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Testing the effect of host availability on endobiont diversity: proposing the single hotel hypothesis

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This study investigates the determinants of endobionts diversity within habitat-forming organisms, employing concepts from Island Biogeographic Theory (IBT) as a prospective explanatory framework. Sponges have long been considered "living hotels" due to the great diversity and abundance of their associated fauna. Various factors have been proposed to influence the composition and diversity of sponge-associated fauna, often relating to individual sponge characteristics, such as volume and oscular diameter. However, studies frequently contradict when identifying the main determinant. Focusing on two common massive sponge species, *Agelas oroides* and *Sarcotragus foetidus*, we collected, dissected, and analyzed 18 sponge specimens of *A. oroides* and 12 of *S. foetidus* from three sites in Crete, Greece (Eastern Mediterranean Sea). The sponges hosted 943 macroinvertebrates belonging to 94 different taxa, half of which were polychaetes. Crustaceans were the most abundant group, with over 50% of the individuals. Contrary to IBT predictions, *A. oroides* from areas with lower sponge abundance (i.e., "single hotel in town"), exhibited higher endofauna densities and richness. Notably, *S. foetidus*, which hosted large numbers of snapping shrimps, presented a different pattern, highlighting the importance of species-specific interactions on endobiont communities. Additionally, the reproductive state of *S. foetidus* correlated with increased endobiont richness, suggesting a potentially overlooked aspect of sponge-endobiont interactions related to the sponge's reproductive state. These results emphasize the importance of sponges as "living hotels" and sponge communities as sources of biodiversity and highlight the complex influence of habitat availability and species-specific interactions on sponge-associated fauna.

Keywords Habitat availability, Invertebrates, Ophiuroidea, Island biogeography, Sponge, Symbiosis

The Theory of Island Biogeography (IBT)[1] has served as a model to predict insular species richness and turnover rates in relation to island size and isolation. Island isolation plays a major role in this hypothesis, which states that islands in closer proximity to one another are expected to have a higher species diversity and richness as they facilitate easier species dispersal[1–3]. Species inhabiting proximate islands may exhibit heightened genetic connectivity, potentially fostering more intricate ecological interactions. These interactions may encompass shared predator-prey relationships and competitive dynamics, suggesting a greater degree of complexity in the ecological dynamics of these closely located island ecosystems[1,4].

Since its inception, the theory has been subjected to extensive experimentation using actual island systems. While most of the scientific literature in the field refers to "terrestrial islands", IBT has been adapted to many "islands of suitable habitat"[5–7] as well as islands in microscale environments such as detritus aggregates and their microbial inhabitants[8]. Meyer (2017)[7] reviewed the adaptation of this theory to diverse marine habitats resembling islands, exploring instances where the theory proves robust and identifying its limitations. Some

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authors have demonstrated that coral reefs may be regarded as islands[9–11] and others have even viewed sponges as "islands", in order to describe the relationship between their volume and the richness of their endofauna[12–14]. However, to the best of our knowledge, only a few studies have explored the idea that habitat-forming organisms, such as sponges with their complex structures[9], function as insular habitats that may influence the diversity of their associated fauna.

Sponges are a dominant component of the oceans' benthos worldwide and are considered ecosystem engineers in many habitats[17,18]. One of their most important roles is providing habitat to a wide variety of endofauna, thereby significantly contributing to marine biodiversity. Thus, sponges have previously been described as "living hotels"[13,14,16,19–23]. The most dominant members of these endobiont communities are commonly polychaetes, crustaceans, and brittle stars[13,16]. Sponge endobionts often use their host for shelter, as a nursery, and in many cases as a food source[24].

This ecological role of sponges has gained increasing research interest over the last few decades for both scientific and conservation purposes. Previous studies have described the relationship between sponges' morphology and the diversity of their inhabitants[12,25,26]. While most studies found that endofauna richness and density increase with sponge volume[12,13,27]some have shown that sponges with lower volumes may harbor higher faunal density[25,28]. However, these differences could be attributed to the intrinsic characteristics such as oscular diameter and canal size of each sponge species, as various sponges have been shown to host unique endofauna communities[12,13].

Recent work by Goren et al.[19] showed similar findings when comparing the endofauna assemblage in massive sponges from shallow and mesophotic habitats along the Mediterranean coast of Israel. Sponges in the mesophotic sponge grounds (MSG) were larger and more abundant than those in the shallow habitats; accordingly, the total richness of endobiont species was almost twice as high in the MSG as in the coastal areas[19]. However, the density and richness of endobionts per liter were significantly lower in the MSG. Since sponges constitute "living hotels", their abundance/isolation, or the availability of "hotels," may have a crucial impact on their inhabitants' diversity and density. We hypothesize that when there is only a "single hotel in town" (or very few), all "guests" will crowd in it, thus increasing richness and density. On the contrary, when there are many "hotels in town", "guests" will spread among them, reducing density and richness in each sponge (habitat). This is contradictory to what is expected in IBT. Here we aim to investigate this "single hotel hypothesis" by studying the endofauna inhabiting two of the most common species of massive sponges living in sublittoral rocky areas in the Eastern Mediterranean Sea.

Materials and methods

Study sites

The study was carried out in three sites at the sublittoral zone (5–15 m) of the north coasts of Crete (Greece, Eastern Mediterranean; Fig. 1): Alykes (35.42°N, 25.01°E; 10–15 m deep), Mades (35.40°N, 25.03°E; 10–15 m) and Voulisma (35.13°N, 25.74°E; 5–10 m). All surveyed sites contained areas with both high and low sponge abundances. Notably, both focal sponge species, *Agelas oroides* (Schmidt, 1864) and *Sarcotragus foetidus* Schmidt, 1862, are present across these sites. The high and low abundance areas in each site were close to each other, with a maximum distance of 20 m, In each site all specimens were collected roughly at the same depth range, with only a couple of meters difference (10–15 m in mades and alykes, and 5–10 m in voulisma), and with no difference in depth across low and high sponge abundance areas. Most sponges were collected from rocks with vertical orientation, although S. foetidus seemed to prefer more (sub-)horizontal surfaces. In both habitats, *A. oroides* occurred and was collected from semi-dark areas, whereas *S. foetidus* specimens were found also in more lighted areas. Rock surfaces in the study sites were generally characterized by low percentage cover of low-lying algae and sessile invertebrates other than sponges[29,30]. Efforts were made to collect the sponges from areas in which all environmental factors were similar, apart from the abundance of sponges.

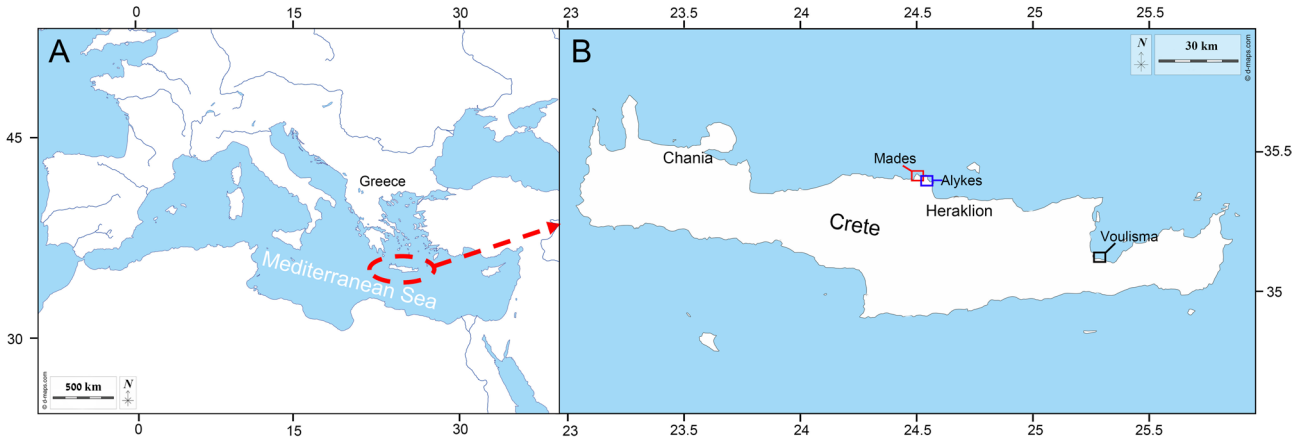

Fig. 1. Maps of (**a**) the Mediterranean Sea (**b**) the island of Crete with the sampling sites (red: Mades, Blue: Alykes, Black: Voulisma).

Sponge cover and abundance Estimation

A quantitative survey was carried out at the different sites to assess the sponge abundance in two areas of each site. The survey was conducted by capturing still images via SCUBA diving. The images were taken only on rocky substrates in a random manner (every two fin strokes). A Canon G16 camera was used, coupled with two parallel laser beams for scale and diving lights. From these images, we created a collection of 25 to 31 quadrats of known dimensions (45 × 30 cm) for each area. Photos were uploaded to CoralNet[31,32]where total sponge coverage and massive sponge coverage were determined using the point count method[33]. Massive sponge abundance was estimated by counting all massive sponge individuals in the photoquadrats.

Sponge and sponge-associated fauna sampling

The sponge species *A. oroides* and *S. foetidus* were chosen as models to investigate the "single hotel hypothesis" because they are massive ecosystem-engineering species, supporting rich associated macroinvertebrate communities[13,16,19] and they are among the most common sponges in Mediterranean rocky beds[34–36]including the study area.

Eighteen specimens of *A. oroides* and twelve specimens of *S. foetidus* were collected in the following manner: In Alykes and Mades sites, we collected three specimens of each species from areas of low sponge abundance, and three more from areas of high sponge abundance. In Voulisma, only specimens of *A. oroides* (three from each area) were collected due to the scarcity of *S. foetidus*. We attempted to collect sponges of roughly the same size.

Sponges were collected via SCUBA diving at 5–15 m depth. The specimens were covered with 40 × 40 cm zip lock bags to avoid loss of motile macrofauna, then detached using a knife, leaving the sponge holdfast attached to the substrate to allow its regeneration. Immediately following collection, specimens were taken to the laboratory, where sponge volume was estimated (via water displacement), and oscular diameter (cm) was measured to control for the possible effect of these parameters on the endofauna abundance and diversity. The associated endofauna was separated from sponge individuals under a stereoscopic microscope by systematic dissection along the canals and cavities of the sponge.

The water and the associated macrofauna remaining in the bags, were sieved through a 0.5 mm mesh. Sponge-associated endofauna was sorted, counted, and identified to the lowest taxonomic level possible. Biomass of associated fauna was estimated after animals of each taxon from a single sponge were dried for a few seconds on absorbent paper. Weighing was done to 0.1 mg accuracy.

Reproductive state of *Sarcotragus foetidus*

During the dissection of sponges, numerous sponge embryos were observed in the mesohyl of the specimens. The embryos were visible to the naked eye, and thereafter, we revisited all sponge individuals and qualitatively assessed the number of reproductive individuals.

Statistical analysis and data access

The volume of *A. oroides* and *S. foetidus* was compared between the two areas by the Mann-Whitney U test, as the data were not normally distributed. The relationships between endobionts' community structure components (species richness, Shannon-Wiener diversity (H'), species evenness (J'), and density) and sponge species, locality, volume, average oscular diameter, and sponge abundance were analyzed. Spearman's rank correlation coefficient was used to examine the relationship between sponge volume and average oscular diameter with the abundance and richness of the associated fauna. Normality was assessed for all data sets using the Shapiro-Wilk test[37]and homoscedasticity was assessed with Levene's test[38].

The variability of the above-mentioned indices across the distinct zones of the surveyed sites was investigated using mixed-design ANOVA to account for fixed and random effects of factors. Data that was not normally distributed was log-transformed. The total biomass of the associated fauna in each sponge was averaged per sponge species and compared between areas (low vs. high sponge abundance) using the Mann-Whitney U test.

Non-Metric Multidimensional Scaling (NMDS) ordination was carried out to assess the similarities between the associated sponge fauna in all sites[39]based on Bray-Curtis dissimilarity matrices[40].

The contribution of associated species to Bray-Curtis dissimilarity among the resulting sample groups was estimated with SIMilarity PERcentages (SIMPER)[41]. Analysis of similarity (ANOSIM) was employed to examine the variation in community composition of the associated assemblages by comparing the similarity of taxa between the sponges, sites, and areas, as well as a pairwise comparison in a post-hoc test[41].

All statistical analyses were performed using the R and R Studio software (versions 4.2.2 and 2023.06.2, respectively)[42,43]. Diversity, richness, evenness, and ordination were calculated using Vegan 2.6-4[44] and Rich 1.0.1 packages[45]. Mixed-design ANOVA was performed using the nlme package[46]with richness as the dependent variable, area (low or high sponge abundance) as the fixed effect, and site and host species as random effects. Estimated marginal means post-hoc test was performed using emmeans 1.11 package. Figures were created using ggplot2 3.4.1[47]. All data is published in the EDI Data repository[48].

Results

Sponge cover and abundance

In all three sites, total sponge coverage and massive sponge coverage in the areas considered as "high abundance" were significantly higher than the "low abundance" area of the same site (Mann-Whitney U test, p-value < 0.0001 for all sites; Fig. 2a & b, Table S1). This was also the case for massive sponge abundance (Mann-Whitney U test, p-value < 0.0001 for all sites; Fig. 2c, Table S1).

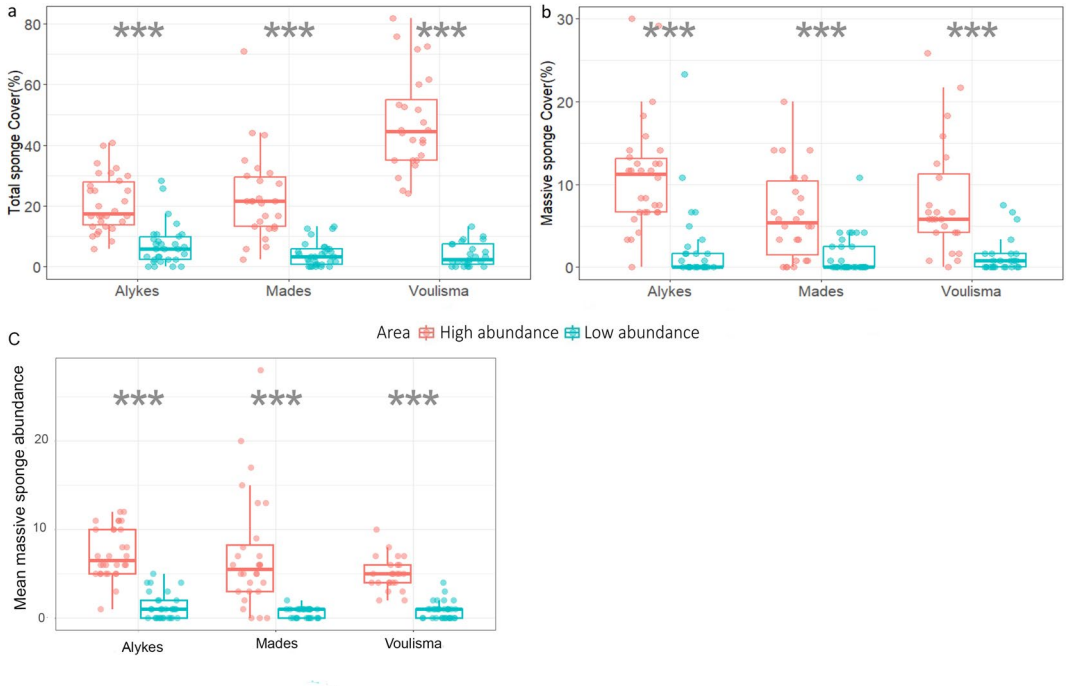

Fig. 2. Box-plots of the mean and 50% and 75% percentiles of sponge coverage at the three sites of Crete (Alykes, Mades and Voulisma). Differences between high and low abundance areas were significant (***<0.001) in: (a) total sponge cover; (b) massive sponge cover; (c) Mean abundance (number) of massive sponges per quadrat.

Sponge species	Area	Oscular diameter (mm)	Sponge volume (ml)	Endobiont density (#/L sponge)	Endobiont Richness			Diversity (H')	Evenness (J')
					Average	Total per area	Per spongespecies		
Agelas oroides	Low abundance	5.5 ± 1.56	243.33 ± 52.68	186.01 ± 96.73	12.67 ± 2.95	80	59	2.7	0.72
	High abundance	6.81 ± 1.75	282.22 ± 56.96	83.2 ± 50.11	10.67 ± 3.84		55	3.37	0.88
Sarcotragus foetidus	Low abundance	3.73 ± 0.34	413.33 ± 92.66 *	87.97 ± 45.45	10 ± 5.06	52	40	2.66	0.76
	High abundance	4.36 ± 1.2	265 ± 90.05 *	94.75 ± 47.95	8.16 ± 3.43		31	2.56	0.74

Table 1. Sponge and endobiont characteristics. A summary of the oscular diameter, sponge volume, endobiont density, richness, diversity and evenness is provided. Data are segregated by sponge species (*Agelas oroides* and *Sarcotragus foetidus*) and category of area by sponge abundance (low and high). Mean values and standard deviations are presented to compare differences between populations. * Statistically significant differences (Mann-Whitney: W = 4.5, p-value < 0.04).

Sponge characteristics

Sponge oscular diameter was not significantly different between high and low abundance areas in either sponge species (Table 1). *Agelas oroides* volume was not significantly different between the two areas, while collected *Sarcotragus foetidus* individuals were significantly larger in the low abundance area (Mann-Whitney: W = 4.5, p-value < 0.04, Table 1). This was due to the low availability of sponges for collection in the low-abundance area.

Endobiont community composition

A total of 943 endobiont specimens were recovered from the 30 sponges collected, belonging to seven phyla (Platyhelminthes, Annelida, Nemertea, Mollusca, Brachiopoda, Arthropoda, Echinodermata; Fig. S1), 15 major groups (classes and orders, when such classification was not possible phyla were mentioned) and 94 taxa (most at the species level, hereafter: species; Table S2). The richest group was Polychaeta with 40 species, followed by Crustacea with 29 species. In both sponge species, these two groups represented 71–77% of endobiont species. These two groups were also the most dominant in terms of abundance, with crustaceans representing 55% of individuals and polychaetes 30%. Another important group in terms of abundance was Ophiuroidea, which comprised 7% of all individuals with four species (66% of individuals belonged to the non-indigenous species *Ophiactis savignyi (Müller & Troschel, 1842)*). The most abundant species were the crustaceans *Gnathia dentata* (G. O. Sars, 1872) (15% of all individuals), *Colomastix pusilla* Grube, 1861 (12.5%), *Synalpheus gambarelloides*

(Nardo, 1847) (11.1%) and the polychaete *Composetia costae* (Grube, 1840) (5%; Table S2). An interesting record was the presence of chironomid larvae of the subfamily Orthocladiinae inside the canals of *A. oroides* (Fig. S1). The two sponge species differed in the major composition patterns of endobionts at the two areas. In *A. oroides* we found similar composition at both high and low abundance areas where polychaetes accounted for ~ 35% of all individuals and crustaceans ~ 55% (Amphipoda, Isopoda and Decapoda; Fig. 3). In *S. foetidus* on the other hand, a completely different pattern of endobionts composition was observed between high and low abundance areas. In high abundance areas crustaceans accounted for 63% and polychaetes for 30% of individuals (Fig. 3), while in low abundance areas polychaetes comprised only 16% of individuals, and crustaceans 49% (Fig. 3). In both sponges Ophiurids were in greater numbers in high abundance areas with 8–25% of individuals, compared to 1-2.5% in low abundance areas (Fig. 3). Mysids were present only in *S. foetidus* in the low abundance areas with 12% of individuals. *Sarcotragus foetidus* also differed from *A. oroides*, in the fact that decapods comprised about half of the crustacean individuals (most of them belonged to *S. gambarelloides*), as opposed to the 12–14% of crustacean individuals in *A. oroides*.

Endobionts richness differed both between sponge species and between areas (Table 1). In *A. oroides* specimens, we found higher endobiont richness with a total of 80 species, an average of 12.67 ± 2.95 species in sponges from low-abundance (59 total) areas and 10.67 ± 3.84 species from high-abundance areas (55 total, Table 1). In *S. foetidus*, lower endobiont richness was observed with a total of 52 species, with an average of 10 ± 5.06 species in sponges from low abundance areas (40 total) and 8.16 ± 3.43 species from high abundance areas (31 total, Table 1). Shannon diversity and Pielou's evenness indices showed high diversity and a balanced endobiont community in *A. oroides* from high abundance areas, and moderately diverse, semi-balanced endobiont communities in *A. oroides* from low abundance areas and *S. foetidus* from both areas (Table 1).

A mixed-effects model including all sites and both sponge species showed that endobiont richness and density were significantly higher in low-sponge-abundance areas compared to high-sponge-abundance areas (Fig. 4a and b; $p < 0.001$ for both variables). Analysis of random effects indicated moderate variability among sites and minimal variability among hosts within sites.

When analyzed separately for each sponge species (pooling across sites), the area effect remained significant for *A. oroides*, with both richness and density of endobionts higher in low-sponge-abundance areas (Fig. 4c and d; richness: $p = 0.046$; density: $p < 0.001$). In contrast, *S. foetidus* showed no significant differences in richness or density between areas.

Post-hoc pairwise comparisons using emmeans (see Table S3) further revealed that the significant area driveneffect for *A. oroides* was consistent across all three sites for density, and in one of three sites for richness (Alykes, $p < 0.01$). For *S. foetidus*, no significant area effects were detected at any site (all $p > 0.05$). When both species were analyzed collectively within each site, only the Mades site showed a significant difference in density between areas ($p = 0.032$), though the trend of higher values in low-abundance areas was observed across all sites (Fig. 4a, b). However, for both sponge species, the biomass of associated fauna per sponge in the high-sponge-abundance area was significantly lower than in the low-sponge-abundance area (0.36 g vs. 0.77 g for

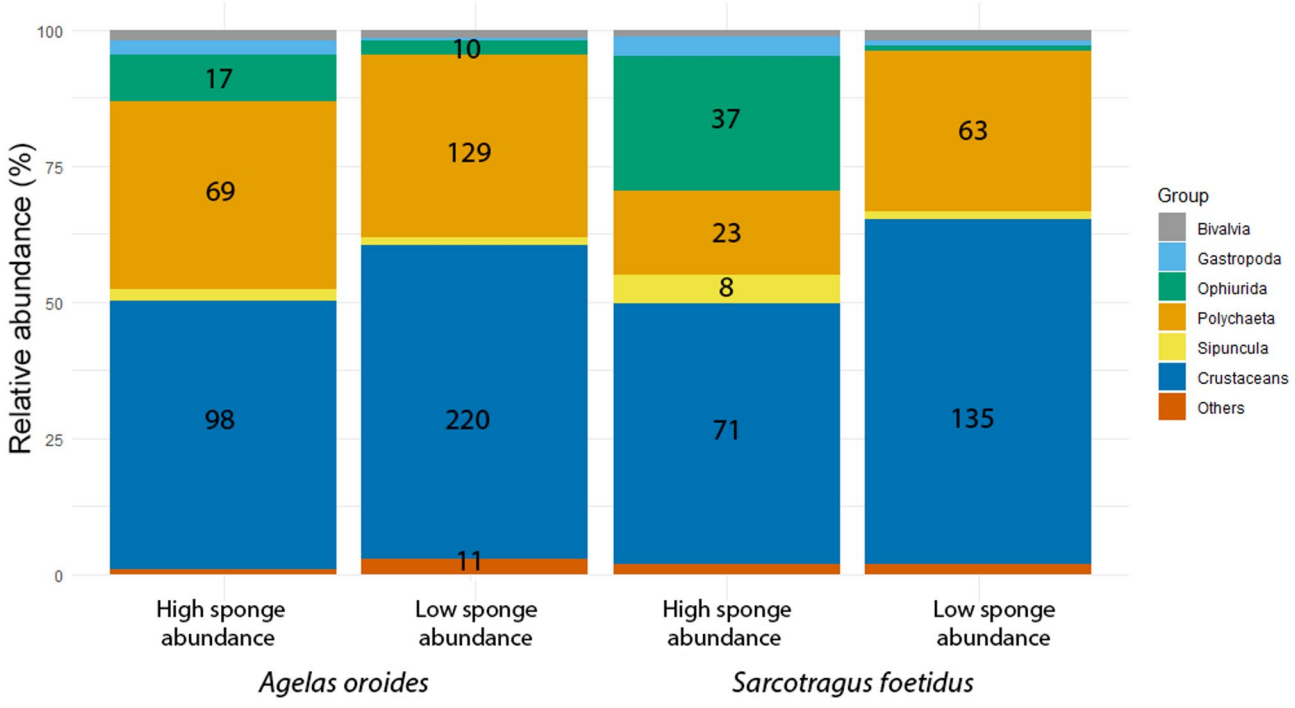

Fig. 3. Relative abundance of 7 major endobiont groups in sponges collected in the study areas. Numbers inside the bars represent the number of individuals found in each group.

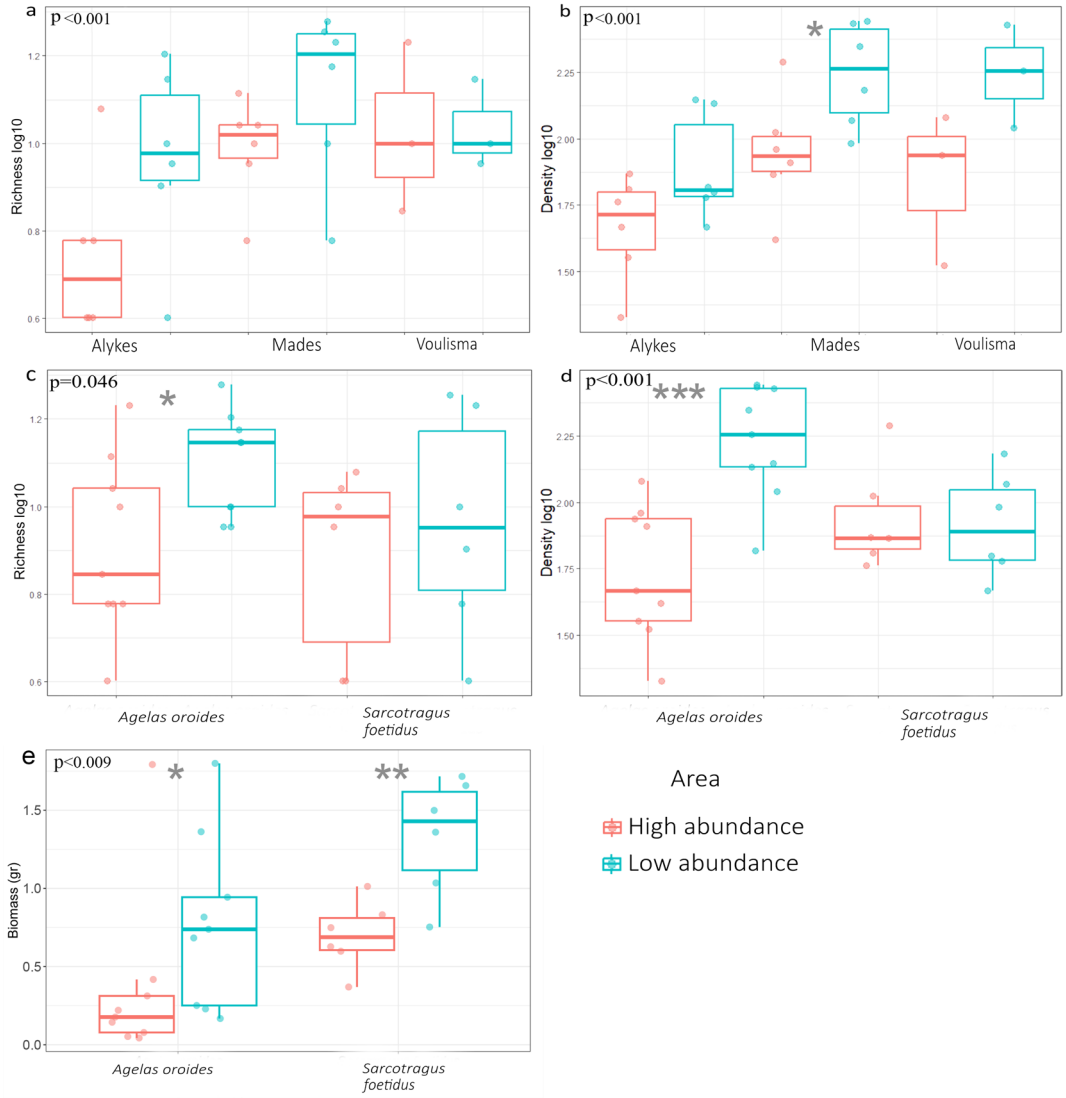

Fig. 4. Box-plots of differences in endobionts' composition in *Agelas oroides* and *Sarcotragus foetidus* collected in high abundance and low abundance areas. Richness and density data are log10 transformed. P-values present results from the mixed-design ANOVA, referring to the difference in richness and density between high and low abundance areas when sites and host are taken as random factors in a and b, and when only sites are taken as a random factor in c and d. Asterisks denote significance in the emmeans post-hoc test (*<0.05, **<0.01, ***<0.001, Tables S3 and S4). (**a**) Endobionts richness and (**b**) Endobiont density in both sponge species, at the three sites: Alykes ($n=6$, $n=6$), Mades ($n=6$, $n=6$) and Voulisma ($n=3$, $n=3$). (**c**) Endobionts richness and (**d**) Density in *Agelas oroides* ($n=9$, $n=9$) and *Sarcotragus foeditus* ($n=6$, $n=6$) in high and low abundance areas. (**e**) Mean of total biomass of the associated fauna in each sponge per sponge species and areas (low vs. high sponge abundance).

A. oroides, W = 16, $p < 0.032$; and 0.68 g vs. 1.34 g for *S. foetidus*, respectively, W = 2, $p < 0.009$; Mann-Whitney U-test; Fig. 4e).

When examining the relationship between sponge volume or oscular diameter and richness or density of endobionts, only one significant interaction was detected: in *A. oroides* a negative correlation was found between sponge volume and endobiont density (Table 2).

Quantitative analyses of endobiont communities revealed distinct patterns of diversity and distribution between the two sponge species. NMDS ordination indicated that endobiont community compositions were primarily separated by sponge species (Fig. 5). These findings were supported by ANOSIM results ($R = 0.46$, p-value = 0.001; Table S4). While the area (low vs. high sponge abundance) had no significant effect on the endobiont communities of *A. oroides*, it accounted for some of the significant differences observed in *S. foetidus* (Table S4).

SIMPER analysis revealed that 12 out of the 94 species explained over 50% of the Bray-Curtis dissimilarity between the endobiont communities in the different sponges and areas (i.e., *S.gambarelloides*, *C. pusilla*, *G. dentata*, *O. savignyi*, Mysida sp. 1, *Syllis gerlachi* (Hartmann-Schröder, 1960), *Composetia hircinicola* (Eisig,

Sponge species Correlation	Richness vs. volume	Density vs. volume	Richness vs. oscular diameter	Density vs. oscular diameter
Agelas oroides	t = −2.04, df = 16, p-value = 0.26, correlation = −0.28	t = −2.91, df = 16, p-value = 0.05*, correlation = −0.63	t = −1.48, df = 16, p-value = 0.2, correlation = −0.314	t = −1.43, df = 16, p-value = 0.46, correlation = −0.18
Sarcotragus foetidus	t = 1.34, df = 10, p-value = 0.29 correlation = 0.33	t = −0.45009, df = 10, p-value = 0.59 correlation = −0.171	t = 0.71011, df = 10, p-value = 0.475 correlation = 0.23	t = 2.06, df = 10, p-value = 0.065 correlation = 0.55

Table 2. Spearman's rank correlation of endobionts' richness and density with sponge volume and oscular diameter in *Agelas oroides* and *Sarcotragus foetidus* collected at the study sites. * Statistically significant differences.

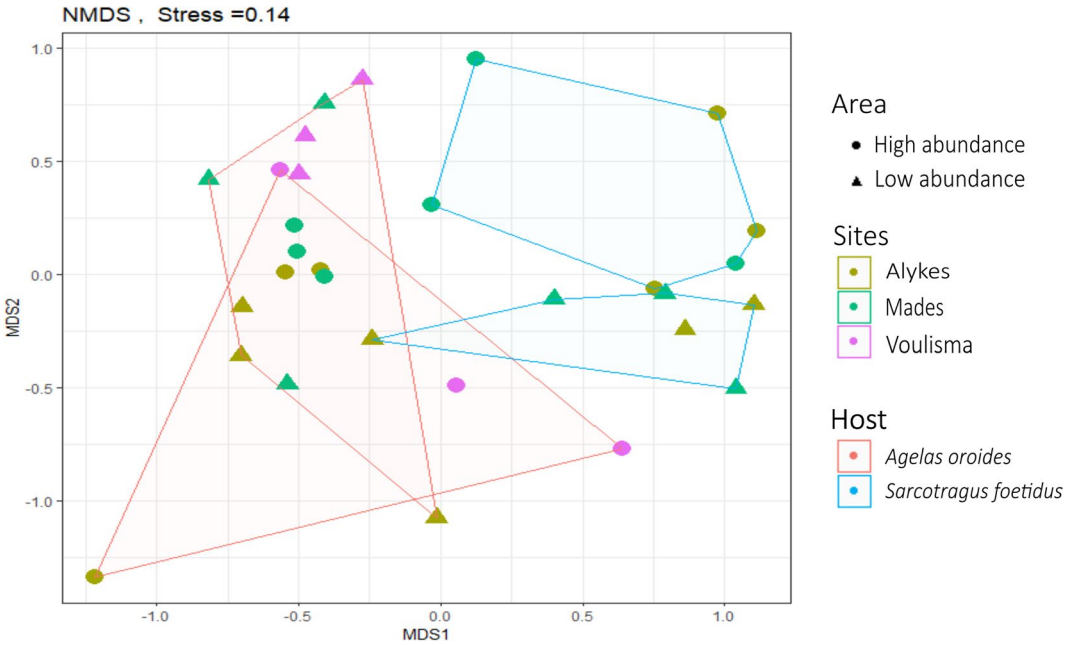

Fig. 5. Non-metric multidimensional scaling (NMDS) ordination of endobiont communities of *Agelas oroides* and *Sarcotragus foetidus* in the three sites; Alykes ($n = 6$, $n = 6$), Mades ($n = 6$, $n = 6$) and Voulisma ($n = 3$, $n = 3$) in high abundance and low abundance areas. The spatial arrangement of points indicates the degree of similarity in endobionts' community composition, with closer points suggesting more similar communities.

	High abundance		Low abundance	
	Density	Richness	Density	Richness
Non reproducing	65.4 ± 7.9 per L_{sponge}	6.6 ± 4.6	87.3 ± 57 per L_{sponge}	6.6 ± 4.6
Reproducing	124.7 ± 63 per L_{sponge}	10 ± 1	91.1 ± 29 per L_{sponge}	14.3 ± 5.5

Table 3. Endobionts density and richness in *Sacotragus foetidus* individuals in different reproductive States at high abundance and low abundance areas. Mean values and standard deviations are presented.

1869), *Neoamphitrite edwardsii* (Quatrefages, 1866), *C. costae*, *Leucothoe spinicarpa* (Abildgaard, 1789), *Tritaeta gibbosa* (Spence Bate & Westwood, 1862) and *Ophiothrix fragilis* (Abildgaard in O.F. Müller, 1789); Table S5).

In *S. gambarelloides*, which contributed most to the dissimilarity in *S. foetidus*, we found a significant negative correlation between its abundance and endobiont richness per L sponge (Spearman correlation, $p < 0.04$; Rho = −0.6).

During the analysis of *S. foetidus*, we found that some collected specimens contained embryos. A linear mixed-effects model showed that *S. foetidus* specimens containing embryos had significantly richer endobiont communities than those without embryos (Table 3). The sponge's reproductive state had a strong effect (p-value = 0.037, SE = 2.2), while the area had a minimal residual effect (SD = 4.45×10^{-5}). The mean endobiont density in reproducing *S. foetidus* was also higher than in non-reproducing individuals, but this difference was not significant, likely due to high variability (Table 3).

Discussion

Many studies have attempted to explain the various factors determining the richness and abundance of endobionts inside sponges, often with contradictory results[13,25,27,49,50]. The factors that have frequently been implicated are usually sponge volume, canal or oscular size, and even the sponges' surrounding environment[12,13,27,50]. In this study, we observed a "single hotel" phenomenon, where higher endobiont densities and richness were found in isolated sponges compared to those in areas of higher sponge availability. This finding contradicts expectations derived from IBT, which posits that isolated habitats typically harbor lower biodiversity.

When testing the widely accepted factors affecting sponge endobiont richness (i.e., oscular diameter and sponge volume), we did not identify any relationship between them and endobiont richness and density in *S. foetidus*. However, *A. oroides* exhibited a significant negative correlation between sponge volume and endobiont density. This relationship, though uncommon, aligns with previous observations[12,25,28]but in these cases, this phenomenon was linked to the fact that sponges with lower volumes tended to have smaller oscular size, and thus, were able to harbor greater densities of smaller taxa. In addition, the smaller openings of the sponge canals may offer greater protection (against predators). Nonetheless, we found no corresponding relationship between sponge volume and oscular size. In our previous study[19]we observed higher endobiont densities in sponges of varying sizes at shallow depths, compared with mesophotic depths, which we suggested was influenced by the low availability of sponges as habitats.

Some studies have treated sponges as "islands of suitable habitat" and followed the IBT[9,14,15]which deals with situations where the insularity of islands (or islands of suitable habitats), are an obstacle for connectivity and colonization of the different species inhabiting them. While most of the species inhabiting the sponges are not obligatory residents of their hosts, we argue that they are a specialized community[14,20]preferring sponges as their habitat to avoid predation, which typically results in higher numbers within sponges compared to the surrounding environment[16,49].

Thus, if we consider sponges as islands, we would expect to find lower richness and densities of endobionts in the more isolated sponges. Contrary to these expectations, we observed higher endobiont densities, richness and biomass in the more isolated sponges. This is intriguing because, while isolated island communities sometimes show greater densities than their closer-together counterparts, the proposed mechanism of this phenomenon – "density compensation" – is tied to species impoverishment, meaning fewer species with larger populations[51]. Our findings do not support this, as the number of species in low sponge abundance areas (isolated "islands") was significantly higher than that in high sponge abundance areas (close-together "islands"; Table 1).

The "island" analogy, while useful, requires careful consideration and adaptation when applied to sponges. It is important to notr that aquatic habitats pose fewer barriers that limit the dispersal of organisms than terrestrial habitats. Moreover, while the differences between low and high sponge abundance areas in this study were significant (Fig. 2), the scale of distance between sponges and between the two habitats (low and high sponge abundance areas) was quite low and measured from a few cm to 20 m at the most, which would probably have no effect on larval stage dispersal. A more fitting perspective might be the framework of habitat availability. Some studies have shown that abundance of several species of fish decreases with lower availability of branching corals – their habitat[52,53]which also agrees with many habitat-fragmentation theories[54]. In our case, however, endobionts' abundance (or density) was higher in areas of lower sponge availability. In some cases, this phenomenon is known as the "crowding effect"[54] and it is suggested to occur shortly after fragmentation. But it is a temporal state, followed by a decrease in abundance, when the habitat can no longer support the numbers of organisms, reaching its carrying capacity. It is unlikely that the high density observed in the present study is the result of such recent fragmentation, as no signs of loss of sponges were seen at any of the sites. Moreover, all the sponges collected from both habitat types were roughly the same size, meaning that they were probably of the same age. A similar pattern was found in spiders that increased their abundance in smaller, fragmented habitats[55]. As opposed to the abovementioned "crowding effect", this was hypothesized to be related to the fact that smaller and more fragmented urban habitats in that study were often more productive, and thus could support higher densities of spiders. We have no reason to believe that sponges at the low abundance areas can provide more food than the ones in high abundance areas. However, if we view sponges as "hotels", or specialized niches that are preferred by their "residents", it stands to reason that limited habitat availability may lead to greater crowding. This was further emphasized by the significantly larger total biomass of associated fauna per sponge in the low-sponge-abundance areas, showing that the reason for the differences was not due to smaller individuals crowding together. In high sponge abundance areas, endobionts may prefer not to crowd in a single "hotel", to avoid potential competition on space and resources[56].

While biomass patterns were the same in both sponge species, and in line with our hypothesis, we observed different patterns of endobiont richness and density between *A. oroides* and *S. foetidus*. In *A. oroides* endobionts richness and density differed significantly between the areas, while in *S. foetidus*, both parameters were not significantly different (Fig. 5). This highlights the importance of species-specific interactions. It is important to note that while the overall mixed-effects model detected a significant effect of area on endobiont richness and density (Fig. 4a, b), the post-hoc analyses revealed that this effect was not uniformly significant across all sites and hosts. Specifically, post-hoc pairwise comparisons (Table S3) showed that the area effect was consistently significant for *A. oroides* across sites, but not for *S. foetidus*. When both species were analyzed together within each site, only the Mades site showed a significant difference in density between areas, although the trend of higher endobiont values in low abundance areas was visible in all sites. This apparent contradiction likely reflects the limited statistical power in subgroup analyses due to small sample sizes, as well as the possibility that the strong effect observed in certain sites (especially Mades) disproportionately influences the overall model results. Thus, while the general pattern supports our hypothesis, the lack of significance in some subgroups should be interpreted with caution and attributed, at least in part, to these methodological constraints. Another constraint is that sponges from Voulisma were collected at shallower depths than those from Mades and Alykes. While

we did not detect other major abiotic differences between sites, it is possible that the reduced magnitude or significance of area effects observed at Voulisma (see Fig. 4, Table S3) may be partially attributable to depth-related factors rather than solely to sponge abundance.

Unlike *A. oroides*, most of the *S. foetidus* collected, hosted groups of the snapping shrimp *S. gambarelloides* (averaging nine individuals per sponge). A total of 105 *S. gambarelloides* individuals were collected, including many ovigerous females; this phenomenon was documented several times[25,27]. While Koukouras et al.[25] suggested that *S. gambarelloides* chose to settle in the sponge *Spongia officinalis* due to its numerous large canals, in our case, it seemed as if *S. gambarelloides* had reshaped the canals of *S. foetidus*, making larger canals that occupy most of the sponge body (authors' personal observation). When looking at the two individuals that did not contain *S. gambarelloides* as well as *S. foetidus* collected in previous studies, we observed different canal structures in comparison with the ones that *S. gambarelloides* inhabited. The presence of snapping shrimps inside sponges was shown to cause structural modifications to the hosts' canals[57]probably by feeding on the sponges[23,58]. Moreover, they are known to compete with other snapping shrimps and invertebrates[23]. This can be further corroborated in our study, where a significant negative correlation was found between the abundance of *S. gambarelloides* and endobiont richness per L sponge (Spearman correlation, $p < 0.04$; Rho = −0.6). Therefore, the presence of *S. gambarelloides* in *S. foetidus* may have affected the richness and abundance of other endobionts and obscured the patterns recorded in *A. oroides*. Furthermore, we found greater endobiont richness in reproducing *S. foetidus* (Table 3), pointing to the significance of the reproductive stage in sponges and suggesting a potentially overlooked aspect of sponge-endobiont interactions. Henkel and Pawlik[49] have shown that brittle stars inhabiting sponges feed on reproductive elements of their hosts. Sponge with embryos and larvae could be an appealing nutritional food source for other invertebrates[59–61]. The observed increase in endobiont richness in reproductive *S. foetidus* (Table 3) underscores the need for further research into these nutritional and ecological implications of these relationships. Both the presence of *S. gambarelloides* and the reproductive state of *S. foetidus* may act as intrinsic factors that influence the diversity of endobionts. While these factors could obscure the direct effects of the "Single Hotel Hypothesis" on some diversity measures, they do not invalidate the broader patterns observed (Fig. 4).

Overall, our study reinforces the vital role of massive sponges as habitat builders, or "living hotels"[16,19,25] and identifies a diverse community of 94 endobiont species across *S. foetidus* and *A. oroides*. The composition of these communities was predominantly influenced by the host species, underscoring the connection between sponge hosts and their associated endobionts.

Only in *S. foetidus* did we observe a significant difference in endobionts' community composition between the areas (low vs. high abundance). However, these differences were relatively weak and can be attributed to the presence of two taxa (Mysida sp. 1 and *O. savignyi*; Table S4, Figs. 3, 4 and 5). This is evident from the NMDS ordination (Fig. 5) and supported by the ANOSIM results. This further emphasizes the connection between the sponge host and its endobiont community. Most *S. foetidus* communities were dominated by *S. gambarelloides*, while other endobionts appeared in lower numbers and more evenly distributed in their frequencies. In *A. oroides* there were several dominant endobiont species (i.e., *G. dentata*, *C. pusilla*, *C. costae*, *N. edwardsii*, *S. gerlachi*, *Syllis corallicola*, Verrill, 1900 *Amphitritides gracilis* (Grube, 1860), *Hesiospina aurantiaca* (M. Sars, 1862)).

Our findings of polychaetes being the richest group, and crustaceans being the most abundant group, agree with most studies on sponge-associated fauna[12,13,16,25,62,63]. Some species found in this study are characteristic sponge-dwellers (e.g., *C. pusilla*, *C. costae*, *L. spinicarpa*, *O. fragilis*), while others have been rarely found in sponges. For example, chironomid larvae are observed here for the second time from marine sponges[19] and are recorded for the first time in such depth (15 m).

The species *G. dentata* and *C. pusilla* are well known sponge inhabitant: *G. dentata* is a parasitic isopod with the genus *Gnathia* being known to largely depend on sponges, inhabiting them as an adult and in some cases also in several juvenile stages[64]. There is no evidence of specificity to a sponge species in this isopod, but our results show high preference to *A. oroides*. *Colomastix pusilla* is an amphipod which appears to be adapted to life in sponges but does not appear to be hosts-specific[16,50,65]. Most polychaete species that can be found in sponges are considered as opportunistic inhabitants that can be found in other microhabitats as well[13,25]. This may also be the case here. However, with regard to *C. costae*, while it can be found outside of sponges, it is a typical sponge dweller, and probably prefers to live in them, but without host specificity[19,20]. In this study, it was the most abundant polychaete species, and was found in all hosts, sites, and areas.

It should also be noted that five non-indigenous species were found among the sponge endobionts (Table S2), including the brittle star *O. savignyi*, a Lessepsian migrant that has been previously found within sponges in the Mediterranean Sea[19,27]. All non-indigenous species have been previously reported from the South Aegean Sea[66]except for *Palaemonella rotumana* (Borradaile, 1898), a decapod species which was found here for the first time from Greek waters and the Aegean Sea[66]. Previous Mediterranean records of this species come from the Israeli and Turkish coasts in the Levantine Sea[67,68].

Conclusions

The results of this study support the initial hypothesis that habitat availability, specifically in the form of sponge abundance, influences the diversity of their endobionts, demonstrating that in a "single hotel" scenario, endobionts will be more crowded than in areas of higher habitat (sponge) availability. In addition, we showed that factors beyond the commonly accepted ones (i.e., volume, size of oscula), can significantly affect endobionts diversity. Notably, the reproductive state of the host and its association with specific endobiont species emerged as important considerations.

On a broader scale, the relationship between diversity and habitat is even more complex than previously understood. It depends not only on the intrinsic characteristics of the habitat but also on its availability, the

relationship between the habitat and its inhabitants, and possibly interactions among the inhabitants themselves. These factors have significant implications for our understanding of biodiversity and for management and conservation strategies, as changes in sponge abundance may influence local diversity in unexpected ways. Although biodiversity within a single sponge is related to sponge abundance, this relationship may not be linear when considering larger areas with high sponge densities. Further research is needed to unravel the connections between sponge/habitat availability, intra-sponge diversity, and area-wide diversity. Factors such as the richness and diversity of massive sponges in an area, interactions between endobionts, sponge-endobiont relationships, and the ecological effects of host reproduction on endobiont communities should be considered. Additionally, exploring these dynamics in other living habitats will also be essential to fully understand the implementation of the single hotel hypothesis.

Data availability

Data are provided as private-for-peer review via the following link: https://doi.org/10.6073/pasta/f0e160f9189b561730982b754eed71c7.

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Author contributions

TI Conceptualization (equal); Writing – original draft (equal); Formal analysis (equal); Visualization (equal); Funding Acquisition (equal); Investigation (equal); Methodology Project Administration; Writing – review and editing (equal); LG Conceptualization (equal); Writing – original draft (equal); Formal analysis (equal); Visualization (equal); Funding Acquisition (equal); Investigation (equal); Methodology (equal); Project Administration (equal); Writing – review and editing (equal); SS Investigation (equal); Writing – review and editing (equal); GC Investigation (equal); Writing – review and editing (equal); Resources (equal); VG Methodology (equal); Project Administration (equal); Writing – review and editing (equal); Resources (equal).

Declarations

Competing interests
The authors declare no competing interests.

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Additional information
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