

The dynamic core microbiome: Structure, dynamics and stability

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15 Abstract

16 The long-term stability of microbiomes is crucial as the persistent occurrence of beneficial microbes and their as-
17 sociated functions ensure host health and well-being. Microbiomes are highly diverse and dynamic, making them
18 challenging to understand. Because many natural systems work as temporal networks, we present an approach that
19 allows identifying meaningful ecological patterns within complex microbiomes: the dynamic core microbiome. On
20 the basis of six marine sponge species sampled monthly over three years, we study the structure, dynamics and sta-
21 bility of their microbiomes. What emerge for each microbiome is a negative relationship between temporal variability
22 and mean abundance. The notion of the dynamic core microbiome allowed us to determine a relevant functional at-
23 tribute of the microbiome: temporal stability is not determined by the diversity of a host's microbial assemblages, but
24 rather by the density of those microbes that conform its core microbiome. The core microbial interaction network
25 consisted of complementary members interacting weakly with dominance of comensal and amensal interactions that
26 suggests self-regulation as a key determinant of the temporal stability of the microbiome. These interactions have
27 likely coevolved to maintain host functionality and fitness over ecological, and even evolutionary time scales.

28 Introduction

29 Microbes form intricate relationships with most animals and plants, with symbiosis postulated as one of the driving
30 forces behind diversifications across the tree of life ([1]). Research on host-microbe symbioses are typically restricted
31 to highly specialized reciprocal interactions with one or a few microbes interacting with a single host, resulting in
32 mutual benefits for both parties ([2, 3]). However, more diverse and complex host-associated microbial communities
33 (hereafter *microbiomes*) are increasingly found in different plant and animal species ([1]). This poses a challenge be-
34 cause the pairwise specificity, coevolution and reciprocity of host-microbe interactions might not explain the structure,
35 dynamics and functioning of microbiomes. The mere existence of multiple microbes interacting with a host suggests
36 that interactions among microbes might also be an important driver regulating the overall abundance and composition
37 of microbiomes and their associated ecosystem stability and functions.

38 The diversity, complexity and highly dynamic nature of microbiomes makes them challenging to understand. We
39 thus require approaches that embrace the complexity and dynamics but still allow identifying meaningful ecological
40 patterns within and across microbiomes. The quest for core microbiomes is a promising avenue. A core microbiome
41 is typically defined cross-sectionally, rather than longitudinally ([4, 5, 6, 7, 8, 9, 10]), thus failing to capture temporal
42 dynamics. However, a core microbiome characterized as a set of microbes consistently present over long periods of

43 time ([11, 12, 13]), is more likely to be important for the development, health and functioning of its host; for example,
44 several aspects of human health, including autoimmune disorders ([14, 15]), diabetes ([16]) and obesity ([17, 5]) can
45 be linked to severe shifts in the gut microbiome. Whether these disorders emerge as a consequence of perturbed
46 core microbiomes (defined longitudinally) still remains to be seen. However, arguably, the long-term stability of the
47 core microbiome is likely critical as the persistent occurrence of beneficial microbes and their associated ecosystem
48 functions ensure host health and well-being ([18, 19, 20, 21, 22]).

49 Despite the recent realizations that complex microbiomes pervade the tree of life, little is known about microbiome
50 dynamics beyond humans. Here we study the structure, dynamics and stability of microbiomes from six coexisting
51 marine sponges (*Porifera*) belonging to different orders that were sampled over 36 consecutive months.

52 Sponges are keystone species in marine coastal areas due to their filter-feeding activities: they regulate primary and
53 secondary production by transferring energy between the pelagic and benthic zones ([23, 24]). Despite their constant
54 influx of water, they maintain highly diverse, yet specific microbiomes with very little intraspecific variation ([25]). As
55 *Porifera* is a sister-group to all other multicellular animals ([26]), their association with microbes is likely the oldest
56 extant form of an host animal-microbe symbiosis ([27, 28, 29]).

57 We analyzed sponge species corresponding to two different groups that differ markedly in numerous traits illustrat-
58 ing their dependence upon their association with microbes. This classification is based on the diversity and abundance
59 of microbes they harbor—High and Low Microbial Abundance (HMA and LMA) sponges. The classification pervades
60 sponge host morphology and physiology; LMA hosts have an interior architecture fitted for pumping large volumes
61 of water, whereas HMA hosts are morphologically adapted to harbor denser microbial assemblages within their tissue
62 ([30, 31]). As a result, LMA hosts are more dependent on nutrient uptake from the water column ([32, 30, 31, 33,
63 34]) compared to HMA hosts that rely more heavily on nutrients produced by their microbial symbionts ([33, 34, 35,
64 36, 37, 38]). These two sets of hosts provide an ideal system from which we can generalize whether the structure and
65 temporal dynamics of complex microbiomes differ across hosts with different eco-evolutionary characteristics and
66 lifestyles.

67 Our general aim is to understand the temporal dynamics of complex microbiomes. More specifically, we try to
68 answer: (i) What is the diversity and community structure of each core microbiome and how does it differ from that of
69 the many transient taxa passing through the host? (ii) What are the temporal dynamics and stability of each microbial
70 taxon and their aggregated effect on the core microbiome? And (iii) what are the likely ecological processes that un-
71 derpin the observed temporal dynamics and stability? We expect the answer to each of these questions to differ across
72 hosts with different lifestyles (i.e., HMA vs. LMA), reflecting their different dependency on their respective micro-

73 biomes. In particular, we expect the core microbiomes harbored by HMA hosts to be more diverse, compositionally
74 similar and less variable over time.

75 **Results**

76 We analyzed six microbiomes—Three belonging to host species classified as HMA (*Agelas oroides*; *Chondrosia reni-*
77 *formis*; and *Petrosia ficiformis*), and three from hosts classified as LMA (*Axinella damicornis*; *Dysidea avara*; and
78 *Crambe crambe*) ([39, 40]).

79 **Opportunistic taxa dominate the sponge microbiome**

80 To better understand the commonness and rarity of the taxa occurring throughout the time series, we divided each
81 microbiome into three different temporal assemblages based on the persistence of individual taxa over the 36 consec-
82 utive months. Core microbiomes were defined as those taxa that were present in more than (or equal to) 70% of each
83 time series (i.e., persisting ≥ 26 months), whereas opportunistic assemblages comprised taxa present in less than (or
84 equal to) 30% of each time series (i.e., persisting ≤ 11 months). Intermediately persistent taxa (i.e., those persisting
85 between 12 and 25 months) formed transient assemblages. This resulted in three temporal assemblages each spanning
86 36 months, with individual taxa not restricted to consecutively occur over the course of the time series. While this cat-
87 egorization is rather arbitrary, it agrees with previous classifications based on temporal occurrences ([41, 42]). *Grime*
88 (1998) for example, suggested a similar approach (the mass ratio hypothesis) to better understand the relationship
89 between plant diversity and ecosystem properties, dividing species into three categories—dominants, subordinates and
90 transients—reflecting their contribution to ecosystem biomass, stability and functioning.

91 As typically observed for macroecological systems (see e.g., [43]), we found that opportunistic assemblages made
92 up the bulk of the total diversity (i.e., species richness) that resulted from the aggregation of all taxa observed through-
93 out the time series with the core microbiomes only representing a small fraction (1.24%) of this diversity (Table 1).
94 Core taxa still represented an important fraction of the monthly diversity in some of the hosts; Compared to LMA hosts
95 that on a monthly basis harbored 19 to 25 times more opportunistic taxa, core taxa were only 4 to 5 times less numerous
96 in HMA hosts (Table 1). As common species are increasingly recognized as key contributors to ecosystem functions
97 ([44, 45, 46]), the observed difference in the number of common taxa may mirror variation in the aforementioned
98 symbiont dependency among HMA and LMA host species, respectively.

99 Core microbiomes are mainly driven by changes in abundance

100 Temporal turnover is an intrinsic property of our definition of core microbiomes, transient and opportunistic assem-
101 blages; for example, as opportunistic taxa persist less than 30% of the total time series, these assemblages are bound
102 to heavily fluctuate in microbial composition. Nevertheless, in order to quantify the temporal turnover of each assem-
103 blage, we applied a measure that disentangles the two additive determinants of temporal turnover: change in species
104 composition and change in total abundance ([47]). We found that core microbiomes were mainly driven by changes in
105 abundance, whereas transient and opportunistic assemblages were governed by changes in species composition (Fig-
106 ures S1). Due to this large turnover, i.e., new taxa rapidly replace extinct taxa, the opportunistic assemblages displayed
107 an overall higher average evenness (0.83 ± 0.17), measured as Pielou's J over time, compared to the core microbiomes
108 (0.64 ± 0.25).

109 Microbiome composition and specificity differ across host species and lifestyles

110 Microbiome composition varied markedly across host species (Figure 1; Phylogenetic composition, Figure S2), with
111 nearly no overlap amongst core microbiomes (Figure 2). The observed community structure was different from the
112 expectation generated by a null-model (Figure S3; See *Supplementary material* for more information). In addition,
113 HMA and LMA host species displayed very different taxonomic profiles (Figure 3). HMA hosts harbored three
114 dominant phyla that accounted for roughly half of their diversity: *Chloroflexi*; *Actinobacteria*; and *Acidobacteria*.
115 Despite the dominance of these three phyla, each HMA host still kept a unique taxonomic fingerprint by harboring
116 other phyla, such as *Gemmatimonadetes*, *Nitrospira*, and *Bacteroidetes*. The core microbiomes of LMA hosts, on the
117 other hand, were largely dominated by taxa from a single phylum—*Proteobacteria*.

118 Sponges typically harbor certain taxa highly specific to the phylum *Porifera*. These “sponge-specific” 16S rRNA
119 gene sequence clusters are monophyletic and span 14 known bacterial and archaeal phyla ([48, 49]). Taxa that fall into
120 these sponge-specific clusters are only detected at very low abundances outside of sponge hosts, e.g., in the seawater
121 and sediment ([27, 50, 25]). Some of these taxa are transmitted vertically from parent to offspring, suggesting sponge-
122 microbe coevolution and cospeciation ([51]). We found that the core microbiomes of HMA hosts harbored a larger
123 proportion of taxa that corresponded to sponge-specific clusters than the cores of LMA hosts (Table 2; Figure S4).
124 Furthermore, these taxa had a higher average monthly abundance in the core microbiomes compared to the transient
125 and opportunistic assemblages (Table S1). Then, despite the fact that identifying what constitutes a core microbiome
126 remains elusive ([6, 25, 9]), the definition of the core used here (i.e., taxa present in at least 70% of the time series)

127 provided a clear distinction in species composition between the core microbiomes and the transient and opportunistic
128 assemblages (Figure 2) that displayed prominent differences in the average monthly abundance of sponge-specific taxa
129 (Table S1) and in their temporal turnover (Figures S1).

130 The innate immune defense of some sponge species can differentiate between pathogens, food bacteria and com-
131 mensals in a manner similar to the adaptive immune system of vertebrates ([52, 53, 54, 55, 56, 57]). Thus, the above
132 findings suggests that sponge-specific clusters, although present in the water column and sediment as part of the rare
133 biosphere ([58, 50]), represent taxa important for host functioning.

134 Core taxa are more stable and abundant

135 The unusual temporal coverage of our dataset allowed us to address a number of fundamental questions related to
136 the temporal variability within and across microbiomes. We computed the mean abundance and the coefficient of
137 variation $CV = \frac{\sigma}{\mu}$ for each taxon's abundance trajectory over time. What emerged for each microbiome was a negative
138 relationship between the coefficient of variation and the log mean abundance: individual core and transient taxa were
139 more stable and abundant than opportunistic taxa. However, in a few microbiomes, abundant conditionally rare taxa
140 (CRTs) greatly outnumbered the abundance of core taxa. CRTs are extremely rare or below detection limit throughout
141 most of the time series, but occasionally reach high abundance ([59]). Our results suggest that the presence of these
142 taxa can have a negative impact on the stability of the focal core microbiome (Figure 4 AB; Figure S5).

143 There are several non-mutually exclusive mechanisms that can underpin the observed relationship between tem-
144 poral variability and mean abundance. First, in agreement with recent observations on a broad range of marine com-
145 munities, neutrality alone is unlikely to explain the high abundance of the most common species ([60]). Second,
146 lower variability can imply the presence of self-regulation (i.e., density dependent processes) at higher population
147 abundances ([61, 62]). Furthermore, on a log-log scale, our observed relationship between temporal variability (now
148 variance σ^2) and mean abundance describes Taylor's power law ([63]). The null expectation of the temporal version
149 of Taylor's law states that the variance scales with the mean abundance following a power law with an exponent equal
150 to 2. This implies that population or community variability is constant. Conversely, if the exponent is less than 2, then
151 the variability in population abundance decreases with increasing mean population abundance, as seen in Figure 4 CD
152 and Figure S6. Third, for large population sizes, as is characteristic of microbial communities like those studied here,
153 environmental stochasticity is more likely than demographic stochasticity to reduce Taylor's power law exponent ([64,
154 65]). Fourth, even weak interactions among species can reduce this exponent; for example, interspecific interactions,
155 such as competition typically lead to smaller fluctuations of common versus rare species within communities ([65])—a

156 result that could be extended to other types of interactions. Below, we explore the contribution of these mechanism to
157 microbiome dynamics and stability in more detail.

158 **Core microbiome density, not diversity, begets its stability**

159 We aggregated all individual microbial population abundances within each temporal assemblage—core, transient, and
160 opportunistic (Figure 5). This revealed two markedly different temporal dynamics across microbiomes: in the hosts
161 *A. oroides*, *C. reniformis* and *C. crambe*, core microbiomes were very dense, i.e., they accounted for the majority of
162 microbiome relative abundance. In contrast, the core microbiomes of hosts *D. avara*, *A. damicornis* and *P. ficiformis*
163 were sparser, and instead transient and/or opportunistic assemblages dominated microbiome relative abundance. We
164 found that dense cores were more stable over time than sparse cores, measured as community-level invariability (the
165 inverse of variability, [66]; Figure 5). The association between core density and stability was also robust to a more
166 stringent definition ($\geq 85\%$) of the core microbiome (Figure S6). For some microbiomes, no taxa persisted on or above
167 this threshold.

168 Community-level stability showed a weak (non-significant) relationship with diversity (species richness; Figure S8
169 A). Instead, we observed a significant positive relationship between community-level stability and the median relative
170 abundance (Figure S8 B). This agrees with some studies that demonstrated a positive relationship between community-
171 level stability and the relative abundance or biomass of common plant species ([67, 68, 69]). Importantly, this suggests
172 that the effect of diversity on stability can be constrained by the dynamics of only a few common and abundant species,
173 as seen in the case of our high-density cores (Figure 5); for example, host species *P. ficiformis* harbored the second
174 largest core diversity ($S=40$, Table 1) that still resulted in the least stable low-density core. On the other hand, sponge
175 species *C. crambe* achieved a stable high-density core by harboring only a few core taxa ($S=8$, Table 1).

176 Furthermore, in agreement with the HMA-LMA dichotomy, the metabolic profiles of *P. ficiformis* and *C. crambe*
177 yet match those of other archetypal HMA and LMA hosts, respectively ([70]). While *P. ficiformis* harbored an unstable
178 low-density core, its core was nonetheless comprised of the largest proportion of sponge-specific clusters (Table 2;
179 Figure S4), suggesting that microbiome stability may not always be a prerequisite for host functioning.

180 **Intraspecific interactions drive core microbiome dynamics**

181 In order to further disentangle the main drivers of core microbiome temporal dynamics, we used a model that de-
182 composes temporal fluctuations in species abundances into three contributions—Interspecific interactions, intraspecific

183 interactions, and environmental variability. Environmental variability includes apart from ecological drift, the aggre-
184 gated effects of the host on the microbial consortium, as well as the external environment acting on the host. While
185 we included several environmental covariates that had been recorded over the 36 months, such as water temperature,
186 salinity and nutrients, our model is able to capture unmeasured effects through the use of latent variables (see *Methods*
187 for more information).

188 We found that intraspecific interactions explained the largest proportion of variation, suggesting that all core taxa
189 on average, experienced strong self-regulation (Figure 6 A). There was a marked difference between HMA and LMA
190 host species in terms of the variation explained by interspecific interactions: In the core microbiomes of the HMA
191 hosts, interspecific interactions had a relatively large effect on the dynamics, whilst this effect was almost negligible
192 in the LMA host species (Figure 6 A).

193 The main drivers we identified for core microbiome temporal dynamics somewhat differ from those commonly
194 reported for other large species-rich systems; for example, studies assuming Lotka-Volterra dynamics in macroeco-
195 logical communities ([71, 72, 73, 74]) or other types of time series analyses applied on free-living marine microbial
196 communities ([75, 76, 77]) often report environmental variability as the major factor affecting population dynam-
197 ics. While environmental variability was an important factor, intraspecific interactions was the single most important
198 driver affecting the dynamics across all core microbiomes. Furthermore, the modeled environmental covariates only
199 accounted for a small fraction of the variation explained by environmental variability (Figure 6 A), indicating that the
200 sponge microbiome may experience a reduced influence of the external environment acting on the host.

201 A large body of theoretical and empirical literature suggests that self-regulation, which we equate here to in-
202 traspecific interactions, is a key determinant of temporal stability ([61, 62]). The simple premise of this regulatory
203 mechanisms is that species abundances decrease per capita growth rates when population abundances are high and vice
204 versa. Recently *Barabás and colleagues (2017)* showed that stability requires the majority of species in a community
205 to experience negative self-effects. Although this work focuses on asymptotic stability (i.e., whether small pertur-
206 bations of species' abundances away from an equilibrium point tend to be dampened, with the system returning to
207 equilibrium) and not on temporal variability, their results in combination with ours suggest that strong self-regulation
208 should also be the norm within microbiomes ([78]).

209 **The core microbiomes are comprised of weak unilateral interactions**

210 The nature and strength of interspecific interactions are pivotal to understand the dynamics of species interaction
211 networks ([79, 80]). Our unique temporal series allows for determining how microbes interact with each other within

212 different host species. Because interspecific interactions were almost negligible in the LMA hosts, we analyzed the
213 most credible network structure of each HMA core microbiome (Figure 7; Figures S9). For these three networks,
214 only a small fraction among the possible interactions were likely to occur (Figures S10), resulting in low network
215 connectance (5-7%). The networks had a skewed distribution of interaction strengths toward many weak and a few
216 strong interactions (Figures S11). This pattern mimics that found in empirical food-webs [81, 82] and mutualistic
217 networks ([83]). Theory shows that skewed distributions of interaction strengths beget stability, and arises during the
218 assembly of persistent communities ([84, 85]).

219 Theory shows that reciprocal interactions such as exploitation $\{+/-\}$, cooperation $\{+/+\}$ and competition $\{-/-\}$
220 differ in their effects on community stability and ecosystem functions ([86, 87, 88, 89, 90, 79, 80]). Specifically,
221 communities consisting of a mixture of unilateral interactions are more stable than those with only reciprocal inter-
222 actions ([80]). We found that amongst all possible interspecific interactions (Figures S12), unilateral interactions in
223 the form of commensalism $\{+, 0\}$ and amensalism $\{-, 0\}$ dominated (Figure 6 B). Reciprocal interactions—cooperative
224 $\{+, +\}$, competitive $\{-, -\}$ and exploitative $\{+, -\}$ interactions were exceptionally rare. The core microbiomes of hosts
225 *A. oroides* and *C. reniformis* were largely dominated by commensal interactions, whereas the core microbiome of host
226 *P. ficiformis* had a higher frequency of amensalism. It was also the only core network that had competitive interac-
227 tions among its members, although at very low frequencies. Sponge-specific clusters, although prevalent in the core
228 microbiomes of HMA hosts were not more connected than other nodes within these networks

229 Certainly, opportunistic and transient taxa can influence the dynamics of the core microbiome. However, we
230 focused on inferring interspecific interactions among core taxa for three main reasons: (1) Computation—Including
231 non-core taxa would increase network size ten folds, and thus not be computationally feasible; (2) Information—There
232 is very little information in taxa only occurring in one or a few timesteps, thus the inference for those taxa would
233 be very poor; and (3) Ecology—Interspecific interactions require species to frequently co-occur. The many occasional
234 taxa observed throughout the time series, especially those occurring at high densities (i.e., the CRTs) are likely acting
235 together with ecological drift as sources of stochastic variability. In our model, the effects of unmodeled interspecific
236 interactions are captured by the inclusion of the latent variables (see *Methods* for more information).

237 **Microbial transmission mode can affect microbiome stability and functioning**

238 High-density cores (i.e., those core microbiomes whose taxa accounted for the majority of abundance) were found
239 in sponge species that transmit microbes vertically from adult to larvae ([91, 92, 93]), whereas low-density cores
240 represent sponge species with larvae largely deprived of microbes ([94, 95, 96]).

241 Vertical transmission provides an evolutionary mechanism for preserving particular combinations of microbes,
242 including their interaction structure and the ecosystem functions that emerge from it ([97]). Evidence from other
243 ecological communities, including the human gut microbiome, suggest that priority effects—the order and timing of
244 species arrivals—determine the interactions among species, and in turn also community assembly and stability ([98,
245 99, 100]). The process of vertical inheritance of microbes likely has similar outcomes as priority effects. Further-
246 more, as pathogenic microbes use cooperative secretions that modify their environment to enhance their growth and
247 expansion ([101, 102]), it is reasonable to assume that commensal microbes do too. We therefore hypothesize that the
248 complementary set of microbes that are vertically transmitted from parent to offspring pre-empt the initial host niche
249 by fast reaching carrying capacity, while simultaneously modifying it in their favor. This would inhibit the subsequent
250 colonization of some microbes, while facilitating the establishment of certain others.

251 As previously mentioned, host species *P. ficiformis* harbored an unstable low-density core, yet it harbored the
252 largest consortia of sponge-specific clusters within its core. This does not only suggest that microbiome stability
253 may not always be a requirement for host functioning, it also indicates that host species *P. ficiformis* achieves HMA
254 archetypal functional characteristics by means of horizontally selecting commensal microbes from the water column,
255 many of which fall into sponge-specific clusters. These sponge-specific microbes are examples of conditionally rare
256 taxa (CRTs) outside the sponge host, but through some recognition mechanism are allowed to flourish within the host.

257 Conclusion

258 Natural systems commonly work as temporal networks ([103]). To increase our understanding of the processes gov-
259 erning microbiome assembly, stability and functioning, this study highlights the importance of defining the core mi-
260 crobiome longitudinally (i.e., analysing temporal dynamics) rather than cross-sectionally. Most studies to date have
261 focused on the human microbiome (see e.g., [104, 13, 105, 79, 100]), with only a few studies exploring temporal dy-
262 namics in other host systems ([11, 106, 107]). By focusing on the six most common sponge species of the temperate
263 Mediterranean benthic community, we successfully characterized microbiome dynamics and stability under natural
264 conditions.

265 The observed negative relationship between temporal variability and abundance that emerged from the analyses
266 of each microbiome is conducive to the notion of the dynamic core microbiome. This notion allowed us to determine
267 that irrespective of host's eco-evolutionary characteristics and lifestyles, it is the density of the core microbiome
268 rather than its diversity that determines the stability of the sponge microbiome. We hypothesize that priority effects

269 mediated by vertical transmission underpins this pattern, which may further suggest that high-density cores confer
270 hosts resistance against the establishment of occasional taxa that sponges are constantly exposed to through their
271 filter-feeding activities. The core microbiome has been proposed as the common taxa shared among microbiomes in
272 an habitat ([108], [6]). Our finding reveals a relevant functional attribute that constitutes an step forward towards the
273 identification and characterization of the so-called core microbiome.

274 We further found that intraspecific self-regulation is much more important for microbiome dynamics than environ-
275 mental forcing. The most credible core interaction networks consisted of members interacting weakly with each other
276 with a dominance of comensal and amensal interactions. Altogether, this suggests that host-associated microbiome
277 dynamics and its emerging interaction structures differ from the temporal dynamics of free-living microbial commu-
278 nities. These interactions have likely coevolved to maintain host functionality and fitness over ecological, and even
279 evolutionary time scales.

280 We have focused on compositional stability over time—a notion inclusive of variation in both species relative abun-
281 dances and species composition. More generally, compositional and functional stability often show complex interde-
282 pendencies ([109]), because, for example, compensatory dynamics between species may reduce functional loss within
283 communities ([110]). For most host species studied here, our results suggest that there may exist a positive relationship
284 between compositional and functional stability. However, for host-associated microbiomes in general, it is difficult to
285 disentangle the effects of compositional stability from the host's own ability to control the identity and abundance of its
286 microbes on the overall functioning. For one pair of hosts, our findings of high-density and low-density cores did not
287 match the notion of a positive relationship between compositional and functional stability. This suggests that, at least
288 for some host species, functioning is achieved by other mechanisms that do not require compositional stability. The
289 relationship between microbiome compositional stability and host functionality will benefit from further investigation
290 that focuses on the temporal dynamics and functioning of the core microbiome.

291 **Methods**

292 **Sponge collection**

293 The sponge species *Agelas oroides*, *Chondrosia reniformis*, *Petrosia ficiformis*, *Axinella damicornis*, *Dysidea avara*
294 and *Crambe crambe* were collected monthly from March 2009 until February 2012 close to the Islas Medas marine
295 reserve in the NW Mediterranean Sea 42°3'0"N, 3°13'0"E by SCUBA at depths between 10-15 metres. Three repli-
296 cates per sponge species (i.e., different individuals per sampling time) and ambient seawater samples were collected.

297 The collected sponge species belong to six different orders that represent common members of the Mediterranean
298 benthic community. Each sponge species were identified based on distinct morphological features. Specimens were
299 sublethally sampled and excised fragments were placed in separate plastic bottles and brought to the surface were
300 they were frozen in liquid nitrogen until DNA extractions. Samples of the ambient water were taken at 5 m depth
301 and poured into three separate 5 L jars. All samples were stored at -80°C until DNA extraction. Aliquots of seawater
302 (300-500 mL each, 1 aliquot per sample jar) were concentrated on 0.2 μ m polycarbonate filters, submerged in lysis
303 buffer and stored at -80°C until DNA extraction.

304 **DNA extraction and sequencing**

305 Following the manufacturers Animal Tissue protocol, 16S rRNA gene sequences were PCR-amplified from sponge
306 samples (n=648) and seawater filters (n=108) using the DNeasy tissue kit (Qiagen, CA, USA), and subsequently
307 submitted to the Research and Testing Laboratory (Lubbock, TX, USA) for gene amplicon pyrosequencing. Samples
308 were amplified with primer 28F and amplicons were sequenced using 454 Titanium chemistry (Roche, CT, USA),
309 producing 250 base pair read lengths in the 5'→3' direction.

310 **Analysis of sequencing data**

311 454 reads were processed in mothur v.1.29.2 ([111]). Raw reads were pooled from replicates belonging to the same
312 sponge species. Fasta, qual and flow files were extracted from binary sff files; sffinfo(...,flow=T). Flow files were
313 then filtered based on barcodes to speed-up the proceeding de-noising process; trim.flow. Sequences were de-noised;
314 shhh.flows(..., lookup= LookUp_Titanium.pat). The LookUp-file is necessary and specific to the 454 technology used.
315 Next the barcode and primer sequences were removed together with sequences shorter than 200bp and/or contained
316 homopolymers longer than 8bp; trim.seqs(..., pdiffs =2, bdiffs =1, maxhomop =8, minlength =200). In order to min-
317 imise computational effort, files were reduced to non identical sequences; unique.seqs. Non redundant sequences were
318 aligned to SILVA 102 reference alignment with default kmer search and Needleman-Wunsch algorithm; align.seqs(...,
319 flip =F). Non overlapping sequences were removed; screen.seqs(..., optimize= end, start= 1044, criteria = 95), in
320 addition to empty columns that were introduced from the alignment process; filter.seqs(...,vertical =T, trump =).
321 Aligned sequences were reduced to non redundant sequences; unique.seqs. To further reduce amplification errors, less
322 abundant sequences were binned to more abundant sequences if they were within 2bp of a difference; pre.cluster(...,
323 diffs =2). Chimeric sequences were identified; chimera.uchime(..., dereplicate =T) and removed; remove.seqs. Se-

324 quences were classified using the RDP reference taxonomy; `classify.seqs(..., template=trainset9_032012.pds.fasta,`
325 `taxonomy=trainset9_032012.pds.tax, cutoff=80)`, and non bacterial lineages were removed; `remove.lineage(...,`
326 `taxon=Mitochondria-Chloroplast-Archaea-Eukaryota-unknown)`. We calculated pairwise distances between aligned
327 sequences; `dist.seqs(..., cutoff=0.050)`.

328 Due to an uneven sequence distribution across samples, we pooled sequences across the three host species repli-
329 cates prior to OTU clustering. As we found a plate effect on the number of sequences, we sub-sampled 1500 sequences
330 from the resulting monthly samples. This number corresponded to the average of the three lowest host-plate averages.
331 Sequences were thereafter clustered into OTUs defined at 97% similarity; `classify.otu(..., label=0.030)` and outputted
332 to an OTU-table (`.shared-file`); `make.shared(..., label=0.030)`.

333 **Identification of sponge-specific clusters**

334 A representative sequence from each OTU was taxonomically assigned using a BLAST 62 search against a curated
335 ARB-SILVA database containing 178 previously identified sponge-specific clusters (SC) ([49]). For each BLAST
336 search, the 10 best hits were aligned to determine sequence similarities. The most similar OTU sequence to the
337 respective reference sequence within the database was then assigned to an SC based on a 75% similarity threshold:
338 (i) a sequence was only assigned to any given SC if its similarity was higher to the members of the cluster than to
339 sequences outside the cluster; and (ii) if its similarity to the most similar sequence within the cluster was above 75%.
340 A majority rule was applied in cases where the assignment of the most similar sequences was inconsistent, and the
341 OTU sequence was only assigned to the SC if at least 60% of the reference sequences were affiliated with the cluster.

342 **Microbiome stability and dynamics**

343 **Temporal turnover**

344 We applied a measure of temporal turnover that describes the extent to which individual OTUs and consequently the
345 microbiome changes over time ([47]). Importantly, this measure decomposes abundance fluctuations into two additive
346 contributions of change due to microbiome composition and total abundance.

Total turnover D between times t and u , ($u > t$) is defined as

$$D(t : u) = \sum_{i=1}^S d_i(t : u) = \sum_{i=1}^S \log \left(\frac{\lambda_{i,u}}{\lambda_{i,t}} \right) p_{i,t} \quad (1)$$

$$= - \sum_{i=1}^S \log \left(\frac{p_{i,t}}{p_{i,u}} \right) p_{i,t} + \left(\frac{\lambda_u}{\lambda_t} \right) \quad (2)$$

$$= D_1(p_t : p_u) + D_2(\lambda_t : \lambda_u) \quad (3)$$

347 where $\lambda_t = \sum_{i=1}^S \lambda_{i,t}$ represent the sum of the expected total abundance of each OTU in the microbiome. The expected
 348 abundance of OTU i in time t , i.e., $\lambda_{i,t}$, $i = 1, 2, \dots, S$ is unknown and therefore needs to be estimated from an observed
 349 time series. $p_{i,t}$ represents the relative abundance of OTU i in time t , and is calculated as $p_{i,t} = \left(\frac{\lambda_{i,t}}{\lambda_t} \right)$. As such, the
 350 total turnover D can be decomposed into D_1 which is related to the amount of change in microbiome composition,
 351 and D_2 reflecting the amount of change in total abundance.

As noted above, the expected abundance needs to be estimated. We thus modeled each time series of time series
 of high-throughput DNA sequence $N_{i,t}$ assuming a Poisson log-linear model with a time-varying mean parameter $\lambda_{i,t}$

$$N_{i,t} \sim Pois(\lambda_{i,t}) \quad (4)$$

$$\log \lambda_{i,t} = \sum_{j=1}^{N_c} X_{t,k} \beta_{k,j} \quad (5)$$

352 where $X_{k,t}$ is a time series of $k = 1, 2, \dots, N_c$ environmental covariates, and $\beta_{k,j}$ is the corresponding regression
 353 coefficient that needs to be estimated. We included temperature, salinity, chlorophyll, bacterial cell density, nitrite
 354 (NO_2), ammonia (NH_4), and phosphate (PO_4) as the N_c environmental covariates. All covariates were standardized
 355 to have zero-mean and unit variance.

356 Community-level stability

We applied a newly developed measures of temporal stability defined as invariability ([66]) at the community-level,
 i.e., for each core microbiome, transient and opportunistic assemblages, respectively. Invariability at the community-
 level is defined as

$$I = \frac{1}{CV(N_{tot})^2} = \frac{(\widehat{N}_{tot})^2}{Var(N_{tot})} \quad (6)$$

357 where \widehat{N}_{tot} and \widehat{N}_i denote the average of the total abundance and the average of the abundance of OTU i over the time
358 series, respectively.

359 **Core dynamics and ecological interactions**

360 We adapted a multivariate first-order autoregressive model assuming Gompertz population dynamics ([112]) to model
361 core dynamics and to infer ecological interactions among core taxa from time series of high-throughput DNA sequence
362 counts. Compared to the commonly used Generalized Lotka–Volterra (GLV) model (see e.g., [113]), the Gompertz
363 model is linear on the log-scale and thus a good approximation of nonlinear dynamics. Furthermore, a severe problem
364 with even the simplest GLV model is that the number of parameters that need to be estimated often is larger than
365 the number of available data points. *Mutshinda and colleagues (2009)* addressed this problem by using Gibbs Vari-
366 able Selection ([114]) in order to induce sparseness: the $N(N + 1)$ interspecific interactions are constrained so that
367 most are shrunk to zero. We further adapted this framework to address two additional challenges of microbiome data.
368 First, to model covariances between a large number of taxa using a standard multivariate random effect is compu-
369 tationally challenging: the number of parameters that has to be estimated when assuming a completely unstructured
370 covariance matrix increases quadratically as the number of taxa increases. We therefore parameterized the residual
371 covariance matrix using a latent variable approach. Latent variables also capture unmeasured effects (e.g., host ef-
372 fects and unmodeled interspecific interactions) which if not accounted for may lead to erroneous inference ([115]).
373 Second, high-throughput DNA sequencing produces compositional data, i.e., non-negative counts with an arbitrary
374 sum imposed by the sequencing platform, which can produce spurious correlations if not properly accounted for (see
375 e.g., [116, 117, 118]). We therefore used a log-linear model with a Poisson likelihood that includes a random effect
376 accounting for sample size. This model produces a likelihood equivalent to that of the logistic normal multinomial
377 model but is more convenient for computation and estimation ([119]).

378 **Process model**

379 To accommodate the time series, we refer to OTU $i \in \{1, \dots, I\}$ in time point $t \in \{1, \dots, T\}$. Let $\mathcal{N}(\mu, \sigma^2)$ denote a
380 univariate normal distribution with mean μ and variance σ^2 , and analogously, let $\mathcal{MVN}(\mu, \Sigma)$ denote a multivariate
381 normal distribution with mean vector and covariance matrix Σ . If we denote $n_{i,t}^*$ as the expectation of $n_{i,t}$ which
382 is the natural logarithm of the observed time series $N_{i,t}$, then on the natural logarithmic scale we have the expected
383 number of 16S rRNA gene sequences from OTU i in time point t within a given core microbiome described by

$$n_{i,t} * |n_{i,t-1} = n_{i,t-1} + r_i \left[1 - \sum_{j=1}^S \frac{\alpha_{i,j} n_{j,t-1}}{k_i} \right] + \sum_{j=1}^{N_c} X_{t,k} \beta_{k,j} + \epsilon_{i,t} \quad (7)$$

$$t = 2, 3, \dots, T; k = 1, 2, \dots, N_c$$

384 where we assume $r_i \sim \mathcal{N}(0, 10)$ and $K_i \sim \text{Exp}(1)$. The coefficients measuring each taxon's response the k -th
 385 environmental covariate are assumed $\beta_{k,j} \sim \mathcal{N}(0, 100)$. We assumed correlated residual responses to the environment
 386 by included temperature, salinity, chlorophyll, bacterial cell density, nitrite (NO_2), ammonia (NH_4) and phosphate
 387 (PO_4) as the N_c environmental covariates potentially influencing the modeled core OTUs. All covariates were
 388 standardized to have zero-mean and unit variance. $\epsilon_{i,t} \sim \mathcal{MVN}(\mathbf{0}, \Sigma)$ represents the residual variance, where Σ is the
 389 residual covariance matrix which was parameterized using latent variables.

390 Latent variables

391 As previously stated, to improve statistical efficiency we parameterized the residual covariance matrix Σ using a latent
 392 variables approach, where the index q runs over the $q = 1, \dots, 2$ latent variables.

$$\epsilon_{i,t} = \sum_{q=1}^2 \eta_{t,q} \lambda_{q,i} + \delta_{i,j} \epsilon_{i,t} \quad (8)$$

$$\epsilon_{i,t} \sim \mathcal{N}(0, \sigma_i^2)$$

$$\Sigma = \lambda \lambda^T + \text{diag}(\sigma_i^2) \quad (9)$$

393 where η denote the latent variables and λ their corresponding factor loadings. Both are assigned standard normal
 394 priors $\mathcal{N}(0, 1)$ with the assumption of zero mean and unit variance to fix the location (see chapter 5, [120]). $\delta_{i,j}$ denote
 395 the Kronecker's delta such that $\delta_{i,i} = 1$ and $\delta_{i,j} = 0$ for $i \neq j$. Thus, the covariance matrix Σ can be computed from
 396 the factor loadings (Equation 9). The diagonal elements of the covariance matrix Σ quantify the amount of residual
 397 variation for OTU i not captured by the modeled environmental covariates.

398 Observation model

399 The time series of high-throughput DNA sequence counts $y_{i,t}$ were modeled as Poisson random variables with means
 400 $\lambda_{t,i}$ satisfying the following log-linear model

$$y_{i,t} \sim \text{Pois}(\lambda_{i,t}) \quad (10)$$

$$\log \lambda_{t,i} = n_{i,t} + \log N_t + \mu N_t \quad (11)$$

$$n_{i,t} \sim \mathcal{MVN}(n_{i,t}^*, \sigma_i^2) \quad (12)$$

401 where $\log N_t$ is an offset accounting for the observed total number of DNA sequences in time t , while $\mu N_t \sim$
402 $\mathcal{N}(0, 100)$ represent the random effect accounting for sample size in time t . Both thus represent the total abundance
403 in time t , and account for the aforementioned compositional nature of high-throughput DNA sequencing data.

404 **Gibbs Variable Selection**

405 As mention above, we used Gibbs Variable Selection ([114]) method in order to constrain the model to only use inter-
406 specific interaction coefficients $\alpha_{i,j}$ for which there were strong support in the data. This was achieved by introducing
407 a binary indicator variable $\gamma_{i,j}$ for $i \neq j$, and assuming $\gamma_{i,j} \sim \text{Bernoulli}(p)$, such that $\gamma_{i,j} = 1$ when OTU j is included
408 in the dynamics of OTU i , and $\gamma_{i,j} = 0$ otherwise. Where there was low support for $\alpha_{i,j}$ in the data, $\gamma_{i,j} = 0$ and the
409 corresponding interaction was excluded from the model. On the other hand, when $\gamma_{i,j} = 1$, $\alpha_{i,j}$ was freely estimated
410 from the data. The parameter p represents our prior belief about the proportion of realized interspecific interactions:
411 we set $p=0.1$, thus assuming that 90% of all interspecific interactions were zero.

412 We used Markov chain Monte Carlo (MCMC) simulation methods through JAGS ([121]) in R ([122]) using the
413 *runjags* package ([123]) to sample from the joint posterior distribution of all the model parameters. We ran 10 in-
414 dependent chains with dispersed initial values for $5e6$ iterations, discarding the first $2e6$ samples of each chain as
415 burn-in and thinned the remainder to every 50th sample. We evaluated convergence of model parameters by visually
416 inspecting trace and density plots using the packages *coda* ([124]) and *mcmcplots* ([125]), as well as using the Geweke
417 diagnostic ([126]). In addition, to ensure good mixing of the parameter $\alpha_{i,j}$, we calculated the number of jumps the
418 parameter $\gamma_{i,j}$ made between its two states, 0 and 1.

419 **Variance partitioning**

420 The total variance V_i affecting the dynamics of core OTU i can be decomposed into additive sources reflecting inter-
421 specific interactions, intraspecific interactions, and environmental variability (i.e., measured environmental covariates
422 and residual variation) as follows,

$$V_i = \overbrace{\left[\frac{r_i}{K_i} \right]^2 \sum_{j \neq i} v_{j,j} \alpha_{i,j}^2}_{\text{Interspecific interactions}} + \overbrace{\left[\frac{r_i}{K_i} \right]^2 v_{i,i}}_{\text{Intraspecific interactions}} + \overbrace{\sum_{q=1}^{N_c} \beta_{i,q}^2 + \sigma_i^2}_{\text{Environmental variability}} \quad (13)$$

423 where $v_{i,i}$ represent the stationary variance for n_i (Equation 11), $\beta_{i,k}^2$ the variance attributable to each k covariate,
 424 and σ_i^2 correspond to the residual variance (the diagonal elements of Σ , Equation 9). As a consequence of Equation
 425 13 the proportion of variation attributed to e.g., interspecific interactions can be calculated as

$$\sigma_{i_{inter}}^2 = \left\{ \left[\frac{r_i}{K_i} \right]^2 \sum_{j \neq i} v_{j,j} \alpha_{i,j}^2 \right\} / V_i \quad (14)$$

426 Finding the most credible network structure

427 To characterize each core microbiome network, we analyzed the interaction structure of the marginal posterior distribu-
 428 tion for the interaction coefficient $\alpha_{i,j}$. The parameter $\alpha_{i,j}$ is a probability distribution, thus containing the probability
 429 of OTU j having a per capita effect on the growth rate of OTU i . This means that we can decompose $\alpha_{i,j}$ into two
 430 marginal posterior distributions—one for interaction sign and another one for interaction strength. We constructed the
 431 core microbiome networks for each HMA host as means of visualizing the most credible network structures. This
 432 was done by mapping the marginal posterior distribution of the average number of links onto $\alpha_{i,j}$, thus extracting
 433 the marginal posterior average number of links with the highest probability of non-zero interactions. As a way of
 434 further validating network structure, we compared the marginal posterior distribution of connectance to the empirical
 435 connectance of each constructed network.

436 Code and Data Availability

437 All data and code will eventually be available at the [Open Science Framework](#).

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443 **Author contributions**

444 JRB and JMM conceived the study. JRB performed all the analyses and wrote the manuscript. JRB and RBO adapted
445 the MAR(1) model. JRB and JMM refined the manuscript. RC and MR collected the data. All authors commented on
446 later versions of the manuscript.

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740 **Tables and Figures**

Table 1: Microbiome diversity by temporal assemblage

	HMA			LMA		
	<i>A. oroides</i>	<i>C. reniformis</i>	<i>P. ficiformis</i>	<i>A. damicornis</i>	<i>D. avara</i>	<i>C. crambe</i>
Core	45 38.4 ± 11.7	33 27.4 ± 11.1	40 32.1 ± 12.3	8 6.7 ± 2.1	6 6.4 ± 2	8 6.4 ± 2.3
Transient	90 41.3 ± 14.4	54 26.4 ± 12.5	140 67.9 ± 30.8	31 12.7 ± 5.9	44 21.4 ± 7.4	41 17.7 ± 6.2
Opportunistic	2658 140 ± 77.7	2436 129.9 ± 66.7	2580 141.4 ± 30.2	2443 126.8 ± 78.1	2763 126.3 ± 42.8	3465 160.1 ± 60.4
Total biome	2793	2523	2760	2482	2813	3514

Notes: For each assemblage, the first row displays the total number of unique taxa (S), while the second row shows the monthly average ($\pm SD$) number of coexisting taxa. The last row shows the total species richness (S_T) of each microbiome.

Table 2: Percentage of taxa within each assemblage and host assigning to sponge-specific clusters.

	HMA			LMA		
	<i>A. oroides</i>	<i>C. reniformis</i>	<i>P. ficiformis</i>	<i>A. damicornis</i>	<i>D. avara</i>	<i>C. crambe</i>
Core	42.2	45.6	60	25	0	12.5
Transient	43.3	40.7	47.1	25.8	9.1	9.8
Opportunistic	22.8	33.9	35.6	22.2	9.5	11.8

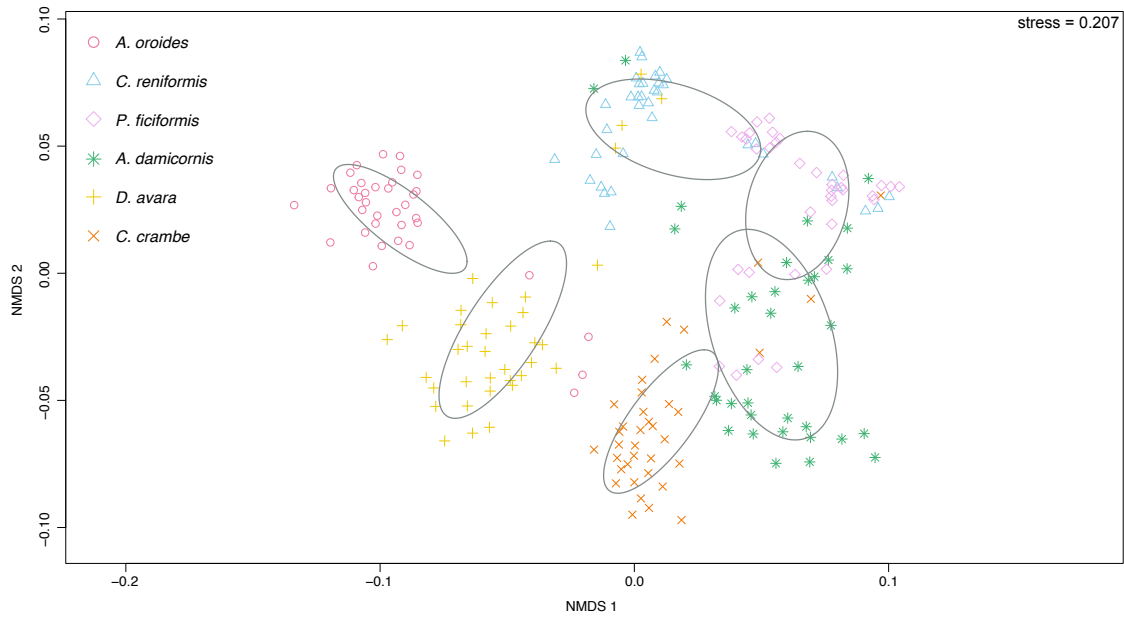


Figure 1: Microbiome compositional similarity across host species. Non-metric multidimensional scaling (NMDS) calculated on Jaccard distances among all 36 monthly samples for each host species ($n=36 \times 6=216$). Colors and shapes denote all monthly samples from a given host species surrounded by an ellipse showing the 95% confidence interval. Red circles *A. oroides*; blue triangles *C. reniformis*; pink diamonds *P. ficiformis*; green stars *A. damicornis*; yellow crosses (+) *D. avara*; and orange crosses (×) *C. crambe*. ANOSIM: $R=0.767$, $P<0.001$

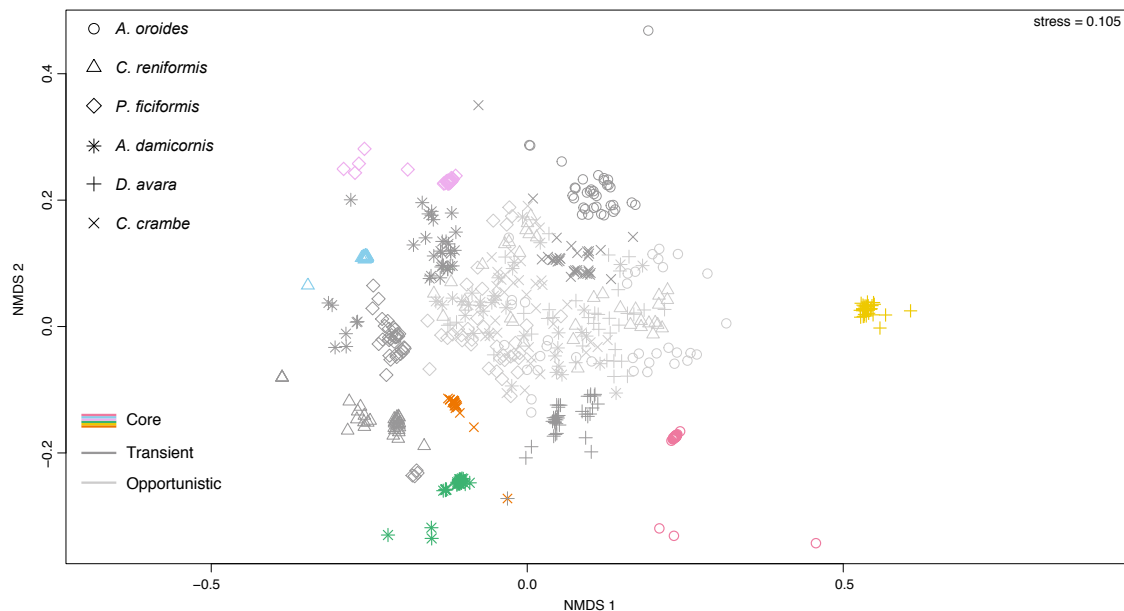


Figure 2: Microbiome compositional similarity across assemblages and host species. Non-metric multidimensional scaling (NMDS) calculated on Jaccard distances among all 36 monthly samples for each host and assemblage ($n=36 \times 6 \times 3=648$). Colors and shapes denote all monthly samples from a given host and assemblage, respectively. Different shapes for each host species: circles *A. oroides*; triangles *C. reniformis*; diamonds *P. ficiformis*; stars *A. damicornis*; crosses (+) *D. avara*; crosses (x) *C. crambe*. Different colors for each core microbiome: red *A. oroides*; blue *C. reniformis*; pink *P. ficiformis*; green *A. damicornis*; yellow *D. avara*; and orange: *C. crambe*. Dark gray denotes transient and light gray opportunistic assemblages, respectively.

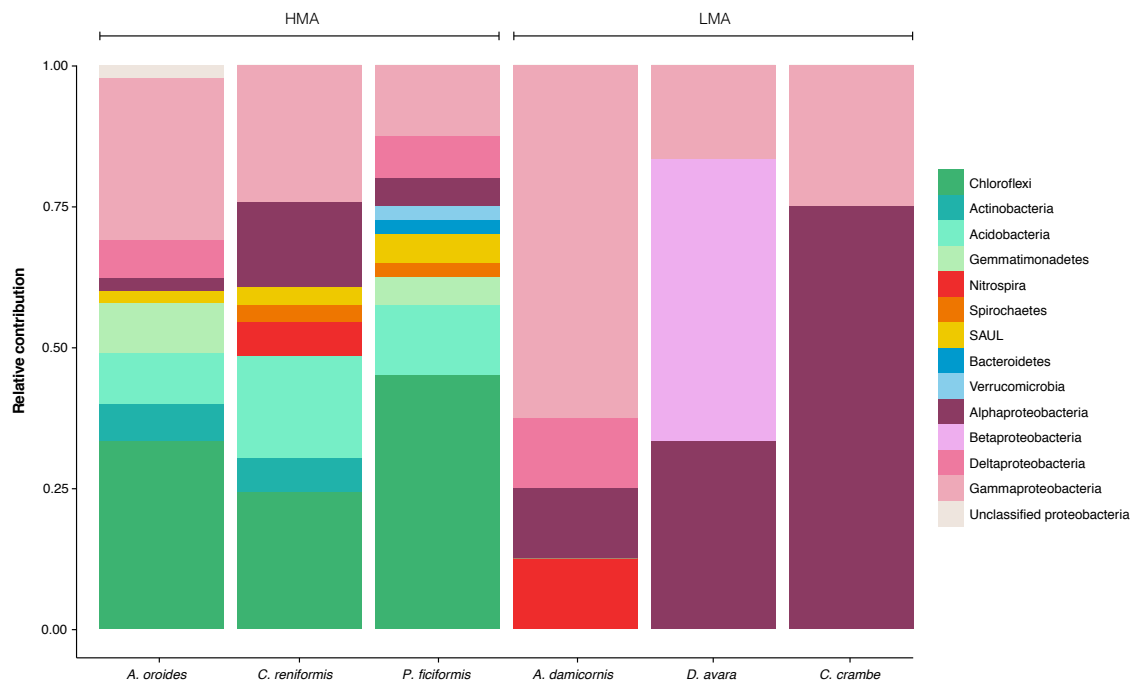


Figure 3: Taxonomic profiles of core microbiomes across host species and lifestyles (HMA vs. LMA). Taxonomic classification at the phylum level of core taxa and their relative contribution to diversity (species richness) for each core microbiome. The core microbiomes of HMA hosts harbored a larger taxonomic diversity than those of LMA hosts.

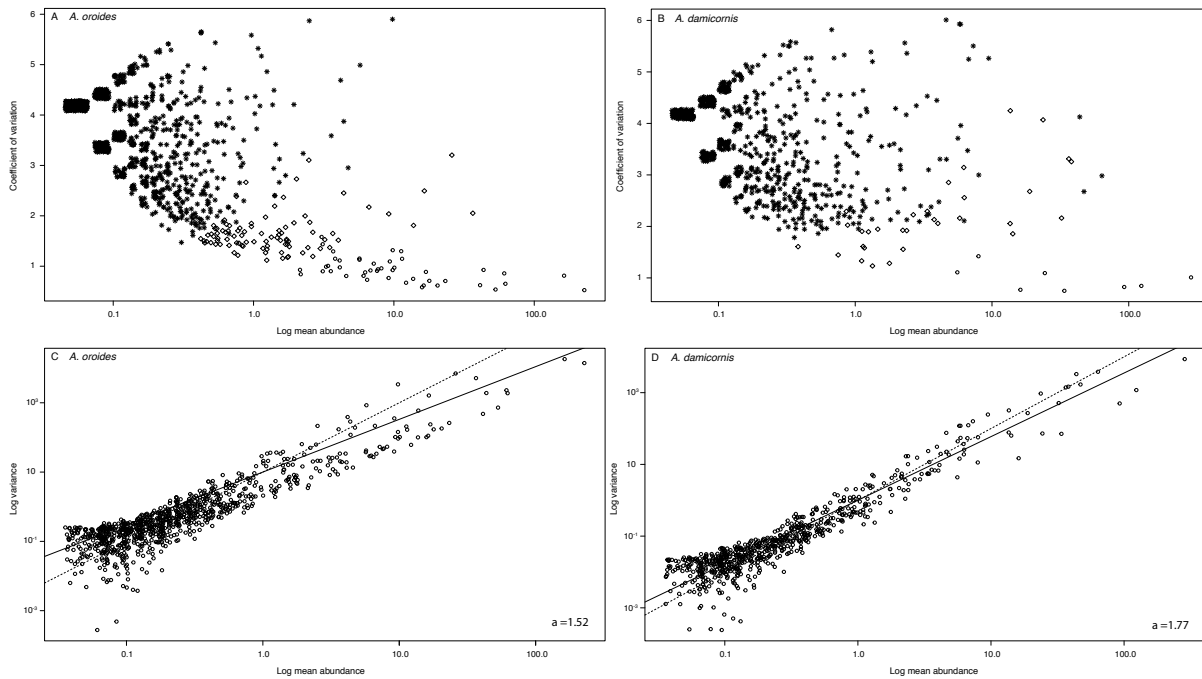


Figure 4: The top panel shows the relationship between temporal variability (CV) and mean log abundance for each taxon's abundance trajectory over time, for host (A) *A. oroides* and (B) *A. damicornis*. Overlaying points have been separated jitter (random noise). Opportunistic, transient and core taxa are represented by stars, diamonds and circles, respectively. Individual core and transient taxa are more stable (Kruskal-Wallis test: $H = 2198$, $df=2$, $P < 0.001$ two-tailed; Dunn's post-hoc test with bonferroni correction; $P < 0.001$) and abundant (Kruskal-Wallis test: $H = 1694$, $df=2$, $P < 0.001$; Dunn's post-hoc test with bonferroni correction; $P < 0.001$ two-tailed) than opportunistic taxa. The bottom panel shows the relationship between log variance and log mean abundance for each taxon's abundance trajectory over time (Taylor's power law), shown for host (C) *A. oroides* and (D) *A. damicornis*. Solid lines represent the null expectation of Taylor's power law, i.e., an exponent $a=2$, and the dashed lines correspond to the exponent of each host's microbiome: 1.52 for *A. oroides* and 1.77 for *A. damicornis*.

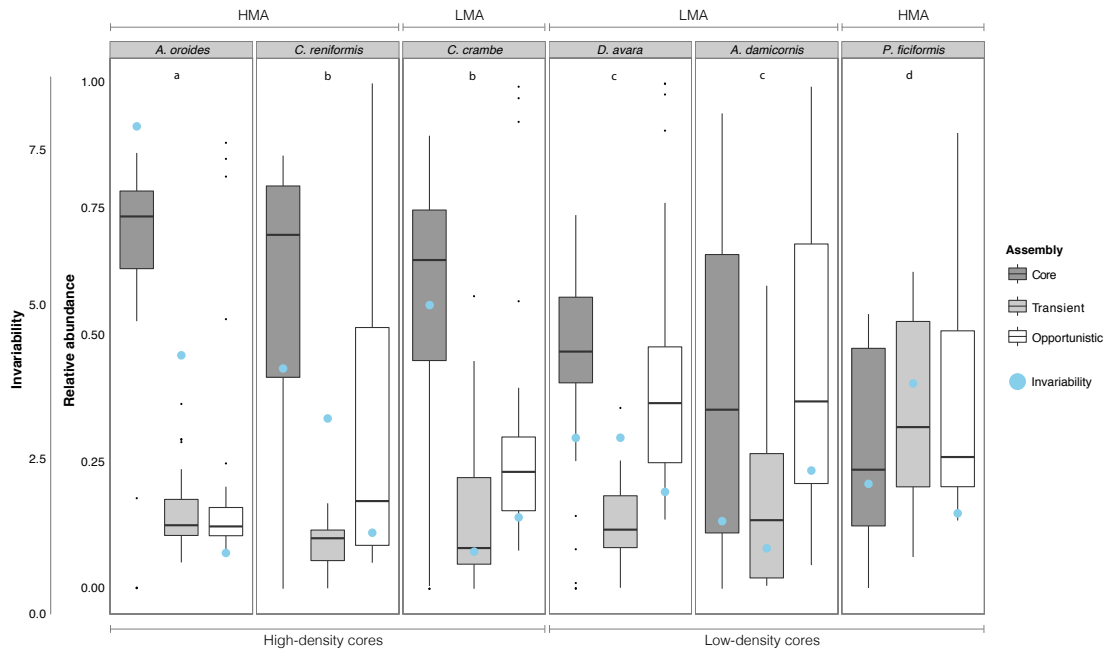


Figure 5: The contribution of each assemblage to microbiome abundance and its aggregated stability across hosts. The inner y-axis shows the contribution to microbiome relative abundance by each assemblage across host species. Each box shows the median including the first and third quartiles (the 25th and 75th percentiles), representing temporal variation. The outer y-axis shows invariability at the community level (blue dots) for each assemblage. The figure is ordered from the highest to the lowest in terms of core microbiome density. Lowercase letters denote different significant scenarios (see Table S2 for more detailed information): (a) The core microbiome was significantly different from the transient and opportunistic assemblages, but transient and opportunistic assemblages were not significantly different from each other; (b) All assemblages were significantly different; (c) The core microbiome and the opportunistic assemblage were not significantly different, but the core microbiome and transient assemblage, and the transient and the opportunistic assemblage were significantly different from each other; and finally (d) No significant differences between any of the assemblages. What emerged was three high-density (scenario a & b), and three low-density (scenario c & d) cores, respectively.

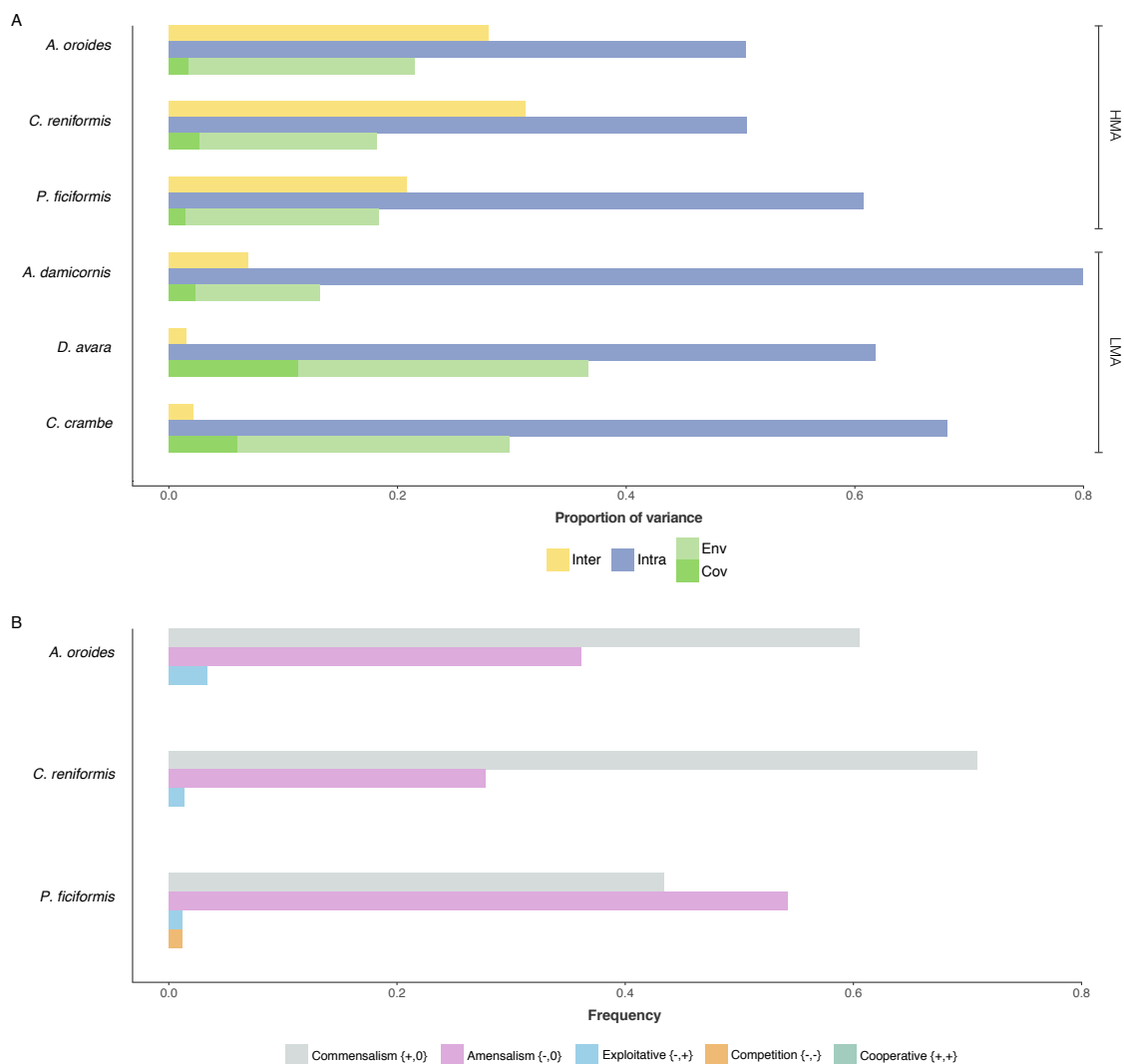


Figure 6: Processes explaining core microbiome dynamics and the frequency of all possible interaction types within HMA core microbiomes. Panel A shows the relative contribution of interspecific (yellow) and intraspecific (blue) interactions and environmental variability (greens) to temporal variation in microbial population abundances across core microbiomes. Environmental variability is decomposed into residual variation (light green, Env) and variation attributed to the modeled environmental covariates (dark green, Cov). In all hosts, core microbiome dynamics were mainly driven by intraspecific interactions. While the modeled environmental covariates explained relatively little variation across core microbiomes, an important driver of the dynamics in HMA cores was interspecific interactions which were almost negligible in LMA cores. Panel B shows the relative frequency of all inferred possible interaction types within HMA cores. This was calculated from the marginal sign posterior distribution of $\alpha_{i,j}$ (see *Methods*). Commensalism $\{+, 0\}$ and amensalism $\{-, 0\}$ were the most frequent interaction types across HMA cores. Competitive $\{-, -\}$ and exploitative $\{+, -\}$ interactions were exceptionally rare. Noteworthy, cooperative interactions $\{+, +\}$ was never inferred.

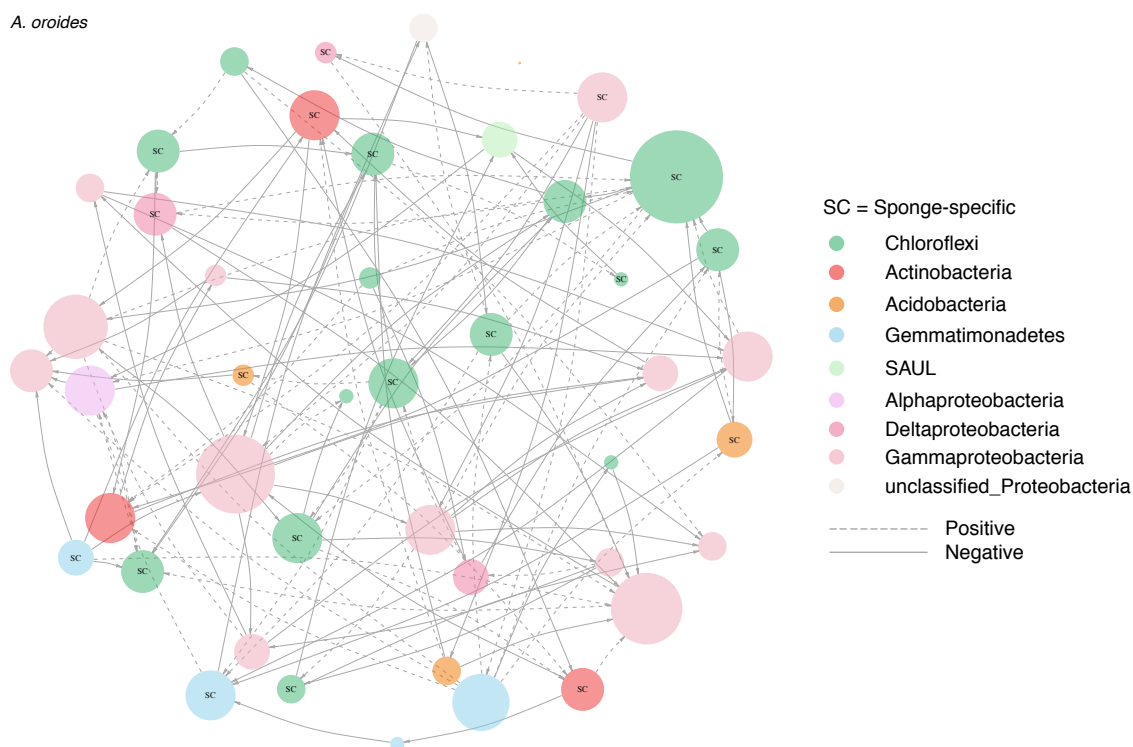


Figure 7: The most credible network structure for HMA host *A. oroides*'s core microbiome. Nodes represent core taxa and links their inferred ecological interactions. Node size is scaled to their degree (i.e. in and out-going links). Colors correspond to different bacterial phyla and dash and solid lines represent positive and negative interactions, respectively. Nodes marked with SC correspond to taxa that assigned to sponge-specific clusters. See Figure S10 for the corresponding link probabilities between OTU i and j , and Figure S9 for the networks belonging to the core microbiomes of HMA hosts *C. reniformis* and *P. ficiformis*. See *Methods* for how the networks were constructed.