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From sampling stations to archipelagos: investigating aspects of the assemblage of insular biota

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ABSTRACT

Aim To investigate the formation of nestedness and species co-occurrence patterns at the local (sampling station), the intermediate (island group), and the archipelago scale.

Location The study used data on the distribution of terrestrial isopods on 20 islands of the central Aegean (Greece). These islands are assigned to two distinct subgroups (Kyklades and Eastern islands).

Methods The Nestedness Temperature Calculator was used to obtain nestedness values and maximally nested matrices, the EcoSim7 software and a modified version of Sanderson (2000) method were used for the analysis of species co-occurrences. Idiosyncratic temperatures of species and the order of species placement in the maximally nested matrices were used for further comparisons among spatial scales. The relationships of nestedness values with beta-diversity, habitat diversity and a number of ecological factors recorded for each sampling station were also investigated.

Results Significant nestedness was found at all spatial scales. Levels of nestedness were not related to beta-diversity or habitat diversity. Nestedness values were similar among spatial scales, but they were affected by matrix size. The species that contributed most to the nested patterns within single islands were not the same as those that produce nestedness at the archipelago scale. There was significant variation in the frequency of species occurrence among islands and among spatial scales. There was no direct effect of ecological factors on the shaping of patterns of nestedness within individual islands, but habitat heterogeneity was crucial for the existence of such patterns. Positive associations among species prevailed at all scales when species per station were considered, while negative associations prevailed in the species per island matrices. All associations resulted from the habitat structure of sampling stations and from particularities of geographical distributions.

Conclusions There was no clear-cut distinction between nestedness patterns among spatial scales, even though different species, and partially different factors, contributed to the formation of these patterns in each case. There was a core of species that contributed to the formation of nested patterns at all spatial scales, while the patterns of species associations suggested that biotic interactions are not an important causal factor. The results of this study suggest that locally rare species cannot be widespread at a higher spatial scale, while locally common species can have a restricted distribution.

Keywords

Aegean Islands, Greece, insular biota, nestedness, spatial scale, species co-occurrence, Temperature Calculator, terrestrial isopods.

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INTRODUCTION

The assembly of insular biotas is one of the recurring major themes in ecological biogeography (Diamond, 1975; Connor & Simberloff, 1979; Weiher & Keddy, 1999). Within the framework of the equilibrium theory, several aspects of insular species assemblages have been subjected to investigation, such as the role of immigration and extinction, species turnover, and the effects of area, habitat diversity and isolation on species richness, as well as patterns of species co-occurrence (Schluter, 1984; Sanderson *et al.*, 1998; Gotelli, 2000; Sanderson, 2000; Gotelli & Ellison, 2002). During the last 15 years, special attention has also been given to the nested structure of insular biotas (Patterson & Atmar, 1986; Wright & Reeves, 1992; Atmar & Patterson, 1993; Kadmon, 1995; Boecklen, 1997; Wright *et al.*, 1998; Sfenthourakis *et al.*, 1999; Weiher & Keddy, 1999; Jonsson, 2001; Mac Nally & Brown, 2001; Fernández-Juricic, 2002). These issues are related to the mechanisms that shape insular communities and especially to the effects of competition and extinction. Nestedness is the expected condition when the species present in a group of islands (real or habitat) come from the same pool, in the absence of strong stochastic effects and local speciation. This means that nestedness should characterize island groups that share a common history and that have not been isolated for a very long time. Special patterns of co-occurrence are indicative of either mutual exclusion (less co-occurrence than expected by chance) or positive species associations (more co-occurrence than expected by chance), with the former commonly interpreted as results of competitive exclusion. These phenomena should be scale-dependent, both in space and time (Lomolino, 1999).

In this paper we attempt to trace the emergence of community assembly patterns as we move from the local (individual island) to the archipelago spatial scale, through the intermediate scale of island subgroups. The main questions we address are the following.

- Is there nestedness among sampling stations within individual islands?
- Is nestedness related to beta-diversity?
- Are the same species responsible for nested patterns at all spatial scales?
- Are the species that are widespread at a local scale also widespread at larger scales?
- Are the patterns of species co-occurrence similar at all spatial scales?
- Is there any role for ecological factors in the shaping of nested patterns?

Our approach herein is based on one case-study for which we have detailed data regarding the distribution of species and ecological factors per sampling station within islands. Of course, more such studies will be needed before we can come to general conclusions. The relationship between local and regional species diversity has been a focus of ecological interest for the last two decades (e.g. Schluter, 1984; Cornell & Lawton, 1992; Caley & Schluter, 1997; Hugueny & Cornell, 2000; Arita & Rodriguez, 2002; Gotelli & Ellison, 2002), but has been addressed mainly

for the more tractable case of perfectly nested samples. This line of research could be expanded to the more general case of non-perfectly nested samples, but to do this, one should have detailed information on how nestedness patterns change through several spatial scales. We believe that our paper contributes also to this discussion.

MATERIALS AND METHODS

We use detailed data on the distribution of terrestrial isopods on central Aegean islands (Greece). The islands investigated are remnants of a continuous landmass (Aegaeis) that connected the Greek mainland with Asia Minor until *c.* 5 Myr BP. They are grouped in two geographical units, the Kyklades and Eastern Islands. The two groups were separated sometime in the Pliocene, but they may have gained some restricted reconnection during the Mindel or Günz glacial period. The Kyklades are more distant from the mainland and have been isolated before the Pleistocene (with restricted local reconnections established for short periods during glacial periods), while the Eastern Islands lie close to the mainland (Asia Minor) and have been isolated for just a few thousand years. In fact, the details of the palaeogeographical history of the area are quite complex and not yet fully resolved. Furthermore, the Kyklades are not a uniform group, since some of the islands have formed temporary connections during the Pleistocenic glacial periods. We made separate analyses for each group, as well as a combined analysis for all the islands. The complete species list, the analysis of biotic similarity, the species-area relationships and a more detailed discussion on the palaeogeography of the region have been presented in Sfenthourakis (1996a,b).

All the islands host Mediterranean-type ecosystems and their habitats are highly heterogeneous. Sampling stations were locations of more or less equal area (around 0.1 km²) distributed over the whole island surface and covering all habitat types exploited by terrestrial isopods. For each sampling station we recorded 48 ecological parameters (as present/absent). In the present analysis we excluded the purely halophilic species and the corresponding coastal habitats because it was not possible to have secure and uniform records of all these species due to the inaccessibility of a large part of the coastal sites (steep rocky shores, etc.). The data matrix used consists of 59 species for 265 stations on 20 islands. This is a subset of the complete dataset for the region, from which the small islets and a few islands that were not sampled in a uniform way (e.g. Anafi, where collecting was done during long walking routes around the island) were excluded.

For the exploration of nestedness patterns we used the Nestedness Temperature Calculator (Atmar & Patterson, 1995). The rationale of this well-known method has been explained in detail by Atmar & Patterson (1993). Here, it suffices to say that higher temperatures are indicative of lower community nestedness, while 'colder' matrices are more nested. The free software developed by the authors calculates a 'Temperature' value (T) for each community and offers the possibility of a Monte Carlo simulation for assessing the statistical significance of this value. It also provides a diagram with the idiosyncratic temperatures of each

species and each sample, as well as the reorganization vector table from which one can identify the position of each species and sample in the maximally nested matrix. Idiosyncratic temperatures are a measure of the deviation of each point (species or sample) from the maximally nested condition, so that higher temperatures are assigned to species (or samples) that contribute more to the community's deviation from perfect nestedness.

This approach to the calculation of nestedness values has been criticised for not using fixed row *and* column sums in the null matrices constructed for estimation of statistical significance (Brualdi & Sanderson, 1999). According to the critics, this strategy leads to extensive Type I errors (finding significant nestedness where it doesn't exist), and they have proposed the construction of a 'null matrix space' consisting of matrices that retain the actual row and column sums. Nevertheless, up to now no one has provided sufficient evidential support that this is what actually happens, with the exception of some artificial matrices with equally rich sites. The criticisms of Brualdi & Sanderson (1999) are valid mainly for the previously applied RANDOM0 and RANDOM1 methods of Patterson & Atmar (1986) that used gaps (species present in poorer sites but absent in richer ones) as a metric, while the Temperature Calculator uses an approach that avoids the drawbacks of these older methods. Furthermore, from a biological point of view, one might argue that a test for significant nestedness should contrast the real data with 'null' communities where species incidences (column sums) may be left free to vary (while retaining the actual site richness, assuming species/area or saturation effects), to take into account the Narcissus effect (Colwell & Winkler, 1984), i.e. that the effects of a process could be underestimated because the community may be already structured by that same process (such as those that could be responsible for the nested structure). Furthermore, Jonsson (2001) has argued against the use of either fixed row or fixed column sums. It is clear that the issue is far from being settled.

A more robust criticism of the Temperature method is that *T* is affected by matrix size (Wright *et al.*, 1998), something we also find in our analyses. Nevertheless, if one does not use the Temperature Calculator as a 'black box' (Fischer & Lindenmayer, 2002), but is aware of its limitations, it is still possible to make relative comparative statements based on its results. The *C* metric of Wright & Reeves (1992) avoids the matrix-size effect, but we preferred to use the Temperature method because of the additional information it offers (idiosyncratic temperatures, reorganization matrix, etc.) which were more crucial for the analyses herein. In addition, this method is used widely in the literature and has become a familiar tool to many researchers.

For the analysis of species co-occurrence we used the Ecosim7 software (Gotelli & Entsminger, 2001; see also Gotelli, 2000). This software calculates four indices of co-occurrence (*C*-score: average number of 'checkerboard' units, Checker: number of never coexisting species pairs, Combo: number of unique species combinations, and *V*-ratio: the ratio of the variance of the column sums to the sum of the row variances) under nine simulation algorithms that are the combinations of fixed, equi-probable and proportional row and column sums. As recommended by its

author, we used the Sim9 algorithm that uses fixed row and column sums (those of the original matrix) because it is less prone to Type I Errors. This algorithm cannot be used for the *V*-ratio index. Also, we did not use the Combo index, as it is not particularly informative in the context of our investigation. The indices of co-occurrence aim to detect deviations from a randomly structured species presence-absence matrix, which is a matrix that has more or less co-occurring species pairs than expected by chance. Therefore, it is crucial to check, not only the statistical significance of the possibly deviant value, but also if it is larger or smaller than that of the random statistic (Gotelli & Entsminger, 2001). By doing this, it is possible to see if the community is structured by interspecific competition or by excess species co-occurrence. In a competitively structured community the values of *C*-score and Checker will be larger than those expected by chance.

Since co-occurrence is a phenomenon that involves specific species combinations (usually, but not exclusively, pairs), the use of 'ensemble' indices, such as *C*-score and Checker, may obscure useful information (Harvey *et al.*, 1983). Therefore, following also the rationale of Sanderson (2000), we applied a modified version of his method that identifies the precise species pairs that co-occur more, or less, often than expected by chance. Using a program we developed in C++, we calculated the frequency of all species pairs' co-occurrences in 5000 null matrices produced by Ecosim7 (using the fixed row and column sums option and the random knight's tour algorithm) for each original matrix, as well as the number of times that these species pairs co-occur in the original matrix. If this latter number fell outside the 5% and 1% confidence intervals of the null matrices' frequency distribution of co-occurrences, we considered the respective pairs as significantly deviating from a random co-occurrence pattern. Species pairs with a number of co-occurrences lying outside the lower limit of the frequency distribution exhibit a negative association ('mutual exclusion'), while those outside the upper limit are positively associated (co-occurring more often than expected by chance). The results of this method can be compared to those of the metrics available in Ecosim for a further evaluation of their performance.

Additional methods and procedures we applied for specific analyses are introduced in the respective sections of Results and Discussion, for reasons of clarity and because they provide a more direct view of our reasoning.

RESULTS AND DISCUSSION

Are sampling stations nested?

Should we expect to find nestedness in species communities within islands? If there are differences in the distribution of species among the various habitats encountered within each island, then we might find a nested pattern, since some expansive species would be widely present, while others might occur locally, in specific localities or habitat types.

In most of the islands in our dataset, sampling stations are significantly nested (Table 1). The levels of nestedness are not very high (most temperature values fall between 20 and 30), and

Table 1 The results of the analysis of nestedness using the Nestedness Temperature Calculator and data from Aegean islands, Greece (terrestrial isopods). For each island, Whittaker's index of diversity is also given

	T	P	F	NoSt	S	I _{sp}	I _{ha}
SAMOS	27.3	2.52e ⁻⁰⁶	25.7	18	29	4.27	3.43
IKARIA	26.5	3.87e ⁻⁰⁸	29.3	19	26	3.41	3.43
KOS	37.6	1.77e ⁻⁰³	31.6	15	29	3.16	3.29
KALYMNOS	20.2	8.9e ⁻⁰⁵	43.7	10	16	2.28	2.67
LEROS	36.4	NS	44.4	7	18	2.25	2.95
NISYROS	22.4	1.61e ⁻⁰²	43.6	7	20	2.29	2.07
PATMOS	39.6	NS	45.3	5	17	1.93	2.46
ASTYPALAI	23.5	3.17e ⁻⁰⁴	36.8	11	20	2.71	2.71
NAXOS	23.7	3.92e ⁻⁰⁶	20.2	19	32	4.94	3.53
ANDROS	26.7	1.04e ⁻¹⁵	31.8	24	26	3.14	3.28
TINOS	37.3	3.88e ⁻⁰³	35.3	13	25	2.82	2.72
PAROS	30.2	7.03e ⁻⁰⁸	41.1	15	18	1.91	2.83
MILOS	26.2	4.93e ⁻⁰²	20.5	13	22	4.87	3.49
KEA	23.7	6.8e ⁻⁰⁶	38.3	15	20	2.61	3.28
AMORGOS	48.9	NS	35.9	11	23	2.78	3.12
KYTHNOS	31.9	2.59e ⁻⁰³	41.8	13	16	2.39	2.54
MYKONOS	42.7	NS	40	10	16	2.5	2.93
SYROS	34.2	6.71e ⁻⁰⁴	33.3	15	20	3	2.79
SIFNOS	12.6	1.03e ⁻⁰⁶	39.2	11	21	2.37	2.92
SERIFOS	28.3	2.07e ⁻⁰⁴	40.6	11	20	2.46	2.67
EASTERN	42.6	2.03e ⁻⁰²	40.3	8	46	2.08	1.23
EASTERN (per station)	19.7	1.02e ⁻⁶³	16.5	98	46	6.04	3.54
KYKLADES	34.6	9.16e ⁻⁰⁹	38.2	12	50	2.32	1.23
KYKLADES (per station)	15.0	2.78e ⁻⁸³	14.5	170	50	6.89	3.67
ALL	37.2	1.58e ⁻¹⁶	33.5	20	59	2.71	1.23
ALL (per station)	13.6	4.53e ⁻¹⁰²	12.5	268	59	7.98	3.62

T = temperature.

P = significance level (Monte Carlo simulation, 50 permutations).

F = matrix fill.

NoSt = number of stations (or islands).

S = number of species.

I_{sp} = Whittaker's index of species diversity (total number of species on each island/mean species number per station).

I_{ha} = index of diversity for environmental variables (total number of variables present in each island/mean number of variables at each station).

are not correlated with matrix fill (F), number of stations (NoSt) or number of species (S), but are significantly correlated (negatively) with the product NoSt × S ($r = -0.59$, $P < 0.001$), that is, with matrix size. No significant nestedness was found in two Eastern islands and two islands of the Kyklades.

The striking difference of nestedness values in the aggregate data (Kyklades, Eastern and All) between the matrices containing species presences per station (more nested) and those containing species presences per island (less nested) is probably a consequence of the large number of rows (stations) in the former matrices. Nevertheless, because the discrepancy of values is quite large, it could also indicate a 'phase transition' when moving from stations to islands.

Is there any relationship between nestedness values and Whittaker's index of diversity?

One could assume that nestedness of stations within each island might be causally related to the species diversity among stations

(beta-diversity). As a first step towards testing this hypothesis we attempted to establish a correlation of nestedness values with an index of beta-diversity. For this purpose we used Whittaker's index (Whittaker, 1975), I_{sp} = total number of species/mean number of species per station, because it uses the same kind of information and also because available data did not permit the use of population density-based indices. There was no correlation of T with I_{sp} ($r = -0.16$, $P > 0.05$), so there was no reason for further elaborations on possible causal connections.

We also calculated a measure of each island's habitat diversity using the same index (I_{ha} in Table 1) and 48 environmental variables coded as present/absent at each station. This index also failed to show any significant correlation with T (at the same time, both indices are significantly correlated with species richness — results not shown).

We should note that the two indices were significantly correlated with each other (for individual islands: $r = 0.75$, $P < 0.001$), meaning that the more diverse islands host a more diverse set of species.

When we calculate the same indices for the groups of islands, we see a negative correlation of T with I_{sp} , suggesting that the more diverse groups are also more nested, a result that does not agree with the basic assumptions of nestedness. There is no other correlation of T at the group level.

Finally, we should note that the Kyklades are more diverse than the Eastern islands for both species and ecological variables, and that the diversities of ecological variables for per-island coded groups are identical.

We also tested the relationship of the serial order of islands in the maximally nested total matrix with their rank according to T , species richness (S), I_{sp} and I_{ha} . The island order, the Spearman rank correlation coefficients, and the partial correlations of ranks are given in Table 2.

The island position in the maximally nested matrix (N) shows significant correlation with species richness and both indices of diversity, meaning that the islands contributing most to the nested structure of the matrix are the richer and more diverse ones. This effect is mainly due to species richness, which is also correlated with rank species diversity, as shown by partial correlation analysis, which shows a significant correlation of richness rank with N . Therefore, the order of islands in the maximally nested matrix is determined solely by species richness, as expected by the methodological procedures of the Nestedness Temperature Calculator, without significant deviations due to habitat or species diversity.

Are the same species responsible for the nested patterns in islands and island groups?

We applied the nonparametric Spearman rank order correlation coefficient to the rank of species in the maximally nested matrices produced by the Nestedness Temperature Calculator in each case (Table 3), to see if the same species are responsible for the observed nested patterns.

Since the ranking of species in the maximally nested matrix does not fully reflect their contribution to the matrix's level of nestedness, we also applied the Spearman rank order correlation on the species ranked according to their idiosyncratic temperatures. Idiosyncratic temperatures are a measure of the contribution of each species to the deviation from perfect nestedness (the higher the temperature, the higher the contribution), or, in other words, its occurrence 'unexpectedness'. There were no significant correlations among the various combinations of islands and aggregate data (with the only exceptions being the significant correlations of aggregate Kyklades and Eastern island data with All).

The results given in Table 3 reveal some interesting cases of unexpected correlations, as well as absence of correlations. The islands of the Eastern group seem to be the most atypical as far as the placement of species in the maximally nested matrices is concerned, since most of them show no correlation with either the species placement in the All, or the aggregate Eastern islands matrix. Almost all correlations are significant when the stations are used in the matrices of the larger island groups (although there are still some exceptions).

Table 2 (a) The rank order of islands according to their nestedness value (ascending T), species richness (descending S), Whittaker's index of species diversity (descending I_{sp}), index of habitat diversity (descending I_{ha}) and their position in the maximally nested total matrix (ascending N). (b) The results of the rank order correlation (r_{sp} — Spearman correlation coefficient) and the partial correlations (partial r) between the first four ranks and N

	T	S	I_{sp}	I_{ha}	N
NAXOS	5	1	1	1	1
MILOS	6	6	2	2	7
SAMOS	9	2	3	3	3
IKARIA	7	3	4	3	6
KOS	16	2	5	4	2
ANDROS	8	3	6	5	4
KEA	5	8	11	5	10
AMORGOS	19	5	9	6	9
LEROS	14	9	18	7	15
MYKONOS	18	11	12	8	18
SIFNOS	1	7	15	9	8
PAROS	11	9	20	10	16
SYROS	13	8	7	11	14
TINOS	15	4	8	12	5
ASTYPALAI	4	8	10	13	13
SERIFOS	10	8	13	14	12
KALYMNOS	2	11	17	14	20
KYTHNOS	12	11	14	15	19
PATMOS	17	10	19	16	17
NISYROS	3	8	16	17	11

	r_{sp}	P	partial r	P
T-N	0.129	n.s.	0.369	n.s.
S-N	0.983	< 0.001	0.915	< 0.001
I_{sp} -N	0.786	< 0.001	-0.005	n.s.
I_{ha} -N	0.707	< 0.001	0.066	n.s.

What is more interesting is the better correlation of certain islands from one island group with the aggregate data of the other island group. These cases are Samos, Amorgos and Syros, as well as Ikaria and Kalymnos but only for the species-per-island data matrix. This result suggests that, even though each island group can be characterized by certain species (endemic or with distribution limits therein), the overall faunal character of central Aegean islands, when judged by the frequency of species occurrence among sites, is mixed. Also, we should note that the correlations between all the combinations of the island groups are highly significant.

Are the species that are widespread within islands the same as those that are widespread at the archipelago scale?

Species appearing in the first few columns of the maximally nested matrices are generally those that are more widespread

Table 3 Spearman's rank correlation coefficient for the order of species placement in the maximally nested matrices produced by the Nestedness Temperature Calculator

	ALL		KYKLADES		EASTERN		ALL st		KYKLADES st		EASTERN st	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
Samos	0.628	< 0.001	<i>0.605</i>	< <i>0.002</i>	n.s.		0.724	< 0.001	<i>0.792</i>	< <i>0.001</i>	0.545	< 0.005
Ikaria	0.397	< 0.05	<i>0.534</i>	< <i>0.01</i>	n.s.		0.538	0.005	<i>0.525</i>	< <i>0.01</i>	0.560	< 0.005
Kos		n.s.		n.s.	0.565	< 0.002	0.404	< 0.05		n.s.	0.620	< 0.001
Kalymnos		n.s.!	<i>0.668</i>	< <i>0.02</i>	n.s.		0.662	< 0.01	<i>0.709</i>	< <i>0.01</i>	0.729	< 0.002
Leros		n.s.!		n.s.	n.s.!		0.571	< 0.02		n.s.	0.610	< 0.01
Nisyros		n.s.		n.s.	0.606	< 0.005	0.447	< 0.05		n.s.	0.761	< 0.001
Patmos		n.s.		n.s.	n.s.		n.s.			n.s.	n.s.	
Astypalaia		n.s.		n.s.	n.s.		0.506	< 0.05		n.s.	0.538	< 0.02
Naxos	0.518	< 0.005	0.543	< 0.002	n.s.		0.656	< 0.001	0.722	< 0.001	<i>0.515</i>	<i>0.05</i>
Andros	0.447	< 0.05	0.564	< 0.005	n.s.		0.641	< 0.001	0.711	< 0.001		n.s.
Tinos		n.s.	0.489	< 0.002	n.s.		0.562	< 0.005	0.637	< 0.001		n.s.
Paros	0.565	< 0.05	0.539	< 0.05	n.s.		0.725	< 0.001	0.719	< 0.001	<i>0.576</i>	< <i>0.02</i>
Milos	0.599	< 0.005	0.632	< 0.002	<i>0.443</i>	< <i>0.05</i>	0.753	< 0.001	0.725	< 0.001	<i>0.710</i>	< <i>0.001</i>
Kea	0.510	< 0.05	0.647	< 0.005	n.s.		0.780	< 0.001	0.834	< 0.001	<i>0.474</i>	< <i>0.05</i>
<i>Amorgos</i>	0.699	< 0.001	0.563	< 0.01	0.698	< 0.001	0.614	< 0.002	0.527	< 0.01	0.669	< 0.002
Kythnos		n.s.		n.s.	n.s.		n.s.		n.s.		n.s.	
Mykonos	0.720	< 0.005	0.806	< 0.001	<i>0.542</i>	< <i>0.05</i>	0.888	< 0.001	0.847	< 0.001	<i>0.771</i>	< <i>0.001</i>
Sifnos	0.594	< 0.005	0.652	< 0.005	n.s.		0.805	< 0.001	0.857	< 0.001	<i>0.501</i>	< <i>0.05</i>
Serifos	0.590	< 0.01	0.640	< 0.005	n.s.		0.836	< 0.001	0.839	< 0.001	<i>0.655</i>	< <i>0.005</i>
<i>Syros</i>	0.504	< 0.05	0.450	< 0.05	0.480	< 0.05	0.653	< 0.002	0.622	< 0.005	0.646	< 0.005
Kyklades	0.893	< 0.001			0.582	< 0.001						
Eastern	0.774	< 0.001										
All st	0.904	< 0.001	0.897	< 0.001	0.739	< 0.001			0.931	< 0.001	0.867	< 0.001
Kyklades st	0.845	< 0.001	0.910	< 0.001	0.501	< 0.002					0.695	< 0.001
Eastern st	0.805	< 0.001	0.706	< 0.001	0.870	< 0.001						

bold: cases of unexpected absence of significant correlation.

italics: cases of unexpected significant correlations (e.g. islands of the Eastern group with Kyklades).

! = marginally not significant.

st = aggregate data per station.

among the sampling units. We checked if the species present in the first 10 positions of each maximally nested matrix are the same between islands, and between islands and island groups.

In sum, 35 species (from a total of 59) are present in the first 10 positions (Table 4), a number indicating a broad spread of wide-spread species among islands. In the Eastern islands there are 27 species, and there are 28 in the Kyklades. However, several of them appear only once or twice, so only 9 and 10, respectively, from these species appear in half or more of the islands in each group. Only 5 of them are common among the two island groups. These 5 species are also among the top 10 species in the All data matrix, as well as in those of the Eastern and Kyklades sets when grouped according to species per island presences. There are some 10 more species that are very common among the top 10 of individual islands, and these also appear in the top 10 of the aggregate matrices.

All the species present in the top 10 of the aggregate (species-per-island) matrices also appear in the per station top 10, although a few of them occur at a low frequency. This means that most species that are widespread at the island group or the archipelago scale are also widespread within most islands, but not vice

versa. Finally, we should also note that the first three 'core' species are the main components (together with the halophilic species excluded from the present analysis) of the region's small islets' isopod fauna (see Sfenthourakis, 1994, 1996b).

Are the patterns of species co-occurrence similar within and between islands?

The results of the C-score and Checker indices (Table 5) show that most islands do not exhibit any significant pattern of co-occurrence, and in those that exhibit such a pattern, the observed values are higher than the simulated, i.e. there is significant mutual exclusion of species. Similarly, in all cases of island groups, the significant values are those indicating more mutually excluded species pairs than expected by chance. The C-score tends to identify more cases of excess 'checkerboard' distributions than the Checker index.

The analysis of species pair co-occurrence (Table 6), however, revealed a quite different picture. Within most islands (17 out of 20), there were species pairs that co-occur more, or less, often than expected by chance, with positive associations prevailing

Table 4 The 'top 10' species of each maximally nested matrix. Column subheaders are the first three letters of each island (or group). The species are given in descending order of total appearances in the top 10 s

	PER ISLAND			PER STATION			EASTERN ISLANDS										KYKLADES												
	ALL	KYK	EAST	ALL	KYK	EAST	SAM	IKA	KOS	KAL	LER	NIS	PAT	AST	NAX	AND	TIN	PAR	MIL	KEA	AMO	KYT	MYK	SIF	SER	SYR			
<i>Porcellionides pruinosus</i>																													
<i>Armadillo officinalis</i>																													
<i>Platyarthrus schoebli</i>																													
<i>Chaetophiloscia cellaria</i>																													
<i>Porcellio obsoletus</i>																													
<i>Porcellio laevis</i>																													
<i>Armadillidium insulanum</i>																													
<i>Leptotrichus kosswigi</i>																													
<i>Trachelipus aegaeus</i>																													
<i>Agabiformius lentus</i>																													
<i>Leptotrichus naupliensis</i>																													
<i>Proporcellio quadriseriatus</i>																													
<i>Orthometopon phaleronense</i>																													
<i>Schizidium hybridum</i>																													
<i>Armadillidium granulatum</i>																													
<i>Armadillidium marmoratum</i>																													
<i>Bathyropa granulata</i>																													
<i>Chaetophiloscia lagoi</i>																													
<i>Armadillidium vulgare</i>																													
<i>Armadillo tuberculatus</i>																													
<i>Chaetophiloscia elongata</i>																													
<i>Porcellio flavomarginatus</i>																													
<i>Platyarthrus lindbergi</i>																													
<i>Protracheoniscus kalyminius</i>																													
<i>Schizidium oertzei</i>																													
<i>Trichoniscus Oedipus</i>																													
<i>Trichoniscus pygmaeus</i>																													
<i>Trichoniscus rhodiensis</i>																													
<i>Protracheoniscus babori</i>																													
<i>Ligidium ghigi</i>																													
<i>Nagurus aegaeus</i>																													
<i>Ligidium cycladicum</i>																													
<i>Paraschizidium album</i>																													
<i>Armadillidium afficum</i>																													
<i>Leptotrichus syrensis</i>																													

Table 5 Results of co-occurrence analysis using three indices that measure: the average number of species-pairs 'checkerboard units' (C-score) among all species pairs; the total number of species-pairs 'checkerboard units' (Checker). A 'checkerboard unit' is the mutual exclusion of each species in any pair of sites. In communities that are competitively structured, the observed C-score and Checker should be significantly larger than expected by chance (Gotelli, 2000)

	C-score				Checker			
	obs	sim	obs < sim	obs > sim	obs	sim	obs < sim	obs > sim
SAMOS	9.782	9.701	0.742	0.263	184.000	179.715	0.746	0.304
IKARIA	8.763	8.448	0.987	0.014	118.000	116.220	0.657	0.407
KOS	6.640	6.441	0.978	0.023	114.000	114.516	0.493	0.565
KALYMNOS	1.942	1.940	0.590	0.453	11.000	7.451	0.990	0.161
LEROS	2.072	2.076	0.533	0.530	35.000	30.586	0.897	0.157
NISYROS	1.105	1.082	0.747	0.292	36.000	36.586	0.534	0.552
PATMOS	0.794	0.753	0.941	0.118	32.000	27.173	0.978	0.051
ASTYPALAIA	3.322	3.325	0.548	0.481	42.000	39.299	0.801	0.269
NAXOS	4.377	4.395	0.464	0.543	246.000	235.958	0.905	0.116
ANDROS	13.203	12.868	0.981	0.021	74.000	71.009	0.698	0.371
TINOS	3.927	3.878	0.772	0.236	102.000	93.199	0.922	0.099
PAROS	6.928	6.774	0.904	0.101	29.000	26.773	0.792	0.299
MILOS	2.824	2.905	0.177	0.844	126.000	122.304	0.900	0.160
KEA	5.489	5.267	0.975	0.028	39.000	37.741	0.687	0.401
AMORGOS	3.450	3.339	0.936	0.068	94.000	87.634	0.981	0.034
KYTHNOS	3.500	3.375	0.896	0.117	37.000	35.155	0.863	0.251
MYKONOS	3.267	3.161	0.965	0.047	44.000	41.183	0.964	0.101
SYROS	5.158	5.227	0.294	0.721	63.000	61.251	0.720	0.362
SIFNOS	1.889	1.527	1.000	0.000	17.000	22.290	0.124	0.936
SERIFOS	2.731	2.613	0.899	0.110	48.000	50.028	0.346	0.750
EASTERN	1.405	1.351	0.976	0.026	219.000	219.402	0.530	0.506
EASTERN st	104.297	102.500	0.995	0.005	462.000	446.687	0.911	0.102
KYKLADES	2.716	2.642	0.985	0.016	277.000	295.055	0.045	0.963
KYKLADES st	154.855	152.823	0.998	0.002	614.000	566.126	0.999	0.002
ALL	7.699	7.533	0.994	0.007	459.000	460.719	0.501	0.522
ALL st	372.996	367.592	1.000	0.000	845.000	772.978	1.000	0.000

bold: cases of significant correlation.

obs = Observed index value.

sim = Mean simulated index value.

obs < sim = p (observed \leq expected).

obs > sim = p (observed \geq expected).

over negative ones (exclusions) in 9 islands and negative prevailing in 6. It is very important to note that almost all of these pairs (72 of 77) appear once and only once, and the remaining five pairs appear in just two of them each. Furthermore, three of these five pairs exhibit an opposite association in each of the two islands (i.e. co-occurring more often than expected by chance in one and less often in the other). At the island group scale (analysis with species per station), there are 298 'deviating' species pairs, 100 in the Eastern islands, 134 in the Kyklades, and 240 in the All islands matrix. Of these pairs, 49 appear in Eastern and All, 91 in Kyklades and All, 6 in Eastern and Kyklades, and 14 in all groups, while 31 are unique to the Eastern islands, 21 to the Kyklades and 84 to All. Again, the positive associations (192) are more abundant than the negative (115), and there are 9 cases of incongruent associations between groups. The analysis of the species per island data matrix gives 66 deviating species pairs, only 5 of which appear in more than one group (3 in both East-

ern and All, and 2 in both Kyklades and All). Of the remaining 61, 7 appear in the Eastern islands, 10 in the Kyklades and 44 in All. The species pairs of this analysis are almost completely different from those of the analysis of stations within islands, a result that is unremarkable as far as negative associations are concerned (because of nonoverlapping geographical distributions), but which is not so predictable for the positive ones. In these data matrices, the negative associations prevail (45 vs. 26, see also Table 6), but the species involved in these associations are mainly species with limited overall geographical distribution among the islands (endemics, etc.).

The results of this analysis are not congruent with those of the Ecosim7 analysis, since negative associations prevail in only one of the islands (Kea) identified by the C-score as 'competitively structured', while three other islands where negative associations are the only significant ones (Kalymnos, Nisyros and Paros), do not have a significant C-score or Checker value. The same is true

Table 6 A summary of the results of the species-pairs association analysis. The number of times each species pair co-occurs in the original matrix was compared to the frequency distribution of this pair's co-occurrences in 5000 random matrices constructed with fixed row and column sums (equal to those of the original matrix) and with the random knight's tour algorithm. Deviations from randomness (negative or positive) were calculated at two significance levels (5% and 1%). Herein we give only the numbers of pairs with significant negative or positive associations for each data matrix

DATA MATRIX	ASSOCIATION negative	s.l.		ASSOCIATION positive	s.l.	
		5%	1%		5%	1%
SAMOS	4	4	0	5	5	0
IKARIA	4	4	0	6	6	0
KOS	2	2	0	4	3	1
KALYMNOS	1	1	0	0	—	—
LEROS	0	—	—	0	—	—
NISYROS	2	2	0	0	—	—
PATMOS	0	—	—	0	—	—
ASTYPALAIA	2	2	0	1	0	1
NAXOS	0	—	—	3	2	1
ANDROS	3	2	1	13	11	2
PAROS	3	2	1	0	—	—
TINOS	3	3	0	1	1	0
MILOS	0	—	—	1	1	0
KEA	3	3	0	0	—	—
AMORGOS	0	—	—	4	4	0
KYTHNOS	0	—	—	0	—	—
MYKONOS	0	—	—	2	1	1
SYROS	2	1	1	2	2	0
SIFNOS	2	2	0	5	1	4
SERIFOS	2	2	0	2	2	0
EASTERN	7	7	0	3	3	0
EASTERN st	44	24	20	56	43	13
KYKLADES	8	8	0	4	4	0
KYKLADES st	53	20	33	81	52	29
ALL	27	22	5	22	18	4
ALL st	89	38	51	151	87	64

for Astypalaia and Tinos, where negative associations exceed the positive. In 9 of the remaining islands, positive associations are more common than negative, in 2 they are equal, and in 3 islands no significantly deviating species pairs were found.

Congeneric species do not show any exceptional pattern of co-occurrence, as shown in Table 7. In the aggregate matrices they participate in the deviating pairs at a percentage that is analogous to their overall participation in the total number of species pairs, while in most of the single island matrices they make no contribution to the deviating pairs. Furthermore, in the few cases where they do appear, they show positive and negative associations at roughly equal proportions. Also, the congeneric species that show negative associations in certain islands (e.g. *Armadillidium insulanum* and *A. vulgare* in Samos) occur together in many other islands at a nondeviating frequency.

There are certain species with profuse participation in the above mentioned associations, and these are mostly species with special habitat requirements, such as hygrophilous (*Ligidium* spp., *Chaetophiloscia* spp., and *Trachelipus aegaeus*), myrmecophilous (*Platyarthus* spp.) and burrowing species (*Agabiformius* spp., *Leptotrichus* spp., and *Proporcellio quadriseriatus*).

The above mentioned results, combined with the fact that the vast majority of species pairs do not appear systematically and consistently, suggest that the patterns of species associations are probably due to indirect factors, such as the habitat structure of sampling stations, or historical events (particularly in the species per island matrices), and do not result from direct biotic interactions (e.g. competitive exclusion). Of course, conclusive evidence for such a hypothesis can be drawn only through direct experimentation, but our results are highly suggestive of this interpretation.

Is there any common ecological feature behind nested patterns?

When we identified the sampling stations that appear in the first 20 positions in the maximally nested matrices of all islands and of the Kyklades and Eastern islands (40 stations in total), as well as those appearing at the first 10 positions in the corresponding matrix of each island, we found that, as expected, these are among the stations hosting the larger numbers of species. The specific stations found among the top 20s contain the whole range of

Table 7 The contribution of congeneric species to the deviations from random co-occurrence. The second and third columns give the total number of species pairs in each matrix and how many of these are among congeneric species, respectively. The fourth and fifth columns give the respective numbers of pairs whose associations deviate from a random co-occurrence pattern. The symbols in parentheses signify the type of association among congeneric species, positive (+) or negative (-)

matrix	all pairs		significantly deviating from random	
	total	congeneric	total	congeneric
SAMOS	406	21	9	2(-)
IKARIA	325	11	10	0
KOS	406	14	6	0
KALYMNOS	120	6	1	0
LEROS	153	9	0	0
NISYROS	190	8	2	1(-)
PATMOS	136	6	0	0
ASTYPALAIIA	190	8	3	0
NAXOS	496	24	3	1(+)
ANDROS	325	11	16	1(+)
PAROS	153	11	3	0
TINOS	300	13	4	0
MILOS	231	13	1	0
KEA	190	6	3	0
AMORGOS	253	11	4	1(+)
KYTHNOS	120	3	0	0
MYKONOS	120	6	2	0
SYROS	190	10	4	0
SIFNOS	210	10	7	1(+)
SERIFOS	190	7	4	0
EASTERN	1035	44	10	1(+)
EASTERN st	1035	44	100	3(1+, 2-)
KYKLADES	1225	54	12	0
KYKLADES st	1225	54	134	4(2+, 2-)
ALL	1711	71	49	3(-)
ALL st	1711	71	240	7(2+, 5-)

ecological variables in more or less the same proportions as in the All station matrix (Fig. 1). There is only a slight overrepresentation of factors that usually lead to a higher concentration of isopod species, such as the presence of running or stagnant water (G1, G2), abundant shelters (I1), rich and humid litter layer (M1, M3), broadleaved or hygrophilic plants (B4, E2, E3), but there was almost no under-representation of any variable. If ecological variables were following the nested pattern of species occurrences, we would expect a significant overrepresentation of the rare variables among the top 20 stations, since the rich sites would include the overall rarer habitat types, but no such trend can be seen. Thus, the rich sites are a diverse assemblage that reflect the overall heterogeneity of Aegean habitats. We should also note that within the top 20 stations of the complete data matrix we find sites from 14 out of the 20 islands (3 from Andros, 3 from Tinos, 2 from Naxos, 2 from Nisyros, and 1 from Samos, Ikaria, Kos, Kalymnos, Leros, Astypalaia, Paros, Kea, Sifnos, and Serifos). Therefore, the patterns of nestedness among stations are mostly shaped by rich stations distributed all over the archipelago, hosting a core of species that are widespread at the archipelago scale plus some locally 'core' species (at the island group scale).

CONCLUSIONS

The analysis of nested species assemblages has been used in a variety of contexts to obtain information pertaining to the assembly of insular biotic communities and to conservation issues. The approaches used have mainly focused on a single scale of community organization, usually the scale of island groups or habitat fragments. But, since biotic communities are not generally random assortments of species, one would expect to find nested patterns at various levels of biotic integration. Herein we attempted a simultaneous analysis of nestedness at three scales, the scale of sampling stations within individual islands, the scale of island groups with a presumed common recent palaeogeographical history, and the scale of the archipelago (that is, an island group with a deeper common history). We found significant nestedness, although not very high, at all three scales. Nested insular assemblages are due to the differential species richness among islands (which usually come in a variety of areas, translated in turn to a variety of species richness values). The nested patterns at the sampling stations scale are similarly due to the differential species richness among sites, which could be related to habitat patchiness. At the same time, for a nested pattern to

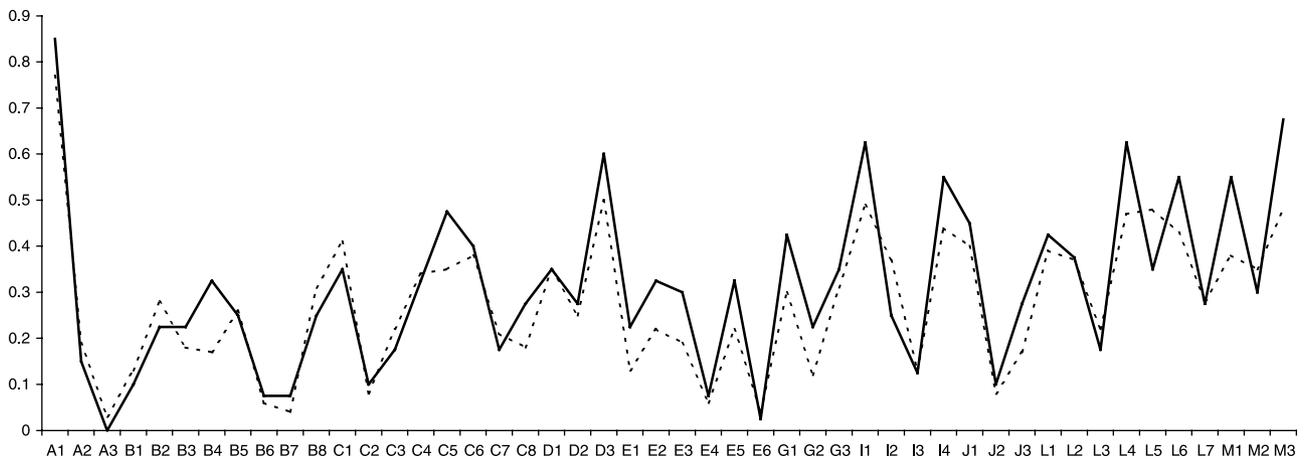


Figure 1 The percentage representation of ecological variables in the top 20 stations appearing in the maximally nested matrices for all islands, Kyklades and Eastern islands (continuous line) compared to that of the total number of stations (dotted line). The horizontal axis shows the codes of ecological variables.

The ecological variables used (coded as present/absent) are the following (individual plant species were coded separately due to their abundance in the respective insular Aegean habitats):

A: Elevation

A1: 0–300 m, A2: 300–600 m, A3: 600–900 m

B: Arboreal vegetation — shrubs (maquis)

B1: *Juniperus* spp., B2: *Pistacia* spp., B3: evergreen *Quercus* spp., B4: broadleaved species, B5: conifers, B6: *Erica* spp., B7: *Arbutus* spp., B8: other species (*Ceratonia*, *Crataegus*, etc.)

C: Herbaceous plants — phrygana

C1: *Sarcopoterium spinosum*, C2: *Cistus* spp., C3: *Genista* spp., C4: *Asphodelus aestivus*, C5: Graminae, C6: other herbs, C7: halophytes, C8: halophytes

D: Cultivated plants

D1: olives, D2: fruit-bearing trees, D3: herbaceous cultivated plants (vegetables, etc.)

E: Riparian vegetation

E1: *Platanus orientalis*, E2: *Arundo donax*, E3: *Nerium oleander*, E4: *Acer* spp., E5: *Myrtus communis*, *Vitex agnus-castus*, etc., E6: dry banks

G: Freshwater

G1: permanent, G2: stagnant, G3: running

I: Shelters

I1: many, I2: scattered, I3: few, I4: stone walls

J: Human impact

J1: buildings, J2: fire, J3: roads

L: Substrate

L1: calcareous, L2: mixed, L3: noncalcareous, L4: sandy soil, L5: intermediate soil, L6: muddy soil, L7: hard soil

M: Litter-layer

M1: rich, M2: present but not rich, M3: wet

appear it is crucial to have a variety of species distribution sizes, with poor sites hosting subsets of the communities present in richer ones. If most species were restricted to a narrow range of habitat types, then we should not expect to find significant nestedness at the sampling station scale. In our case, the modest levels of nestedness found indicate an intermediate situation, with several widespread species (about one fourth of the species) and more that have a narrower distribution. The nested patterns at the island-group scale are due to the fact that all islands ‘draw’ species from a common species pool, with deviations of perfect nestedness caused by extinctions, violation of the ‘common pool’ assumption (e.g. via local speciation, distant immigrants, etc.), other stochastic processes, and/or increased habitat heterogeneity among islands. This means that the causality behind nestedness

partially differs at the two scales, with habitat heterogeneity being the main common factor.

Whittaker’s index is a robust measure of between-site (beta) diversity (Magurran, 1988; Cameron, 1992), but it is not correlated with levels of nestedness. The only determinant of nestedness values in our case was a matrix-related parameter, namely the product of species richness with number of sites (i.e. the matrix size). This means that the richer the matrix, the more nested it is. This result, combined with the modest values of nestedness found, suggest that the nested pattern is mainly due to some widespread species that are encountered more often as one explores more sampling stations. If this is true for within-island communities, then one would want to see if these species are widespread also at the island-group scale. The maximally nested

matrices produced by the Nestedness Temperature Calculator are a nice tool for this kind of data exploration. Both the position of each species in these matrices and their idiosyncratic temperatures can be used for the evaluation of such questions. The first value gives a measure of how widespread each species is, while the second adds a measure of its 'occurrence unexpectedness' (in the sense that it contributes to the matrix's deviation from perfect nestedness). Our analysis showed that besides a small number of 'hardcore' species (less than 10% of the total species pool), there is a loose core (around 25%) of species that contribute to the nested patterns at all scales of analysis. Nevertheless, the species that are widespread within individual islands are not necessarily widespread within the island groups, but there are no species widespread at the island-group scale that are not also widespread within islands. This means that, at least in the case of Aegean terrestrial isopods, species cannot be locally rare but geographically widespread, while they can be locally common but geographically rare. Nested patterns at large scales are mainly formed by locally common species.

When species per site data are considered, species tend to co-occur more often than expected by chance at all scales, meaning that mutual exclusion among isopod species pairs is not common. When species per islands are considered, there are more cases of species that co-occur less often than expected by chance, but these are mainly species that have a restricted or irregular overall distribution within the study area, and in any case they do coexist at several sites. There is no difference between the co-occurrence patterns of congeneric and other species pairs. Patterns of co-occurrence thus seem to be determined by habitat properties and overall geographical distribution, probably due to the complex palaeogeography of the region, and not by biotic interactions among species. Gotelli & Ellison (2002) reached a similar conclusion in their analysis of ant assemblages at two geographical scales, even though at the local scale they did not find any significant deviation from random occurrences. At the regional scale (which corresponds to our species per island datasets) they did find less co-occurrence than expected by chance in one (forest) of the two habitat types they examined, which they attributed mainly to the differential responses of species to various environmental factors.

The identification of particular species-pairs' associations, a method originally developed by Sanderson (2000), is a useful tool for detailed analyses of species co-occurrence, and should be evaluated further as an alternative to the C-score, Checker and other indices of 'overall community structure', to determine the relative merits and drawbacks of each approach.

Ecological factors thus play an indirect role in the formation of patterns of community structure, making up a heterogeneous habitat background that leads to increased variability in species richness, which is necessary for the occurrence of nested patterns within islands. Therefore, as long as there is a relatively high ecological heterogeneity, we can expect to find nested patterns at all scales of analysis.

Finally, we should note that the Temperature method, even though it tends to give lower values (higher levels of nestedness) in large matrices, offers some valuable tools for the detailed study of

biotic communities. Of special interest are the idiosyncratic temperatures of species and sites, and the order of species and sites placement in the maximally nested matrices. These clues can be used for a point-by-point exploration and description of nested patterns, and should attract more attention from the students of insular biotic assemblages.

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