asia Minor including nearby islands (DAI), shorter distance from either mainland (DSH), absolute shorter distance (including the islands near Asia Minor) (DAS).

Besides the above mentioned ordering variables, we also ordered islands according to their species richness and, for the isopod matrix, a measure of habitat diversity (as in Sfenthourakis 1994). Both variables are significantly correlated with area, but the exact ordering of islands is different in each case.

Additionally, for the snail data set, we used the area of limestone as another ordering variable (instead of absolute area), since the presence of land snails is positively correlated with limestone (Schmidt 1955, Ant 1963, Mylonas 1982).

Finally, we used the sequence of islands in the maximally packed matrices of the temperature method as another ordering variable in the departures method of Lomolino.

In order to check the correlation of the parameters used in the departures method, we used the Pearson product-moment correlation coefficient. Area is positively correlated with species richness and uncorrelated with isolation (measured as distance from continental Greece, but the same is true for all other distances too, see Table 1). On the other hand, species richness of isopods and snails is positively correlated with habitat diversity and limestone area, respectively (Table 1). Additionally, there is no correlation between isolation and species richness. Curiously, the slope of the species-area regressions (log-transformed data) is the same (0.24) for both isopods and snails (Table 1).

Results and discussion

Is there significant nestedness in the data sets?

According to the results obtained by applying the method of Atmar and Patterson (1993), all data sets present significant nestedness (Table 2). The matrices without singletons are less nested than the complete and those without endemic species. Also, the matrices without endemics are more nested than the complete ones. These tendencies indicate that species with single presence tend to occur on higher ranked islands (islands on upper part of maximally packed matrices), therefore they do not decrease nestedness. On the contrary, endemic species expectedly reduce nestedness, but not to a very significant degree. The distribution of endemics does not conform with the inclusive hierarchical pattern that is the premise of nestedness, since their occurrence is due to independent evolutionary processes.

It is of particular interest that, not only the temperature variability patterns, but also the absolute temperature values are almost identical for both data sets (snails and isopods), despite their differences in species richness. In fact, the temperatures of isopod matrices are always slightly smaller than those of snails, but these differences are negligible. This is a strong indication of a common underlying causal pattern, probably related to similar features of these two animal groups.

The "departures" test of Lomolino for both animal groups (Table 3) gives statistically significant nestedness for the matrices of distance from continental Greece and of shorter distance. Absolute shorter distance gives significant nestedness for snails, but marginally not significant for isopods. Area, distance from Asia Minor and distance from Asia Minor including islands do not result in significant nestedness in both groups. It is important to note that even though distance is not correlated with species richness (see Table 1), its role in the formation of the species assemblages appears only when species composition is taking into account. The reverse is true for area.

Finally, habitat diversity for isopods and limestone area for land snails are important nesting factors.

Table 2. The temperature (according to the methodology of Atmar and Patterson 1993) of the isopod and snail matrices (Tm), the possibility of finding a cooler matrix after 50 random permutations (p(T<Tm)), the mean temperature of the permutated matrices (Ta) and its standard deviation (SD), the percentage of matrix fill and the number of species in each matrix (N).

Matrix	Tm	p(T<Tm)	Ta(SD)	%fill	N
Isopods (total)	35.03	9.44e-10	62.36(4.54)	38	57
Snails (total)	35.19	2.74e-16	63(3.43)	31.8	87
Isopods (excl. singletons)	36.79	9.65e-09	61.19(4.34)	45.4	47
Snails (excl. singl.)	37.63	2.39e-12	62.94(3.66)	42.3	62
Isopods (excl. endemics)	32.24	5.80e-16	63.58(3.91)	42.5	48
Snails (excl. endemics)	32.68	1.43e-14	63.75(4.08)	35.6	70

Percent of perfect nestedness (%PN) is low (11–20%), compared with the values obtained by the temperature method. However, the two methods estimate nestedness using different metrics, are not directly comparable. Actually, when matrices are ordered according to minimum "temperature", significant nestedness is exhibited only in the isopod data set. This is a counter-intuitive result, that could be due to this difference. The temperature method uses a topologically constrained metric, that assigns higher value to unexpected presence of species at the lower right part of the matrix, where usually depauperate islands and occasional species are lying. On the other hand, the departures method of Lomolino gives equal weight to any unexpected presence (departures are merely added, without any weighting procedure). The choice between the two alternatives depends on assumptions about the idiosyncratic distributions of species. For example, is the "unexpected" presence of a species on a poor and small island due to stochastic processes, to the presence of a nearby large island, or to other ecological/historical factors? If there is strong departmentalisation of the archipelago, e.g. due to palaeogeographical reasons, more "unexpected" presences would be expected.

At the same time, we observe that the sorting of islands in the temperature method differs from the sorting according to other factors. This means that the sorting of islands in the distance or area sorted matrices is far from optimal (in the sense of highest possible nestedness in each matrix, as defined by the temperature method). Additionally, the island sorting (temperature method) in the isopod matrices is different from (although significantly correlated with) that of the snail matrices, as species richness is differentially ordered among the two data sets. The most obvious common element, trivial as it is, is the presence of the larger and richer island (Naxos) at the first row of all matrices. It is of particular interest that different island sortings in matrices with different species numbers lead to almost identical temperatures, under all modifications (exclusion of singletons or endemics).

Area, distance or other factors?

Having confirmed the presence of statistically significant nestedness in both data sets, we checked for possible causal factors. One immediate approach could be the testing of correlation of the island sorting according to the Temperature method with the island sorting according to external factors, such as area, distance, etc. (see Patterson et al. 1996). In Table 4 we give the Spearman rank order correlations between these sortings. Only area, limestone area and habitat

Table 3. The departures (D), the proportion of random runs with fewer departures (p) for 1000 permutations, and the percent of perfect nestedness (%PN), calculated according to Lomolino (1996). The sorting factors used were: area, distance from continental Greece (DCG), distance from Asia Minor (DAM), distance from Asia Minor including coastal islands (DAI), absolute shorter distance (DAS), shorter distance (not taking into account the coastal islands) (DSH), results of temperature method (T), habitat diversity as estimated for terrestrial isopods (H), and limestone area (Ca). Statistically significant nestedness shown in bold. Dm = mean number of departures in 1000 permutated matrix.

	D		p		%PN	
	Isopods (Dm = 104)	Snails (Dm = 173)	Isopods	Snails	Isopods	Snails
Area	100	163	0.24	0.15	3.64	6
DCG	**85**	**138**	**0.003**	**0**	**18**	**20**
DAI	108	188	0.79	0.942	7.4	−8.5
DSH	**87**	**154**	**0.008**	**0.03**	**16**	**11**
DAM	95	162	0.066	0.146	9	6
DAS	95	**145**	0.066	**0.002**	9	**16**
T	**87**	157	**0.008**	0.066	**16**	9
H	**85**		**0.003**		**18**	
Ca		**154**		**0.03**		**11**

Table 4. Spearman rank order correlations between the island sorting according to the Temperature method and the sortings according to other factors. Abbreviations as in Table 3. (p levels in parentheses, ns = not significant).

	A	H/Ca	DCG	DAM	DAS	DSH	DAI
isopods (total)	0.49 (ns)	**0.61** (0.020)	0.13 (ns)	0.22 (ns)	0.17 (ns)	0.15 (ns)	0.23 (ns)
(excl. singl.)	**0.53** (0.049)	**0.62** (0.019)	0.19 (ns)	0.18 (ns)	0.17 (ns)	0.17 (ns)	0.26 (ns)
(excl. end.)	**0.54** (0.047)	**0.63** (0.015)	0.10 (ns)	0.14 (ns)	0.08 (ns)	0.09 (ns)	0.15 (ns)
snails (total)	**0.79** (<0.001)	**0.82** (<0.001)	0.29 (ns)	0.21 (ns)	0.42 (ns)	0.27 (ns)	0.26 (ns)
(excl. singl.)	**0.71** (0.004)	**0.78** (0.001)	0.39 (ns)	0.17 (ns)	0.46 (ns)	0.35 (ns)	0.27 (ns)
(excl. end.)	**0.73** (0.003)	**0.74** (0.003)	0.32 (ns)	0.23 (ns)	0.43 (ns)	0.30 (ns)	0.31 (ns)

diversity are significantly correlated. All distance measures lead to low correlations, in both isopods and snails. Nevertheless, this approach does not sufficiently address the problem of causality, because maximum nestedness (that is, what the Temperature method calculates) in any realistic matrix would be found in a sorting that is very close to that of derceasing species richness. Given the high correlation of species richness with area and habitat diversity (Table 1), the above mentioned results are almost trivial. This problem has not been considered by Patterson et al. (1996), who found a very high correlation between elevation and nestedness in Andean bat assemblages by this method. Elevation was also very highly correlated with species richness.

In order to avoid this shortcoming, we proceeded with the "departures" test of Lomolino, which is not sensitive to correlations between factors. According to the premises of the method, higher nestedness in an area sorted matrix means that extinction has been the main causal factor for nestedness, while immigration would lead to higher nestedness in distance sorted matrix. We present results only for significantly nested matrices plus area.

The results are somewhat different between the two animal groups (Table 6). Area explains more than half of the departures in the isopod shorter distance matrix, while it is not important for the departures in snail matrices. Habitat diversity (isopods) is a significant explanatory factor for shorter distance. On the other hand, limestone area explains more than half of the departures in all snail matrices except for absolute shorter distance. Distance from continental Greece and shorter distance explain area and limestone area for snails, while they are not significant for isopods. Absolute shorter distance does not explain any departures in either group.

These results indicate the following:

The importance of distance from continental Greece is confirmed for isopods, as its departures cannot be explained by any other factor.

The effect of shorter distance in isopods can be attributed to habitat diversity and area, two factors that are strongly correlated. Taking into account that habitat diversity gives significant nestedness while area does not, it could be assumed that the former is the most probable causal factor of nestedness between the two.

Since distance from continental Greece does not explain habitat diversity departures, both factors can be postulated as contributors to observed nestedness in the isopod matrix.

In snails the patterns are more complicated. Distance from continental Greece and shorter distance are explained by limestone area, but at the same time limestone area is itself explained by these two factors.

Absolute shorter distance is neither explained by nor explains any other factors, while area is explained by most factors without explaining any.

Therefore, nestedness in the land snail matrix can be attributed to the combined effect of distances from adjacent mainlands and limestone area.

Since the island sorting resulting from the "temperature" method is different, albeit correlated in some cases, from the sorting by other factors (see Table 5), we estimated their partial effect on it (Table 6). Only shorter distance can explain more than half of the departures in the isopod matrix, while no factor is significant for land snails. This means that the pattern of nestedness in the maximally nested matrix of isopods is closer to the pattern in the shorter distance matrix than to any other, a result that could not be predicted by the rank correlations approach. Combined with the fact that shorter distance and temperature give identical degree of nestedness, and taking into account that shorter distance is explained by habitat diversity (which in turn does not explain "temperature"), we have to assume that shorter distance too has some underlying influence in the structuring of isopod nestedness patterns.

On the other hand, in land snails the pattern of nestedness in the maximally packed matrix is completely unrelated to that of any other factor.

Conclusions

Nestedness is a common pattern in the insular distributions of organisms. Nevertheless, the causal factors leading to this pattern are not easily deciphered. In this paper we attempted an investigation of the role of some factors that could be involved in the building of nested-

Table 5. The ranking of islands according to the various sorting factors used (abbreviations as in Table 3).

Area	DCG	DAM	DAI	DAS	DSH	Ca	H	Tiso	Tmol
Naxos	11	5	2	6	12	1	1	1	1
Andros	1	4	6	1	1	3	2	3	2
Paros	10	8	5	10	11	2	8	12	3
Tinos	4	3	4	5	4	8	3	2	5
Milos	9	14	14	13	10	11	9	4	9
Kea	2	10	13	2	2	6	4	8	4
Amorgos	12	1	3	8	9	4	5	5	6
Kythnos	3	11	11	3	3	10	6	14	10
Mykonos	7	2	1	4	7	14	12	11	14
Syros	5	7	7	7	5	12	7	9	7
Thira	13	9	10	14	14	13	13	13	13
Serifos	6	12	12	9	6	7	11	7	11
Sifnos	8	13	9	11	8	5	10	6	8
Anafi	14	6	8	12	13	9	14	10	12

ness, comparing the patterns displayed by two different animal groups at the same archipelago and evaluating the performance of two distinct methodological approaches. The two animal groups show considerable similarities in nestedness patterns, but also exhibit certain differences as far as the causality of nestedness is concerned. The surprising similarity in the quantitative measure of their nestedness could be attributed to their resemblance in mobility and ecological demands. Land snails and terrestrial isopods have relatively low dispersal capabilities, their populations are restricted to small areas, generally they cannot tolerate arid conditions, they respond in a comparable way to several ecological parameters such as humidity and substrate, and they exploit similar habitats. Humid and calcareous sites sustain more diverse communities, and such sites are generally restricted and patchily distributed on Aegean islands. As a result, extinction patterns are probably similar for the two groups, leading to the observed similarity in estimates of nestedness, and the important role of habitat diversity and limestone area as explanatory factors.

On the other hand, according to the established palaeogeography of the region (see Fig. 2), there has been considerable departmentalisation of the Aegean islands throughout the Pliocene and the Pleistocene. This procedure has been complex, with repeated connections and disconnections among different subgroups of islands, as well as between some islands and adjacent mainlands. Additionally, during the Miocene, the entire Aegean region was a continuous landmass, connecting continental Greece with Asia Minor. The faunal constitution of the two animal groups may has been influenced by different events, leading to different modern distributional patterns. In this case, the effects of distance on patterns of nestedness could have resulted not from differential immigration, in the sense of barrier crossing, but from the differential departmentalisation of the biogeographically distinct sub-groups of islands. If both continental Greek and Asian elements had contributed to the faunal constitution, we would

expect shorter or absolute shorter distance to be the most important explanatory factors. However, if continental Greek elements were prevailing, distance from continental Greece would be the major factor. In our results, after partitioning out the multiple effects between factors, we see that isopod nestedness is explained solely by distance from continental Greece, while that of snails is better explained by absolute shorter distance. This may indicate that the two groups have different histories. Perhaps the separation from continental Greece has affected the isopod fauna, while the snail fauna has been principally affected by the older separation from Asia Minor. Our approach to immigration is consistent with the reasonable hypothesis that nestedness in species assemblages of poor immigrants, such as snails and isopods, should be mainly extinction guided, at least in continental archipelagos (cf. Cook and Quinn 1995).

Taking into account the overall results of the departures method, we can see the interplay between extinction and "immigration". We propose that in our case, "immigration" should be translated to older distribu-

Table 6. P values of the binomial test, assuming that more than half of the departures of the matrices sorted according to the factors given in rows are explained by the factors in columns (at a = 0.05). Statistically significant values in bold. Abbreviations as in Table 3. na = non applicable (partial departures less than half). Only factors that lead to significant nestedness have been included in each case.

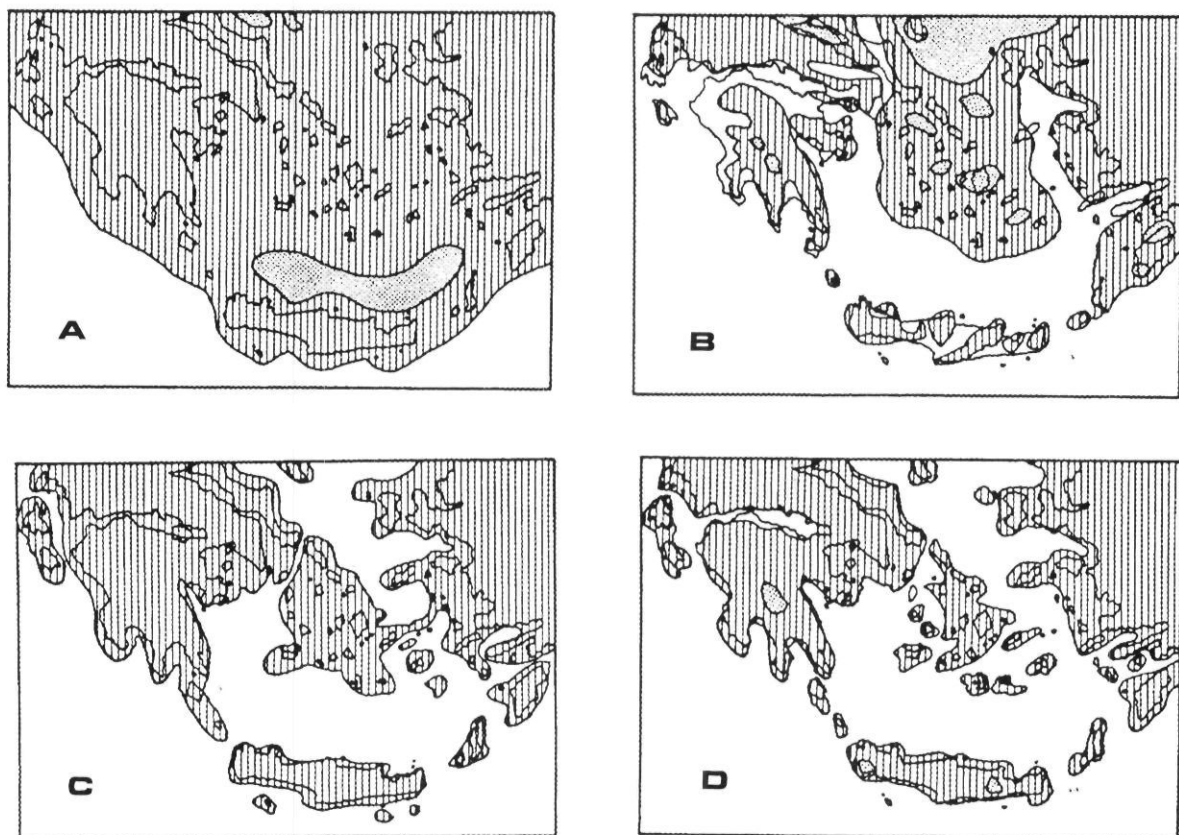|		Area	H/Ca	DCG	DAS	DSH
Area	isopods		na	ns	na	ns
	snails		0.001	0.005	na	0.02
H/Ca	isopods	na		na	na	ns
	snails	ns		0.001	ns	0.001
DCG	isopods	na	ns		na	na
	snails	na	0.001		na	na
DAS	isopods	0.05	0.05	na		na
	snails	ns	na	na		na
DSH	isopods	0.001	0.001	na	na	
	snails	ns	0.005	na	na	
T	isopods	na	ns	ns	ns	0.001
	snails	na	na	na	na	na

Fig. 2. Snapshots of the palaeogeographic history of the study area since middle Miocene (adapted from Giokas 1996). A: middle Miocene, B: lower Pliocene, C: 800000 BP, D: 450000 BP. Hatched area stands for land and dotted area for lakes.

tional patterns. In complex cases, such as the Aegean archipelago, the premises of the method should be properly adjusted in order to take into consideration other known factors. The method itself provides a useful tool for the analysis of patterns that emerge from diverse procedures, such as palaeogeography, habitat structure etc. On the other hand, it is not so strong in documenting levels of nestedness, as shown by its inconsistency with the temperature method for snails. The temperature method is more robust in estimating levels of nestedness, nevertheless it is a mostly descriptive tool that does not directly address biologically interesting questions, since nestedness is common in almost all real insular distributions of organisms. It is possible to biologically evaluate its results by investigating the idiosyncratic temperatures of species, but in our case (results not shown) they could not provide any useful insight, since there was no obvious pattern in their behaviour. Both endemic and widespread species, as well as species with different types of limited distribution, exhibit high idiosyncratic temperatures.

Further examination of more sorting factors, using more groups of organisms with a variety of dispersal capabilities and ecological demands will provide a deeper understanding of the causality of nestedness patterns. Wright et al. (1998) give a thorough evaluation of different metrics for measuring nestedness, but unfortunately they do not include the departures method in their analysis. The "C"-type metrics they propose as more robust require the use of some null models of species' distributions for its estimation, therefore introducing another source of dispute on which is the most appropriate such model (e.g. Cook and Quinn 1998). The departures method, with all its possible shortcomings, avoids such inference. A possible direction towards improvement of this method could be the differential weighting of the departures according to their position in the matrix. Departures found in lower rows, when the matrix is sorted in descending order, should have more weight, since the "abnormal" occurrence of a species in a more depauperate island is more unexpected than a similar occurrence on a higher ranked island. Such a procedure could reduce the noise of stochastic events, since even under a stochastic model of species distribution more "singular" occurences are likely to be found on richer islands. Nevertheless, nestedness should not be viewed in a purely mathematical way, but in a biologically relevant perspective.

References

Ant, H. 1963. Faunistische, ökologische und tiergeographische Untersuchungen zur Vebreitung der Landschnecken in Nordwestdeutschland. – Abh. Landes-Mus. Münster 25: 1–125.

Atmar, W. and Patterson, B. D. 1993. The measure of order and disorder in the distribution of species in fragmented habitat. – Oecologia 96: 373–382.

Atmar, W. and Patterson, B. D. 1995. The nestedness temperature calculator: a visual basic program, including 294 presence-absence matrices. – AICS Res., Univ. Park, NM and The Field Museum, Chicago, IL.

Cook, R. R. and Quinn, J. F. 1995. The influence of colonization in nested species subsets. – Oecologia 102: 413–424.

Cook, R. R. and Quinn, J. F. 1998. An evaluation of randomization models for nested species subsets analysis. – Oecologia 113: 584–592.

Cutler, A. 1991. Nested faunas and extinction in fragmented habitats. – Conserv. Biol. 5: 496–505.

Giokas, S. 1996. The differentiation of the genus *Albinaria* in the Hellenic region. – Ph.D. thesis, Univ. of Athens, Greece (in Greek with English abstract).

Hecnar, S. J. and M'Closkey, R. T. 1997. Patterns of nestedness and species association in a pond-dwelling amphibian fauna. – Oikos 80: 371–381.

Kadmon, R. 1995. Nested subsets and geographic isolation: a case study. – Ecology 76: 458–465.

Lomolino, M. V. 1996. Investigating causality of nestedness of insular communities: selective immigrations or extinctions? – J. Biogeogr. 23: 699–703.

Lomolino, M. V. and Davis, R. 1997. Biogeographic scale and biodiversity of mountain forest mammals of western North America. – Global Ecol. Biogeogr. Lett. 6: 57–76.

Mylonas, M. 1982. The zoogeography and ecology of the terrestrial molluscs of Cyclades. – Ph.D. thesis, Univ. of Athens, Greece (in Greek with English abstract).

Patterson, B. D. 1987. The principle of nested subsets and its implications for biological conservation. – Conserv. Biol. 1: 323–334.

Patterson, B. D. 1990. On the temporal development of nested subset patterns of species composition. – Oikos 59: 330–342.

Patterson, B. D. and Atmar, W. 1986. Nested subsets and the structure of insular mammalian faunas and archipelagoes. – Biol. J. Linn. Soc. 28: 65–82.

Patterson, B. D. and Brown, J. H. 1991. Regionally nested patterns of species composition in granivorous rodent assemblages. – J. Biogeogr. 18: 395–402.

Patterson, B. D., Pacheco, V. and Solari, S. 1996. Distributions of bats along an elevational gradient in the Andes of south-eastern Peru. – J. Zool. 240: 637–658.

Schmidt, H. A. 1955. Zur Abhangigkeit der Entwicklung von Gehaüseschnecken von Kalkgehalt des Bodens. – Arch. Moll. 84: 167–177.

Schoener, T. W. and Schoener, A. 1983. Distribution of vertebrates on some very small islands. 1. Occurrence sequences of individual species. – J. Anim. Ecol. 52: 209–235.

Sfenthourakis, S. 1994. Biogeography, systematics and ecological aspects of terrestrial isopods in central Aegean islands. – Ph.D. thesis, Univ. of Athens, Greece (in Greek with English abstract).

Sfenthourakis, S. 1996a. The species-area relationship of terrestrial isopods (Isopoda; Oniscidea) from the Aegean archipelago (Greece): a comparative study. – Global Ecol. Biogeogr. Lett. 5: 149–157.

Sfenthourakis, S. 1996b. A biogeographic analysis of terrestrial isopods (Isopoda, Oniscidea) from central Aegean islands (Greece). – J. Biogeogr. 23: 687–698.

Simberloff, D. and Levin, B. 1985. Predictable sequences of species loss with decreasing area-land birds in two archipelagoes. – N. Z. J. Ecol. 8: 11–20.

Simberloff, D. and Martin, J. 1991. Nestedness of insular avifaunas: simple summary statistics masking complex species patterns. – Ornis Fenn. 68: 178–192.

Worthen, W. B., Carswell, M. L. and Kelly, K. A. 1996. Nested subset structure of larval mycophagous fly assemblages: nestedness in a non-island system. – Oecologia 107: 257–264.

Wright, D. H. and Reeves, J. H. 1992. On the meaning and measurement of nestedness of species assemblages. – Oecologia 92: 416–428.

Wright, D. H. et al. 1998. A comparative analysis of nested subset patterns of species composition. – Oecologia 113: 1–20.

Appendix A. The complete data matrices for terrestrial isopods and land snails. Species endemic in the study area are indicated with asterisks.

A. Terrestrial isopods

	Tylos ponticus	Ligia italica	Ligidium cycladicum*	Ligidium ghigii	Haplophiloscia couchi	Haplophiloscia hirsuta	Stenophiloscia vandeli	Stenoniscus pleonalis	Philoscia dalmatica	Chaetophiloscia cellaria	Chaetophiloscia elongata	Trichoniscus lindbergi	Trichoniscus oedipus	Trichoniscus rhodiensis	Trichoniscus sp. aff. bureschi*	Trichoniscus sp. aff. pygmaeus*	Monocyphoniscus canensis	Cretoniscellus strinatii	Haplophthalmus thermophilus	Rodonicus anophthalmus	Bathytropa granulata	Platyarthrus beieri	Platyarthrus lindbergi	Platyarthrus schoebli	Agabiformius lentus	Agabiformius obtusus	Agabiformius spatula	Leptotrichus nauphensis	Leptotrichus kosswigi	Leptotrichus panzeri	Leptotrichus syrensis	Proporcellio quadriseriatus	Porcellio lamellatus	Porcellio laevis	Porcellio obsoletus	Porcellio flavomarginatus	Porcellio werneri*	Porcellionides pruinosus	Orthometopon phaleronense	Trachelipus aegeus	Nagurus aegeus	Armadillo officinalis	Armadillo tuberculatus	Schizidium hybridum	Schizidium oertzeni	Schizidium tinum*	Trichodillidium malickyi*	Echinarmadillidium cycladicum	Armadillidium vulgare	Armadillidium marmoratum	Armadillidium atticum	Armadillidium insulanum	Armadillidium granulatum	Armadillidium ameglioi	Paraschizidium aegaeum*	Paraschizidium album	Paraschizidium sp. aff. atticum*
Naxos	1	1	0	0	1	1	1	0	0	1	0	0	0	1	1	1	0	0	1	0	0	0	1	1	1	0	1	1	1	0	0	1	0	1	1	1	0	1	0	1	1	1	1	0	0	0	1	0	1	0	0	1	1	0	0	0	1
Andros	1	1	0	0	1	1	1	0	1	1	1	0	1	1	0	0	1	1	0	0	0	0	1	1	1	0	1	1	1	0	0	1	0	1	1	1	1	1	0	1	0	1	1	0	1	0	0	0	1	1	0	1	1	0	0	0	0
Paros	1	1	0	0	1	1	1	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	1	0	0	1	1	0	1	1	1	1	0	1	0	0	0	1	1	0	1	1	0	1	1	0
Tinos	1	1	0	0	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	1	0	1	1	1	0	1	1	0	0	0	1	0	0	0	1
Milos	0	1	0	0	0	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	1	0	1	0	0	1	0	0	0	1	1	0
Kea	1	1	0	0	1	1	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	1	0	1	0	0	0	1	1	0	0	1	1	0	1	0	0	0
Amorgos	1	1	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	1	0	1	0	0	0	1	0	1	1	1	1	0	0	0	0	1	1	0	1	0	0	0	0	1	0
Kythnos	1	1	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	1	0	1	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0
Mykonos	1	1	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	1	1	1	0	0	0	0	1	1	0	1	1	0	0	1	0	0
Syros	1	1	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	0	1	0	0	0	1	1	0	0	1	0	0	0	0	1	1	1	0	1	1	0	0	0	0	0
Thira	1	1	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0
Serifos	1	1	0	0	1	1	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	1	0	1	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0
Sifnos	1	1	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Anafi	1	1	0	0	1	1	1	0	0	1	0	0	1	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	1	1	1	1	0	0	1	0	0	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0

Appendix A. Cont.

B. Land snails

Species	Naxos	Andros	Paros	Tinos	Milos	Kea	Amorgos	Kythnos	Mykonos	Syros	Thira	Serifos	Sifnos	Anafi
Albinaria coerulea	1	1	1	0	0	1	0	0	1	1	1	0	0	1
Albinaria discolor	0	0	0	0	0	1	0	0	1	0	0	0	1	0
Albinaria turrita	0	0	0	0	1	1	0	1	0	0	0	0	0	0
Bulgarica denticularia	0	1	0	1	0	0	1	0	1	0	0	0	0	0
Caecilioides acicula	1	1	1	0	1	0	1	1	0	0	0	1	0	0
Caecilioides subsaxana	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Caecilioides tumulorum	1	0	0	1	0	1	0	1	0	0	0	0	0	0
Caracollina lenticula	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Cernuella candiota	1	0	1	1	1	0	0	1	0	1	0	1	1	1
Cernuella profuga	1	1	1	0	1	1	1	0	1	0	1	1	1	0
Cernuella sp.	0	1	0	0	1	1	1	0	0	0	1	1	1	1
Cernuella syrensis	1	1	1	1	1	1	0	1	0	0	1	0	0	1
Cernuella virgata	0	0	0	0	1	0	0	0	1	0	1	0	0	0
Chondrus zebra	0	1	0	1	0	1	0	1	0	0	0	0	0	0
Chondrula bergeri	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Cochlicella acuta	1	1	1	1	1	0	0	1	0	1	0	1	0	0
Daudebardia rufa	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Deroceras cycladicum*	1	0	0	0	0	0	0	0	0	0	1	0	0	0
Deroceras kevensis*	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Deroceras laeve	0	0	0	0	1	0	0	1	0	0	0	0	0	0
Deroceras melium*	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Deroceras oertzeni*	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Deroceras parium*	1	0	1	0	0	0	0	0	0	0	0	0	0	0
Deroceras seraphinum*	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Deroceras sp.	0	0	0	0	0	0	0	0	1	0	0	0	0	1
Deroceras thersites	1	1	1	0	1	0	1	0	1	0	0	0	0	0
Eobania vermiculata	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Eopolita protensa	0	0	0	0	1	0	0	0	0	0	0	0	1	1
Ferussacia folliculus	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Granopupa granum	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Helicella conspurcata	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Helicella obvia	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Helicigona cyclolabris	1	0	0	1	0	1	0	0	1	0	0	0	1	0
Helicigona sphaeriostoma	1	0	0	0	1	0	0	0	0	0	0	0	0	1
Helicopsis krynickii	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Helix aperta	0	0	1	0	1	0	0	0	0	0	0	1	0	0
Helix aspersa	1	1	1	1	0	0	0	0	1	0	1	0	1	0
Helix figulina	1	1	0	0	0	0	1	0	1	1	0	0	0	0
Helix godetiana*	1	0	0	0	0	0	0	1	0	0	0	0	0	1
Helix nucula	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Idyla bicristata	0	1	0	1	0	0	1	0	1	0	1	0	0	0
Lauria cylindracea	1	1	1	1	0	0	1	0	0	1	1	1	1	0
Limax conemenosia	0	1	1	1	1	0	0	0	0	0	1	1	1	0
Limax flavus	0	0	0	0	0	0	0	0	0	1	0	0	0	0

Appendix A. Cont.

B. Land snails

Species	Milos	Kea	Amorgos	Kythnos	Mykonos	Syros	Thira	Serifos	Sifnos	Anafi
Lindholmiola lens	0	1	0	1	0	0	0	0	0	1
Mastus anaphiensis*	0	0	0	0	0	0	0	0	0	1
Mastus dirphicus	0	0	0	0	0	0	0	0	0	0
Mastus eturbeculatus	1	0	1	0	1	0	1	1	1	0
Mastus pusio	0	0	0	1	0	1	1	1	0	0
Mastus turgidus	0	0	1	0	0	0	0	0	0	0
Metafruticicola andria*	0	0	1	0	1	0	1	0	0	0
Metafruticicola graphicotera*	1	0	0	0	0	0	0	0	0	1
Metafruticicola pellita	1	0	0	0	0	1	0	1	0	1
Milax gagates	1	0	1	0	0	0	0	1	0	0
Monacha cartusiana	0	0	0	0	0	0	0	0	0	0
Monacha n.sp.*	0	0	0	0	0	0	0	0	0	0
Monacha olivieri	0	1	0	1	0	0	0	0	0	0
Monacha rothi	1	0	1	0	1	1	1	1	1	1
Orculella scyphus	0	1	0	1	0	0	0	0	1	1
Orculella sp.dol.	0	1	1	0	0	1	1	1	1	0
Orcula biasolettiana	0	1	0	0	0	0	0	0	0	0
Oxychilus cyprius	0	1	0	0	0	0	0	0	0	0
Oxychilus hydatinus	1	1	1	1	1	1	1	1	1	1
Oxychilus samius	0	0	0	0	0	0	0	0	0	0
Pagodulina sp.	0	0	0	0	0	0	0	0	0	0
Pyramidula chorismenostoma	0	1	1	1	0	1	1	0	1	0
Pyramidula n.sp.*	0	0	1	0	0	0	0	0	0	0
Pyramidula rupestris	0	0	0	0	0	0	0	0	0	0
Rumina decollata	1	1	0	1	0	1	1	1	1	1
Rupestrella philippi	1	1	1	1	0	1	1	1	1	0
Rupestrella rhodia	0	0	1	0	0	0	0	0	0	0
Tandonia cretica	0	0	0	0	0	0	0	0	1	0
Tandonia sowerbyi	0	1	0	0	0	0	0	0	1	0
Theba pisana	1	0	0	1	0	0	1	0	1	0
Trochoidea cretica	1	0	1	1	1	1	0	1	1	1
Trochoidea didyma	1	0	1	1	1	1	1	1	1	1
Trochoidea pyramidata	0	0	0	0	0	1	1	1	0	1
Trochoidea syphnicus*	1	0	0	1	0	1	0	0	1	0
Truncatellina sp.	0	0	0	0	1	0	0	0	0	0
Vitrea clessini*	1	1	0	1	1	0	0	1	0	1
Vitrea contracta	0	1	0	0	1	0	1	0	1	0
Vitrea keana*	0	1	0	0	0	0	0	0	0	0
Vitrea pygmaea	0	0	0	1	0	0	0	0	0	0
Vitrina sp.	0	1	0	0	0	0	0	0	0	0
Zebrina stokesi*	0	0	1	0	0	0	0	0	0	0
Zonites anaphiensis*	0	0	0	0	0	0	0	0	0	1
Zonites pergamulatus	0	0	1	0	0	0	0	0	0	0