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Sponge-Associated Polychaetes: Not a Random Assemblage

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Polychaetes are among the most common marine organisms, and in many habitats they dominate both in species richness and abundance. They are often found in association with other organisms. Specifically, sponges with their complex three-dimensional internal architecture, are known to host a great diversity of polychaetes. Due to the fact that a large number of sponge-associated polychaete species are known to be common on other substrates, most studies agree that they represent an opportunistic part of the sponge-inhabiting assemblage, without any selection of species tightly associated with sponges. The current study aimed to shed light on polychaetes affinity to sponges. We applied Clarke and Warwick's taxonomic distinctness indices and test for random assembly, to a dataset compiled of 13 publications that provided polychaete species lists from massive-sponges across the Mediterranean Sea, and compared them with benthic-polychaete species lists from all of the Mediterranean and its zoogeographical regions. These indices are considered to be independent of sampling efforts and setting, and can be applied on presence/absence data, making it possible to compare data from multiple studies. We further compared the trophic structure of sponge-associated polychaetes between the Mediterranean's zoogeographical regions. Our results show that the trophic structure of the sponge-associated polychaete community, was found to be stable across the entire Mediterranean Sea. Moreover, randomization tests showed that at almost all observational scales (e.g., study, region, Mediterranean) the phylogenetic diversity is not assembled at random, and that sponge-associated polychaete communities are composed of taxonomically related species. These results support the statement that polychaete assemblages inhabiting sponges are not a transient facultative assembly of species, but rather stable, diverse and specialized communities which are well adapted for life in this habitat.

Keywords: taxonomic distinctness, symbiosis, community ecology, biodiversity, Porifera, Annelida, Mediterranean Sea

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INTRODUCTION

Sponges have a great ecological and economic value, in part due to their three-dimensional complex structure, which supports rich metazoans communities, by providing micro-habitats and ideal shelters (Gerovasileiou et al., 2016). A major component of these communities are polychaetes (phylum: Annelida), often the dominant group in terms of abundance, richness, or biomass (Pansini, 1970; Rützler, 1976; Amoureux et al., 1980; Pansini and Daglio, 1980;

Alos et al., 1981; Peattie and Hoare, 1981; Westinga and Hoetjes, 1981; Dauer, 1984; Koukouras et al., 1985, 1992, 1996; Voultsiadou-Koukoura et al., 1987; Cinar and Ergen, 1998; Çinar et al., 2019). Sponge-associated fauna, and specifically sponge-associated polychaetes, have been studied extensively around the world, from the tropics to the poles (Klitgaard, 1995; Ribeiro et al., 2003; Abdo, 2007; Fiore and Jutte, 2010; Schejter et al., 2012; Kersken et al., 2014; Gerovasileiou et al., 2016). Among polychaetes, only a few species may be considered truly obligatory to sponges, presenting adaptations to life within a sponge, e.g., parasitic forms such as *Dorvillea sociabilis*, *Branchiosyllis exilis*, *Branchiosyllis oculata*, *Haplosyllis spongicola*, *Exogone* spp., or commensal forms such as *Potamilla symbiotica*, *Hydroides spongicola*, and *Sphinther arcticus* (Martin and Britayev, 1998). However, in most cases the nature of the relationships between the polychaetes and their sponge hosts remains unknown. Moreover, most studies agree that polychaetes represent an opportunistic part of the sponge-inhabiting assemblage, without any selection of species tightly associated with sponges (Long, 1968; Frith, 1976; Alos et al., 1981; Koukouras et al., 1985, 1996; Gherardi et al., 2001). The main reason for the latter statement is due to the fact that a large number of sponge-associate polychaete species are known to be common on other substrates, therefore, their composition is related to the polychaete fauna of the surrounding benthos, rather than to the sponge itself (Long, 1968; Alos et al., 1981; Peattie and Hoare, 1981; Koukouras et al., 1985, 1996). By contrast, Westinga and Hoetjes (1981) and Koukouras et al. (1985) have stated that sponge-associated fauna constitutes a real "ecological community" characterized by a constant composition.

Based on the above statement and on our own observations, we hypothesize that sponge-associated polychaetes communities are not a random assembly. The current study examined this apparent discrepancy and aimed to shed light on polychaetes affinity to (massive) sponges. Massive sponges are defined in the "Thesaurus of sponge morphology" (Boury-Esnault and Rützler, 1997) as large compact sponges without definable shape. Most of the studies investigating sponge-inhabitants deals with massive sponges, as they usually contain large oscula and inner spaces, that can support greater diversity of organisms. By using data mined from the literature and applying Clarke and Warwick's randomization test (1998), we wished to determine the extent to which sponge-associated polychaete species lists represent random subset from the larger benthic polychaete species pool (Clarke and Warwick, 1998; Warwick et al., 2002; Somerfield et al., 2009). We further aimed to find whether polychaetes constitute a constant and stable community inside sponges, across several zoogeographic regions.

MATERIALS AND METHODS

Faunistic Data Collection and Taxonomic Updating

In order to obtain the entire available information on sponge-inhabiting polychaete assemblages reported from the Mediterranean Sea, literature describing sponge-associated macroinvertebrates communities was examined. In total 13 publications provided polychaete species lists from massive-sponges along the Mediterranean covering a time span of 95 years (Santucci, 1922; Pansini and Daglio, 1980; Alos et al., 1981; Koukouras et al., 1985, 1996; Voultsiadou-Koukoura et al., 1987; Cinar and Ergen, 1998; Gherardi et al., 2001; Gerovasileiou et al., 2016; Pavloudi et al., 2016; Papatheodoulou et al., 2019; Çinar et al., 2019; Goren et al., 2021). In accordance with previous studies, the Mediterranean Sea was divided to five zoogeographic zones (**Figure 1**; Arvanitidis et al., 2002; Voultsiadou, 2009; Chatzigeorgiou et al., 2017). Literature data were incorporated into a Microsoft Excel database along with zoogeographic (study area, region, and entire Mediterranean Sea), ecological (feeding guilds), and taxonomical information.

Species distribution data in the Mediterranean Sea were compiled from the literature (Campoy, 1979; Ben-Eliahu and Boudouresque, 1995; Arvanitidis, 2000; Bellan, 2001; Arvanitidis et al., 2002; Çinar, 2005; Castelli et al., 2008; Coll et al., 2010; Gil, 2011; Çinar et al., 2014; Mikac, 2015; Faulwetter et al., 2017), to construct the master list of benthic polychaeta and subsequent regional lists, including lists of only sponge-associated polychaetes. Species known to be exclusively pelagic have been excluded from this inventory. The corresponding higher taxonomic classification was based on what is proposed in the World Register of Marine Species (WoRMS). Polychaete species were assigned to feeding guilds categories according to Fauchald and Jumars (1979), Jumars et al. (2015) and the PolyTraits website (Faulwetter et al., 2014). Five categories of trophic guilds were used: carnivores, herbivores, omnivores, deposit feeders and filter feeders.

Statistical Analysis

Pearson correlation was used to test the relationship between the number of studies conducted in a region and the number of sponge-associated polychaete species found in it. It was also used to test if there is a correlation between the number of polychaete species and the number of host sponge species studied in each region. An initial binary matrix was constructed for species' presence/absence in the Mediterranean areas. Bray Curtis dissimilarity coefficients were utilized to create a similarity matrix (Legendre and Legendre, 1998), that was used for both cluster analysis (group average linkage) and non-metric multidimensional scaling (nMDS). Analyses were performed using R version 3.6.1 (R Core Team, 2019), RStudio (Rstudio Team, 2020), and the Vegan package (Oksanen et al., 2013).

Taxonomic Relatedness and Test for Random Assembly

In order to test whether sponge-associated polychaete species lists are randomly assembled, from those of the benthic polychaete species pools in the respective and larger geographic regions, we employed a hierarchical approach. Three successive levels of comparison in the analysis have been defined: (a) study, (b) region (Levant Sea, Aegean Sea, Central Basin, Adriatic Sea, and Western Mediterranean), and (c) master (Mediterranean species pool; **Figure 2**).

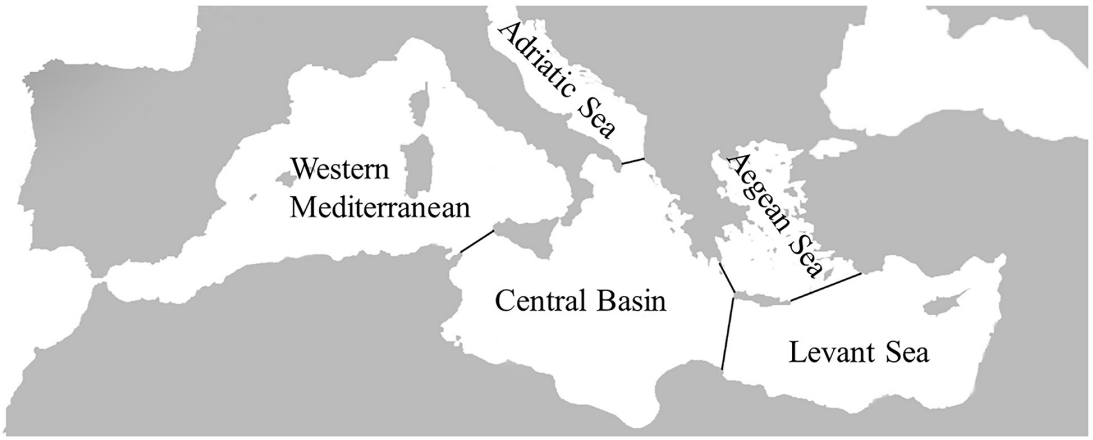

FIGURE 1 | Map of the Mediterranean Sea and the Zoogeographic zones within it considered in this study.

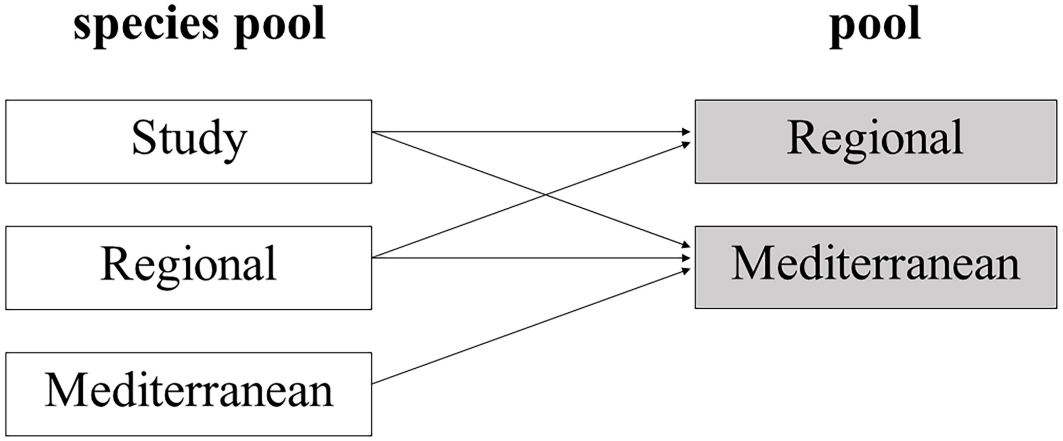

FIGURE 2 | Diagram representing the different levels of comparisons in the taxonomic relatedness analysis.

We used the two indices of taxonomic relatedness, the average taxonomic distinctness ($\Delta+$) and the variation in taxonomic distinctness ($\Lambda+$) (Clarke and Warwick, 1998, 2001). The indices were calculated for each of the locations from the 13 published studies. These indices were selected because they have been shown to be insensitive to sample-size and sample-effort (Clarke and Warwick, 2001). Both indices use the presence/absence data: $\Delta+$ calculates the average path length between every pair of species using the information on their higher taxonomic classification within a sample; the $\Lambda+$ index assesses how evenly the species are distributed, in higher taxonomic categories. The 95% confidence limits of the expected distribution of both indices' values were calculated by simulations derived from the randomly constructed subsets of species from the regional (Western Mediterranean, Central Basin, Adriatic, Aegean, and Levant Basin) and the Mediterranean benthic polychaete species pools. The $\Delta+/\Lambda+$ values calculated for the local (each study), regional and Mediterranean sponge-associated polychaete species-pools, were then superimposed on these funnel-shaped confidence limits. Data points which fall outside the relevant 95% contour imply a statistically significant departure from expectation (Clarke and Warwick, 2001), and indicate that species are more or less (above or below the funnel, respectively) closely related to each other than would be expected if they were assembled at random.

Four taxonomic levels were considered; species, genus, family, and order. Branch lengths between the taxonomic classes were defined following Clarke and Warwick (2001). We assumed equal step lengths between each successive taxonomic level, setting the path length ω to 100 for two species connected at the highest possible level (taxonomically coarsest). So, the weights are $\omega = 25$ (same genus, but different species), $\omega = 50$ (same family but different genera), $\omega = 75$ (same order but different families) and $\omega = 100$ (different orders).

We further modified the methodology suggested by Somerfield et al. (2009), we used a randomization test in

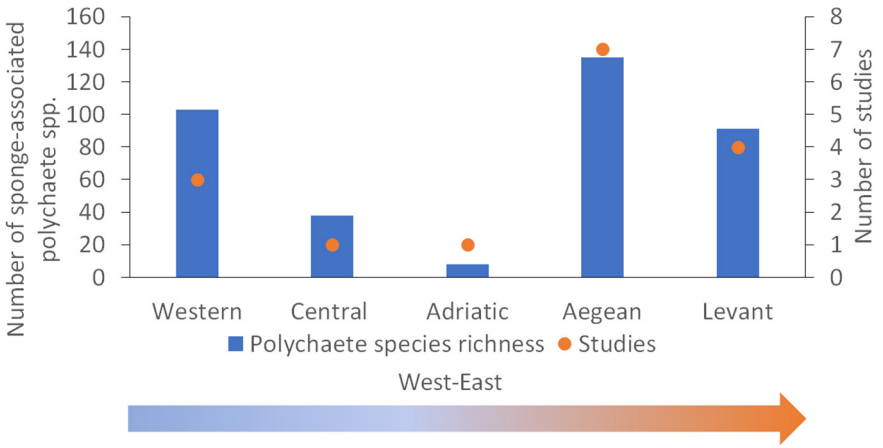

FIGURE 3 | The number of polychaete species reported from sponges in the Mediterranean Sea and the number of studies considered in this research.

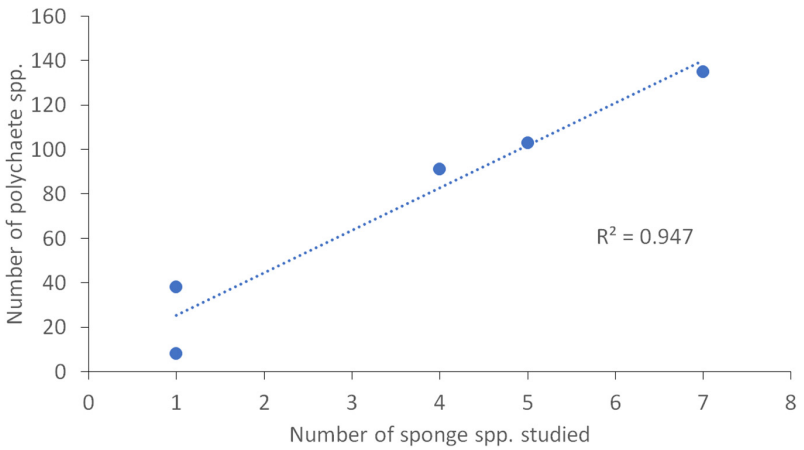

FIGURE 4 | Correlation between the number of sponge-associated species and the number of host sponge species studied in each zoogeographic region in the Mediterranean Sea.

which the criterion set was that if species inhabiting sponges are assembled randomly from the larger, local, regional, and Mediterranean benthic pools, than on average, 95% of the calculated indices values, should fall within the 95% probability limit set for these tests. All analyses were performed using the PRIMER v.7 (Clarke and Warwick, 1998).

RESULTS

Literature study showed that in total 210 polychaete species from 30 families were recorded (**Supplementary Table 1**) in 11 species of host sponges (**Supplementary Table 2**). The sponge-associated polychaete species represent ∼19% of the benthic polychaete fauna of the Mediterranean and about 43% of the families. The number of species reported from sponges in the Mediterranean and the number of studies considered in this research are shown in **Figure 3**. No clear pattern of an increase or a decrease in richness was found according to geographic gradients. The sponge-associated polychaete fauna of the Aegean was found to be the richest, but it is also the best studied area (seven studies), while the Adriatic and the Central Basin are by far the most impoverished and least studied (with one study each area). There is a strong positive correlation between the number of species in a region and the number of studies conducted in it (Pearson correlation, df = 3, Rho = 0.91, $p = 0.03$). A similar positive correlation was found between the number of polychaete species and the number of host sponge species studied in each region (Pearson correlation, df = 3, Rho = 0.97, $p = 0.004$; **Figure 4**).

Estimation of resemblance among the polychaete species of the five Mediterranean regions by group-average-linkage cluster analysis, revealed a similarity of 40% between the Western Mediterranean and the Aegean and Levant Seas. The first two regions had a 50% similarity between them. These results are visualized in an nMDS ordination (**Figure 5**).

An estimation of the resemblance among the polychaete families (not shown) of the five Mediterranean regions yielded

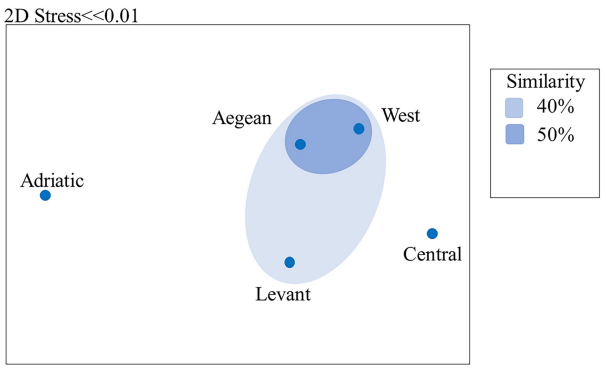

FIGURE 5 | Resemblance of sponge-associated polychaete assemblages in the Mediterranean regions demonstrated in nMDS plot. Similarity was calculated by group-average-linkage cluster-analysis.

the same pattern but with 60% similarity between the Aegean, Levant and Western Mediterranean, and 70% similarity between the Aegean Sea and the Western Mediterranean.

Five feeding guilds were characterized in the list of the sponge-associated polychaetes in the Mediterranean Sea (**Figure 6**): carnivores (72 spp.), deposit feeders (54 spp.), omnivores (40 spp.), filter feeders (39 spp.), and herbivores (10 spp.). Carnivores were the richest group in the Western Mediterranean, the Aegean and the Levant Seas, followed by omnivores. In the Adriatic Sea, both carnivores and omnivores were the most speciose groups, and in the Central Mediterranean, omnivores were the richest group followed by carnivores. The trophic composition, did not differ between the regions. As the Adriatic Sea had only eight species, it was excluded from this analysis.

Taxonomic Distinctness and Test of Random Assembly

The taxonomic relatedness indices for the Mediterranean regions are presented in **Figure 7**. The values of $\Delta+$ and $\Lambda+$ calculated for the regional sponge-associated polychaete species-pools, are superimposed on the simulated 95% confidence limits funnel of the expected distribution derived from the Mediterranean benthic-polychaete species-pool. Only the Adriatic Sea fell within the 95% confidence limits of the $\Delta+$ funnel, and the $\Lambda+$ funnel. This indicates a skewed aggregation of species into higher taxa for the other Mediterranean regions, thus rejecting the hypothesis of random assembly. The same result was obtained for almost all comparisons of study vs. region, and region vs. region. These results are summarized in **Figure 8**, which specifies the percentage of samples falling within the 95% confidence limits of the funnel in each group of comparisons. In all scales of observation, less than 95% of the tests can be considered to be assembled at random.

DISCUSSION

The relationship between sponges and their associated macrofaunal communities has been studied in the Mediterranean Sea more intensively than anywhere else in the world. However, this study is the first to consider sponge-associated polychaete communities on a large biogeographic scale. The sponge-associated polychaetes are usually considered to be facultative transient part of the community, whose composition is probably governed mostly by the zoogeographic region (Pavloudi et al., 2016) and nearby habitats (Voultsiadou-Koukoura et al., 1987; Çinar et al., 2002; Ávila and Ortega-Bastida, 2015). Our results, suggest that it is a specialized community, and that the species in it tend to be more closely related to each other than would be expected if species were assembled at random from the regional or Mediterranean species pool.

Only at the very local scale (study), some of the communities could be considered as a random assembly of the regional pool. These cases probably represent the effect of specific sponge species and individuals' morphology as well as sponge internal architecture, on the diversity and community composition of the polychaetes. The sponge general morphology (Koukouras

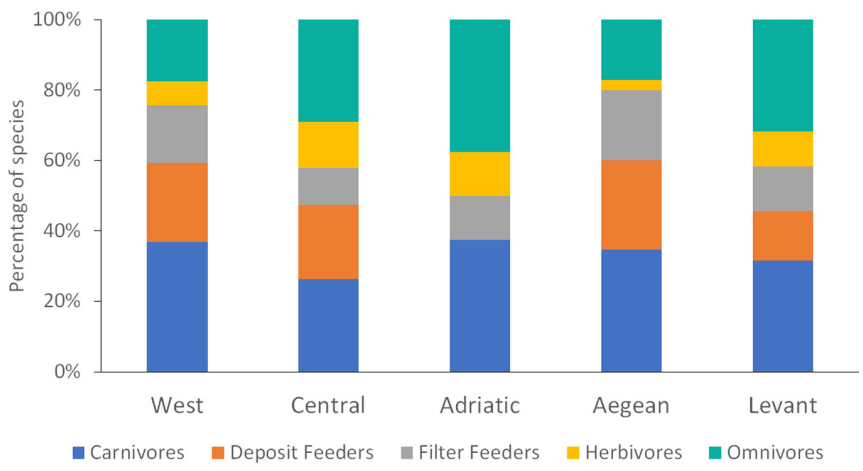

FIGURE 6 | The trophic composition of sponge-associated polychaetes found in five regions of the Mediterranean Sea.

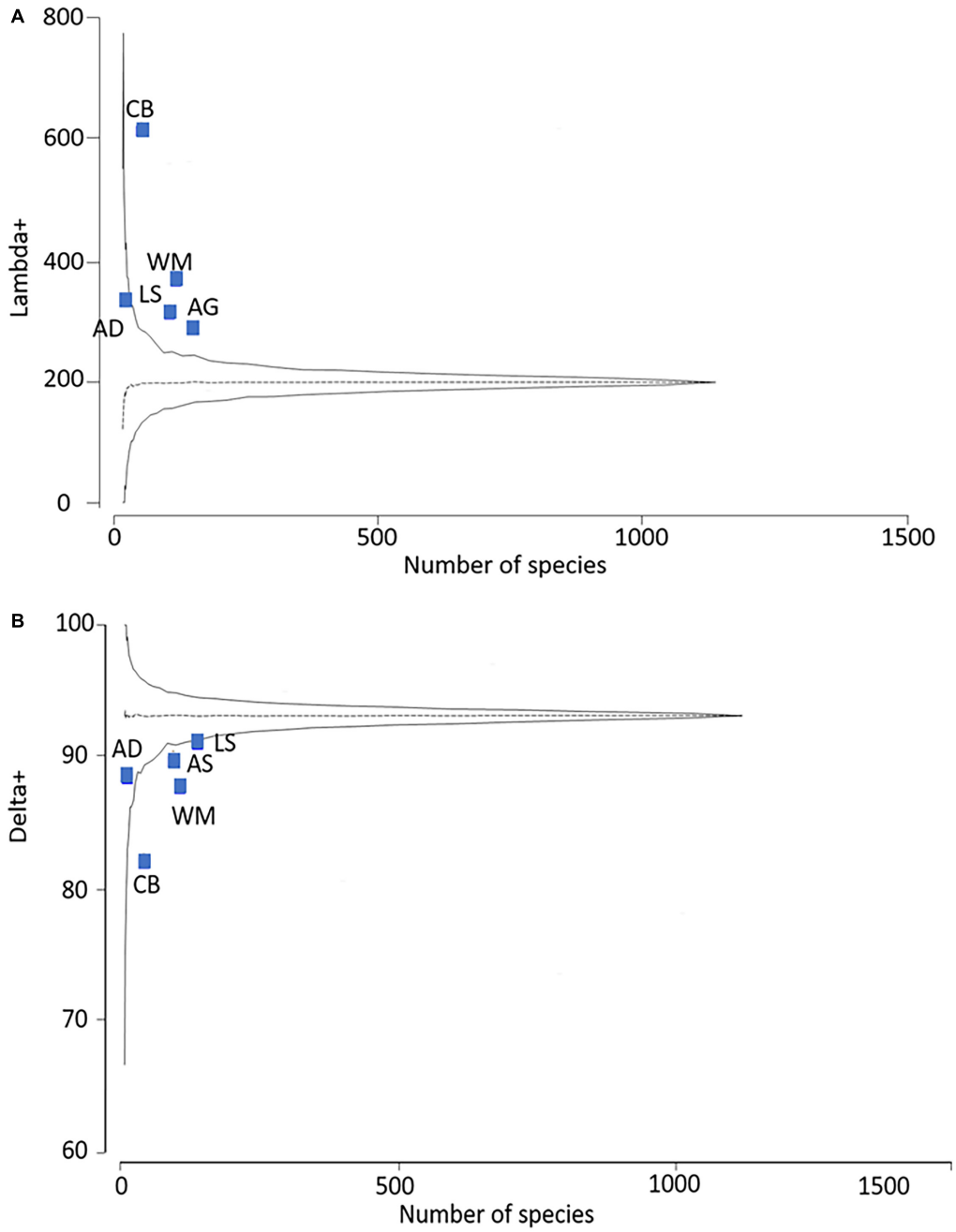

FIGURE 7 | (A) Average taxonomic distinctness (AvTD) and **(B)** Variation in taxonomic distinctness (VarTD) for the Mediterranean regions superimposed on the 95% confidence limits funnel curve for the expected values of the Mediterranean benthic polychaetes master list. The central line represents the mean value. AD, Adriatic Sea; AS, Aegean Sea; CB, Central Basin; LS, Levant Sea; WM, Western Mediterranean.

et al., 1996); diameter and volume of canals (Koukouras et al., 1996; Ávila and Ortega-Bastida, 2015); sponge volume (Cinar and Ergen, 1998; Ávila and Ortega-Bastida, 2015); the presence of an ectosome (Gherardi et al., 2001); oxygen saturation within sponge areas; and the dynamics of water flow within them (Leys et al., 2011). All of which create many potential sub-habitats within the sponge, that probably have a profound effect on the composition of their inhabitants' communities.

Greater taxonomic similarity of the sponge-associated polychaetes shown by the low $\Delta+$ and high $\Lambda+$, indicate that environmental conditions, rather than inter-specific interactions, are probably the dominant force in shaping their communities (Elton, 1946; Webb, 2000; Somerfield et al., 2009). This suggests that in general, habitat conditions (i.e., sponge conditions), play a greater role in shaping its inhabitants' community than historical evolutionary processes. A decrease in $\Delta+$ and an increase in

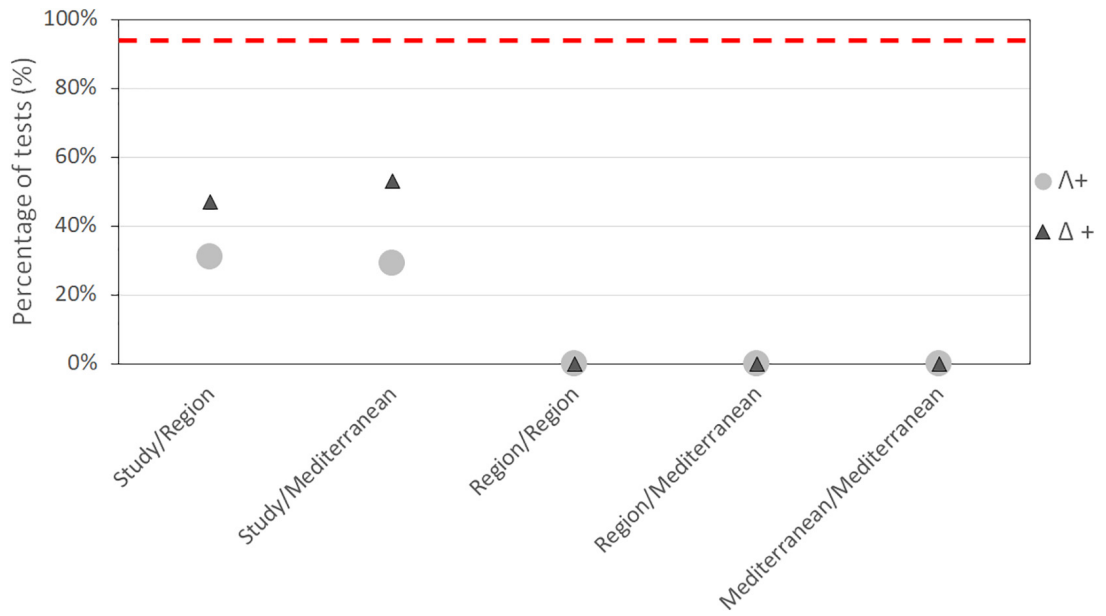

FIGURE 8 | Summary of randomization tests at all spatial scales. Values on the y-axis show the percentage of species lists for which the calculated taxonomic relatedness indices values (Δ+ and Λ+) fall within the 95% confidence limits of the simulated funnels. The dashed line represents the 95% threshold for which it might be reasonable to assume that the hypothesis of assembly at random cannot be rejected.

Λ+ are considered to be a feature of degraded environments (Clarke and Warwick, 2001; Warwick et al., 2002), but since the richness of sponge-associated polychaete communities is rather high compared with polychaete communities from other habitats in the Mediterranean (Box et al., 2010; Chatzigeorgiou et al., 2017), it should not be considered as an indication of habitat degradation. Rather it indicates that the polychaete communities inhabiting sponges share similar ecological adaptations to survive in this specific habitat, i.e., they are a specialized community.

The trophic structure of the sponge-associated polychaete community, remains stable across the entire Mediterranean Sea. No meaningful differences between the ratios of feeding guilds in each region (except for the Adriatic Sea which suffered from lack of data) were found. The main guild was carnivores, as it is often the case in other areas of the world (Frith, 1976; Westinga and Hoetjes, 1981; Dauer, 1984). This finding further undermines the notion of random assembly of sponge-associated polychaete communities.

No relationship was found between the sponge-associated polychaete community composition with major zoogeographic patterns that affect the entire benthic fauna, such as the North-West to South-East gradient of decreasing diversity that was found in benthic polychaetes and other organisms in the Mediterranean, which relates to differences in salinity and temperatures (Arvanitidis et al., 2002; Voultsiadou, 2009). This finding may be linked to the stability of polychaete communities inside of sponges. However, this latter result can also be attributed to the uneven research effort across the Mediterranean Sea, as areas such as the Aegean Sea, with five studies considered in this work, had greater richness than the Adriatic or the Central Basin, with a single study in each. Both cluster analysis and nMDS support this notion, and show that regions with higher richness, were more similar to each other.

Taken together, the results of this study show the importance of sponges as ecosystem engineers in temperate marine environment as they provide shelter and habitat to diverse assemblages of invertebrates. The results further emphasize that polychaete assemblages inhabiting sponges are not a transient facultative assembly of species, but rather stable, diverse and specialized communities which are well adapted for life in this habitat. However, in order to better understand the engineering function of the hosting sponges and their relationship with their surroundings and associated fauna, further research on the role of sponge morphology and zoogeographical gradients on sponge-associated fauna is necessary, especially in the Mediterranean Sea.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

LG organized the database and wrote the first draft of the manuscript. LG and TI performed the statistical analysis. All authors contributed to the conception and design of the study, manuscript revision, and read and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2021.695163/full#supplementary-material

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