



**HAL**  
open science

# The dynamic core microbiome: Structure, dynamics and stability

Johannes Björk, Robert O'hara, Marta Ribes, Rafel Coma, José Montoya

► **To cite this version:**

Johannes Björk, Robert O'hara, Marta Ribes, Rafel Coma, José Montoya. The dynamic core microbiome: Structure, dynamics and stability. 2020. hal-03043059

**HAL Id: hal-03043059**

**<https://ut3-toulouseinp.hal.science/hal-03043059>**

Preprint submitted on 15 Dec 2020

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

# The dynamic core microbiome: Structure, dynamics and stability

Johannes R. Björk<sup>1,6\*</sup>, Robert B. O'Hara<sup>2,3</sup>, Marta Ribes<sup>4</sup>, Rafel Coma<sup>5</sup>, and José M. Montoya<sup>6</sup>

<sup>1</sup>University of Notre Dame, Notre Dame, United States

<sup>2</sup>Biodiversity and Climate Research Centre, Frankfurt, Germany

<sup>3</sup>Department of Mathematical Sciences, NTNU, Trondheim, Norway

<sup>4</sup>Institute of Marine Sciences (ICM-CSIC), Barcelona, Spain

<sup>5</sup>Centre d'Estudis Avançats de Blanes (CEAB-CSIC), Blanes, Spain

<sup>6</sup>Theoretical and Experimental Ecology Station, CNRS-University Paul Sabatier, Moulis, France

<sup>1\*</sup> *rbjork@nd.edu (Corresponding author)*

<sup>2</sup> *bob.ohara@ntnu.no*

<sup>3</sup> *mribes@icm.csic.es*

<sup>4</sup> *coma@ceab.csic.es*

<sup>5</sup> *josemaria.montoyateran@sete.cnrs.fr*

February 6, 2018

## 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  $\geq 26$  months), whereas opportunistic assemblages comprised taxa present in less than (or  
84 equal to) 30% of each time series (i.e., persisting  $\leq 11$  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 ( $0.83 \pm 0.17$ ), measured as Pielou's J over time, compared to the core microbiomes  
108 ( $0.64 \pm 0.25$ ).

## 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  $\sigma^2$ ) 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  $\mu$ 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  $\mu$  and variance  $\sigma^2$ , and analogously, let  $\mathcal{MVN}(\mu, \Sigma)$  denote a multivariate  
381 normal distribution with mean vector and covariance matrix  $\Sigma$ . 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  $\Sigma$  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  $\Sigma$  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  $\eta$  denote the latent variables and  $\lambda$  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  $\Sigma$  can be computed from  
 396 the factor loadings (Equation 9). The diagonal elements of the covariance matrix  $\Sigma$  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  $\sigma_i^2$  correspond to the residual variance (the diagonal elements of  $\Sigma$ , 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](#).

#### 438 Acknowledgements

439 JRB. was supported by an FPI Fellowship from the Spanish Government (BES-2011-049043), JMM. was supported by  
 440 the French Laboratory of Excellence Project ‘TULIP’ (ANR-10-LABX-41; ANR-11-IDEX-002-02) and by a Region

441 Midi-Pyrenees Project (CNRS 121090) and RC and MR were supported by a Spanish Government Project (CGL2013-  
442 43106-R) and by a grant from the Catalan Government (2014SGR1029).

### 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.

### 447 **References**

- 448 [1] Margaret McFall-Ngai et al. “Animals in a bacterial world, a new imperative for the life sciences”. In: *Pro-*  
449 *ceedings of the National Academy of Sciences* 110.9 (2013), pp. 3229–3236.
- 450 [2] Rosario Gil et al. “Extreme genome reduction in *Buchnera* spp.: toward the minimal genome needed for  
451 symbiotic life.” In: *Proceedings of the National Academy of Sciences of the United States of America* 99.7  
452 (2002), pp. 4454–4458.
- 453 [3] Spencer V. Nyholm and Margaret J. McFall-Ngai. “The winnowing: Establishing the squid-vibrio symbiosis”.  
454 In: *Nature Reviews Microbiology* 2.8 (2004), pp. 632–642.
- 455 [4] Matthias H. Tschöp, Philip Hugenholtz, and Christopher L. Karp. “Getting to the core of the gut microbiome.”  
456 In: *Nature biotechnology* 27.4 (2009), pp. 344–346.
- 457 [5] Peter J. Turnbaugh et al. “A core gut microbiome in obese and lean twins.” In: *Nature* 457.7228 (2009),  
458 pp. 480–484.
- 459 [6] Ashley Shade and Jo Handelsman. “Beyond the Venn diagram: the hunt for a core microbiome”. In: *Environ-*  
460 *mental Microbiology* 14.1 (2012), pp. 4–12. ISSN: 1462-2920. DOI: [10.1111/j.1462-2920.2011.](https://doi.org/10.1111/j.1462-2920.2011.02585.x)  
461 [02585.x](https://doi.org/10.1111/j.1462-2920.2011.02585.x).
- 462 [7] Susanne Schmitt, Ute Hentschel, and Michael W. Taylor. “Deep sequencing reveals diversity and community  
463 structure of complex microbiota in five Mediterranean sponges”. In: *Hydrobiologia* 687.1 (2012), pp. 341–  
464 351.
- 465 [8] Tracy D. Ainsworth et al. “The coral core microbiome identifies rare bacterial taxa as ubiquitous endosym-  
466 bionts”. In: *The ISME Journal* 9.10 (2015), pp. 2261–2274. ISSN: 1751-7362.

- 467 [9] Carmen Astudillo-García et al. “Evaluating the core microbiota in complex communities: A systematic inves-  
468 tigation”. In: *Environmental Microbiology* 19.4 (2017), pp. 1450–1462. ISSN: 1462-2920. DOI: [10.1111/  
469 1462-2920.13647](https://doi.org/10.1111/1462-2920.13647).
- 470 [10] Alejandra Hernandez-Agreda, Ruth D. Gates, and Tracy D. Ainsworth. “Defining the Core Microbiome in  
471 Corals’ Microbial Soup”. In: *Trends in Microbiology* 25.2 (2017), pp. 125–140. ISSN: 0966-842X. DOI: [10.  
472 1016/j.tim.2016.11.003](https://doi.org/10.1016/j.tim.2016.11.003).
- 473 [11] Johannes R. Björk et al. “Specificity and temporal dynamics of complex bacteria-sponge symbiotic interac-  
474 tions”. In: *Ecology* 94.12 (2013), pp. 2781–2791. DOI: [10.1890/13-0557.1](https://doi.org/10.1890/13-0557.1).
- 475 [12] Jeremiah J. Faith et al. “The long-term stability of the human gut microbiota.” In: *Science* 341.6141 (2013),  
476 p. 1237439.
- 477 [13] Gilberto E. Flores et al. “Temporal variability is a personalized feature of the human microbiome.” In: *Genome  
478 biology* 15.12 (2014), p. 531.
- 479 [14] June L. Round and Sarkis K. Mazmanian. “The gut microbiota shapes intestinal immune responses during  
480 health and disease”. In: *Nat Rev Immunol* 9.5 (2009), pp. 313–323. ISSN: 1474-1733. DOI: [10.1038/  
481 nri2515](https://doi.org/10.1038/nri2515).
- 482 [15] Jose U. Scher and Steven B. Abramson. “The microbiome and rheumatoid arthritis”. In: *Nat Rev Rheumatol*  
483 7.10 (2011), pp. 569–578. ISSN: 1759-4790. DOI: [10.1038/nrrheum.2011.121](https://doi.org/10.1038/nrrheum.2011.121).
- 484 [16] Junjie Qin et al. “A metagenome-wide association study of gut microbiota in type 2 diabetes”. In: *Nature*  
485 490.7418 (2012), pp. 55–60.
- 486 [17] Ruth E. Ley et al. “Microbial ecology: human gut microbes associated with obesity.” In: *Nature* 444.7122  
487 (2006), pp. 1022–3.
- 488 [18] Amber L. Hartman et al. “Human gut microbiome adopts an alternative state following small bowel trans-  
489 plantation”. In: *Proceedings of the National Academy of Sciences* 106.40 (2009), pp. 17187–17192. DOI:  
490 [10.1073/pnas.0904847106](https://doi.org/10.1073/pnas.0904847106).
- 491 [19] Catherine A. Lozupone et al. “Diversity, stability and resilience of the human gut microbiota”. In: *Nature*  
492 489.7415 (2012), pp. 220–230.
- 493 [20] David A Relman. “The human microbiome: ecosystem resilience and health”. In: *Nutr Rev* 70.Suppl 1 (2013),  
494 pp. 1–12.

- 495 [21] Ilseung Cho and Martin J. Blaser. “The human microbiome: at the interface of health and disease.” In: *Nature*  
496 *Reviews Genetics* 13.4 (2012), pp. 260–270.
- 497 [22] Bayan Missaghi et al. “Perturbation of the Human Microbiome as a Contributor to Inflammatory Bowel Dis-  
498 ease”. In: *Pathogens* 3.3 (2014), pp. 510–527.
- 499 [23] Jasper M De Goeij et al. “Surviving in a Marine Desert: The Sponge Loop Retains Resources Within Coral  
500 Reefs”. In: *Science* 342.October (2013), pp. 108–110.
- 501 [24] Martina Coppari et al. “The role of Mediterranean sponges in benthic–pelagic coupling processes: *Aplysina*  
502 *aerophoba* and *Axinella polypoides* case studies”. In: *Journal of Experimental Marine Biology and Ecology*  
503 477.April (2016), pp. 57–68.
- 504 [25] Torsten Thomas et al. “Diversity, structure and convergent evolution of the global sponge microbiome”. In:  
505 *Nature Communications* 7.11870 (2016).
- 506 [26] Paul Simion et al. “A Large and Consistent Phylogenomic Dataset Supports Sponges as the Sister Group to All  
507 Other Animals”. In: *Current Biology* (2017). ISSN: 0960-9822. DOI: [10.1016/j.cub.2017.02.031](https://doi.org/10.1016/j.cub.2017.02.031).
- 508 [27] Micheal W Taylor et al. “Sponge-associated microorganisms: evolution, ecology, and biotechnological poten-  
509 tial”. In: *Microbiology and Molecular Biology Reviews* 71.2 (2007), pp. 295–347.
- 510 [28] Ute Hentschel et al. “Genomic insights into the marine sponge microbiome”. In: *Nature Reviews Microbiology*  
511 10.9 (2012), pp. 641–654.
- 512 [29] Zongjun Yin et al. “Sponge grade body fossil with cellular resolution dating 60 Myr before the Cambrian”.  
513 In: *Proceedings of the National Academy of Sciences* 112.12 (2015), E1453–E1460. DOI: [10.1073/pnas.](https://doi.org/10.1073/pnas.1414577112)  
514 [1414577112](https://doi.org/1414577112).
- 515 [30] Jeremy B. Weisz, Niels Lindquist, and Christopher S. Martens. “Do associated microbial abundances impact  
516 marine demosponge pumping rates and tissue densities?” In: *Oecologia* 155.2 (2008), pp. 367–376.
- 517 [31] Marie Lise Schläppy et al. “Evidence of nitrification and denitrification in high and low microbial abundance  
518 sponges”. In: *Marine Biology* 157.3 (2010), pp. 593–602.
- 519 [32] Eroteida Jiménez and Marta Ribes. “Sponges as a source of dissolved inorganic nitrogen: Nitrification medi-  
520 ated by temperate sponges”. In: *Limnology and Oceanography* 52.3 (2007), pp. 948–958. ISSN: 1939-5590.  
521 DOI: [10.4319/lo.2007.52.3.0948](https://doi.org/10.4319/lo.2007.52.3.0948).

- 522 [33] Christopher J. Freeman and Robert W. Thacker. “Complex interactions between marine sponges and their  
523 symbiotic microbial communities”. In: *Limnology and Oceanography* 56.5 (2011), pp. 1577–1586.
- 524 [34] Manuel Maldonado, Marta Ribes, and Duyl van Fleur C. “Chapter three - Nutrient Fluxes Through Sponges:  
525 Biology, Budgets, and Ecological Implications”. In: *Advances in Sponge Science: Physiology, Chemical and  
526 Microbial Diversity, Biotechnology*. Vol. 62. Advances in Marine Biology. Academic Press, 2012, pp. 113–  
527 182. DOI: <https://doi.org/10.1016/B978-0-12-394283-8.00003-5>.
- 528 [35] Marta Ribes et al. “Functional convergence of microbes associated with temperate marine sponges”. In: *Envi-  
529 ronmental Microbiology* 14.5 (2012), pp. 1224–1239. ISSN: 1462-2920. DOI: [10.1111/j.1462-2920.  
530 2012.02701.x](https://doi.org/10.1111/j.1462-2920.2012.02701.x).
- 531 [36] Christopher J. Freeman et al. “Quality or quantity: is nutrient transfer driven more by symbiont identity and  
532 productivity than by symbiont abundance?” In: *The ISME Journal* 7.6 (2013), pp. 1116–25.
- 533 [37] Christopher J. Freeman, Cole G. Easson, and David M. Baker. “Metabolic diversity and niche structure in  
534 sponges from the Miskito Cays, Honduras.” In: *PeerJ* 2 (2014), e695.
- 535 [38] Ericka Poppell et al. “Sponge heterotrophic capacity and bacterial community structure in high- and low-  
536 microbial abundance sponges”. In: *Marine Ecology* 35.4 (2014), pp. 414–424.
- 537 [39] Volker Gloeckner et al. “The HMA-LMA Dichotomy Revisited: an Electron Microscopical Survey of 56  
538 Sponge Species.” In: *The Biological bulletin* 227.1 (2014), pp. 78–88.
- 539 [40] Patrick M. Erwin et al. “Stable symbionts across the HMA-LMA dichotomy: low seasonal and interannual  
540 variation in sponge-associated bacteria from taxonomically diverse hosts”. In: *FEMS Microbiology Ecology*  
541 91.910 (2015), fiv115.
- 542 [41] J. P. Grime. “Benefits of plant diversity to ecosystems: immediate, filter and founder effects.” In: *Journal of  
543 Ecology* 86 (1998), pp. 902–910.
- 544 [42] Anne E Magurran and Peter A Henderson. “Explaining the excess of rare species in natural species abundance  
545 distributions”. In: *Nature* 422. April (2003), pp. 714–716.
- 546 [43] Brian J. McGill et al. “Species abundance distributions: Moving beyond single prediction theories to integra-  
547 tion within an ecological framework”. In: *Ecology Letters* 10.10 (2007), pp. 995–1015.

- 548 [44] Melinda D. Smith and Alan K. Knapp. “Dominant species maintain ecosystem function with non-random  
549 species loss”. In: *Ecology Letters* 6.6 (2003), pp. 509–517. ISSN: 1461-0248. DOI: [10.1046/j.1461-  
550 0248.2003.00454.x](https://doi.org/10.1046/j.1461-0248.2003.00454.x).
- 551 [45] Kevin J. Gaston and Richard A. Fuller. “Commonness, population depletion and conservation biology”. In:  
552 *Trends in Ecology & Evolution* 23.1 (2008), pp. 14–19. DOI: [https://doi.org/10.1016/j.tree.  
553 2007.11.001](https://doi.org/10.1016/j.tree.2007.11.001).
- 554 [46] Rachael Winfree et al. “Abundance of common species, not species richness, drives delivery of a real-world  
555 ecosystem service”. In: *Ecology Letters* 18.7 (2015), pp. 626–635. ISSN: 1461-0248. DOI: [10.1111/ele.  
556 12424](https://doi.org/10.1111/ele.12424).
- 557 [47] Hideyasu Shimadzu, Maria Dornelas, and Anne E. Magurran. “Measuring temporal turnover in ecological  
558 communities”. In: *Methods in Ecology and Evolution* 6.12 (2015), pp. 1384–1394. ISSN: 2041-210X. DOI:  
559 [10.1111/2041-210X.12438](https://doi.org/10.1111/2041-210X.12438).
- 560 [48] Ute Hentschel et al. “Molecular Evidence for a Uniform Microbial Community in Sponges from Different  
561 Oceans Molecular Evidence for a Uniform Microbial Community in Sponges from Different Oceans”. In:  
562 *Applied and Environmental Microbiology* 68.9 (2002), pp. 4431–4440.
- 563 [49] Rachel L. Simister et al. “Sponge-specific clusters revisited: A comprehensive phylogeny of sponge-associated  
564 microorganisms”. In: *Environmental Microbiology* 14.2 (2012), pp. 517–524.
- 565 [50] Michael W. Taylor et al. “‘Sponge-specific’ bacteria are widespread (but rare) in diverse marine environments”.  
566 In: *The ISME Journal* 7 (2013), pp. 438–443.
- 567 [51] Robert W Thacker and Christopher J. Freeman. “Chapter two - Sponge–Microbe Symbioses: Recent Ad-  
568 vances and New Directions”. In: *Advances in Sponge Science: Physiology, Chemical and Microbial Diversity,  
569 Biotechnology*. Vol. 62. Advances in Marine Biology. Academic Press, 2012, pp. 57–111. DOI: [https :  
570 //doi.org/10.1016/B978-0-12-394283-8.00002-3](https://doi.org/10.1016/B978-0-12-394283-8.00002-3).
- 571 [52] C. R. Wilkinson. “Microbial associations in sponges. III. Ultrastructure of the in situ associations in coral reef  
572 sponges”. In: *Marine Biology* 49.2 (1978), pp. 177–185.
- 573 [53] Markus Wehrl, Michael Steinert, and Ute Hentschel. “Bacterial uptake by the marine sponge *Aplysina aereo-*  
574 *phoba*”. In: *Microbial Ecology* 53.2 (2007), pp. 355–365.



- 575 [54] Matthias Wiens et al. “Toll-like receptors are part of the innate immune defense system of sponges (Demo-  
576 spongiae: Porifera)”. In: *Molecular Biology and Evolution* 24.3 (2007), pp. 792–804.
- 577 [55] Torsten Thomas et al. “Functional genomic signatures of sponge bacteria reveal unique and shared features of  
578 symbiosis.” In: *The ISME Journal* 4.12 (2010), pp. 1557–1567.
- 579 [56] Benedict Yuen, Joanne M. Bayes, and Sandie M. Degnan. “The characterization of sponge nlr provides in-  
580 sight into the origin and evolution of this innate immune gene family in animals”. In: *Molecular Biology and*  
581 *Evolution* 31.1 (2014), pp. 106–120.
- 582 [57] Sandie M. Degnan. “The surprisingly complex immune gene repertoire of a simple sponge, exemplified by  
583 the NLR genes: A capacity for specificity?” In: *Developmental and Comparative Immunology* 48.2 (2015),  
584 pp. 269–274.
- 585 [58] Nicole S. Webster et al. “Deep sequencing reveals exceptional diversity and modes of transmission for bacterial  
586 sponge symbionts”. In: *Environmental Microbiology* 12.8 (2010), pp. 2070–2082.
- 587 [59] Ashley Shade and Jack A. Gilbert. “Temporal patterns of rarity provide a more complete view of microbial  
588 diversity”. In: *Trends in Microbiology* (2015), pp. 1–6.
- 589 [60] Sean R. Connolly et al. “Commonness and rarity in the marine biosphere”. In: *Proceedings of the National*  
590 *Academy of Sciences* 111.23 (2014), pp. 8524–8529. DOI: [10.1073/pnas.1406664111](https://doi.org/10.1073/pnas.1406664111)
- 591 [61] Ilkka Hanski. “Density Dependence, Regulation and Variability in Animal Populations”. In: 330.1257 (1990),  
592 pp. 141–150. ISSN: 09628436.
- 593 [62] Peter A Henderson and Anne E Magurran. “Direct evidence that density-dependent regulation underpins the  
594 temporal stability of abundant species in a diverse animal community”. In: *Proceedings of the Royal Society*  
595 *B: Biological Sciences* 281.1791 (2014), pp. 20141336–20141336.
- 596 [63] L. R. Taylor. “Aggregation, Variance and the Mean”. In: *Nature* 189 (1961), pp. 732–735. URL: [http:](http://dx.doi.org/10.1038/189732a0)  
597 [//dx.doi.org/10.1038/189732a0](http://dx.doi.org/10.1038/189732a0).
- 598 [64] R. M. Anderson et al. “Variability in the abundance of animal and plant species”. In: *Nature* 296 (1982),  
599 pp. 245–248.
- 600 [65] A. M. Kilpatrick and A. R. Ives. “Species interactions can explain Taylor’s power law for ecological time  
601 series”. In: *Nature* 422 (2003), pp. 65–68.

- 602 [66] Bart Haegeman et al. “Resilience, invariability, and ecological stability across levels of organization”. In:  
603 *bioRxiv* (2016). DOI: [10.1101/085852](https://doi.org/10.1101/085852).
- 604 [67] Wayne Polley H., Brian J. Wilsey, and Justin D. Derner. “Dominant species constrain effects of species di-  
605 versity on temporal variability in biomass production of tallgrass prairie”. In: *Oikos* 116.12 (2007), pp. 2044–  
606 2052. DOI: [10.1111/j.2007.0030-1299.16080.x](https://doi.org/10.1111/j.2007.0030-1299.16080.x).
- 607 [68] Takehiro Sasaki and William K. Lauenroth. “Dominant species, rather than diversity, regulates temporal sta-  
608 bility of plant communities”. In: *Oecologia* 166.3 (2011), pp. 761–768. DOI: [10.1007/s00442-011-  
609 1916-1](https://doi.org/10.1007/s00442-011-1916-1).
- 610 [69] Zhiyuan Ma et al. “Climate warming reduces the temporal stability of plant community biomass production”.  
611 In: *Nature Communications* 8 (2017), p. 15378.
- 612 [70] Teresa Morganti et al. “Trophic niche separation facilitates co-existence of high and low microbial abundance  
613 sponges is revealed by in situ study of carbon and nitrogen fluxes”. In: *Limnology and Oceanography* (In  
614 press).
- 615 [71] Crispin M. Mutshinda, Robert B. O’Hara, and Ian P. Woiwod. “A multispecies perspective on ecological  
616 impacts of climatic forcing”. In: *Journal of Animal Ecology* 80.1 (2011), pp. 101–107.
- 617 [72] Pablo Almaraz and Daniel Oro. “Size-mediated non-trophic interactions and stochastic predation drive assem-  
618 bly and dynamics in a seabird community”. In: *Ecology* 92.10 (2011), pp. 1948–1958.
- 619 [73] Carlos Martorell and Robert P. Freckleton. “Testing the roles of competition, facilitation and stochasticity on  
620 community structure in a species-rich assemblage”. In: *Journal of Ecology* 102.1 (2014), pp. 74–85.
- 621 [74] Elizabeth E. Crone. “Contrasting effects of spatial heterogeneity and environmental stochasticity on population  
622 dynamics of a perennial wildflower”. In: *Journal of Ecology* 104.2 (2016), pp. 281–291. ISSN: 1365-2745. DOI:  
623 [10.1111/1365-2745.12500](https://doi.org/10.1111/1365-2745.12500).
- 624 [75] Jack A. Gilbert et al. “Defining seasonal marine microbial community dynamics”. In: *The Isme Journal* 6  
625 (2011), pp. 298–308.
- 626 [76] Jed A. Fuhrman, Jacob A. Cram, and David M. Needham. “Marine microbial community dynamics and their  
627 ecological interpretation”. In: *Nature Reviews Microbiology* 13 (2015). Review Article, pp. 133–146. DOI:  
628 <http://dx.doi.org/10.1038/nrmicro3417>.

- 629 [77] Carina Bunse and Jarone Pinhassi. “Marine Bacterioplankton Seasonal Succession Dynamics”. In: *Trends in*  
630 *Microbiology* 25.6 (2017), pp. 494–505. DOI: <https://doi.org/10.1016/j.tim.2016.12.013>.
- 631 [78] György Barabás, Matthew J. Michalska-Smith, and Stefano Allesina. “Self-regulation and the stability of  
632 large ecological networks”. In: *Nature Ecology & Evolution* 1.12 (2017), pp. 1870–1875. DOI: [10.1038/  
633 s41559-017-0357-6](https://doi.org/10.1038/s41559-017-0357-6).
- 634 [79] Katharine Z. Coyte, Jonas Schluter, and Kevin R. Foster. “The ecology of the microbiome: Networks, competi-  
635 tion, and stability”. In: *Science* 350.6261 (2015), pp. 663–666. ISSN: 0036-8075. DOI: [10.1126/science.  
636 aad2602](https://doi.org/10.1126/science.aad2602).
- 637 [80] Akihiko Mougi and Michio Kondoh. “Food-web complexity, meta-community complexity and community  
638 stability”. In: *Scientific Reports* 6.24478 (2016). DOI: [http://doi.org/10.1038/srep24478](https://doi.org/10.1038/srep24478).
- 639 [81] R. T. Paine. “Food-web analysis through field measurement of per capita interaction strength”. In: *Nature*  
640 355.6355 (1992), pp. 73–75. DOI: [10.1038/355073a0](https://doi.org/10.1038/355073a0). URL: [http://dx.doi.org/10.1038/  
641 355073a0](http://dx.doi.org/10.1038/355073a0).
- 642 [82] Mark C. Emmerson and Dave Raffaelli. “Predator-prey body size, interaction strength and the stability of a  
643 real food web”. In: *Journal of Animal Ecology* 73.3 (2004), pp. 399–409.
- 644 [83] Diego P. Vazquez et al. “The strength of plant–pollinator interactions”. In: *Ecology* 93.4 (2012), pp. 719–725.
- 645 [84] Kevin McCann, Alan Hastings, and Gary R Huxel. “Weak trophic interactions and the balance of nature”. In:  
646 *Nature* 395.6704 (1998), pp. 794–798.
- 647 [85] Stefano Allesina and Si Tang. “Stability criteria for complex ecosystems”. In: *Nature* 483.7388 (2012), pp. 205–  
648 208. DOI: [10.1038/nature10832](https://doi.org/10.1038/nature10832).
- 649 [86] Akihiko Mougi and Michio Kondoh. “Diversity of Interaction Types and Ecological Community Stability”.  
650 In: *Science* 337.6092 (2012), pp. 349–351.
- 651 [87] Akihiko Mougi and Michio Kondoh. “Stability of competition–antagonism–mutualism hybrid community and  
652 the role of community network structure”. In: *Journal of Theoretical Biology* 360 (2014), pp. 54–58. ISSN:  
653 0022-5193. DOI: [http://dx.doi.org/10.1016/j.jtbi.2014.06.030](https://dx.doi.org/10.1016/j.jtbi.2014.06.030).
- 654 [88] Akihiko Mougi and Michio Kondoh. “Adaptation in a hybrid world with multiple interaction types: a new  
655 mechanism for species coexistence”. In: *Ecological Research* 29.2 (2014), pp. 113–119. ISSN: 1440-1703.  
656 DOI: [10.1007/s11284-013-1111-4](https://doi.org/10.1007/s11284-013-1111-4).

- 657 [89] Miguel Lurgi, Daniel Montoya, and Jose M. Montoya. “The effects of space and diversity of interaction types  
658 on the stability of complex ecological networks”. In: *Theoretical Ecology* 9.1 (2016), pp. 3–13. ISSN: 1874-  
659 1746. DOI: [10.1007/s12080-015-0264-x](https://doi.org/10.1007/s12080-015-0264-x).
- 660 [90] Alix M.C. Sauve, Colin Fontaine, and Elisa Thébault. “Structure-stability relationships in networks combining  
661 mutualistic and antagonistic interactions”. In: *Oikos* 123.3 (2014), pp. 378–384.
- 662 [91] C. Levi and P. Levi. “Embryogenesis of *Chondrosia reniformis* (Nardo), demosponge ovipare, et transmission  
663 des bactéries symbiotiques”. In: *Ann Sci Nat Zool* 18 (1976), pp. 367–380.
- 664 [92] María J. Uriz, Turon Xavier, and Becerro Mikel A. “Morphology and Ultrastructure of the Swimming Larvae  
665 of *Crambe crambe* (Demospongiae, Poecilosclerida)”. In: *Invertebrate Biology* 120.4 (2001), pp. 295–307.
- 666 [93] Susanne Schmitt et al. “Molecular microbial diversity survey of sponge reproductive stages and mechanistic  
667 insights into vertical transmission of microbial symbionts”. In: *Applied and Environmental Microbiology* 74.24  
668 (2008), pp. 7694–7708.
- 669 [94] E. Lepore et al. “The ultrastructure of the mature oocyte and the nurse cells of the ceractinomorpha *Petrosia*  
670 *ficiformis*”. In: *Cahiers De Biologie Marine* 36 (1995), pp. 15–20.
- 671 [95] Ana Riesgo and Manuel Maldonado. “Differences in reproductive timing among sponges sharing habitat and  
672 thermal regime”. In: *Invertebrate Biology* 127.4 (2008), pp. 357–367.
- 673 [96] Manuel Maldonado and Ana Riesgo. “Gametogenesis, embryogenesis, and larval features of the oviparous  
674 sponge *Petrosia ficiformis* (Haplosclerida, Demospongiae)”. In: *Marine Biology* 156.10 (2009), pp. 2181–  
675 2197.
- 676 [97] John N. Thompson. *The geographic mosaic of coevolution*. University of Chicago Press, 2005.
- 677 [98] Jonathan M. Chase. “Stochastic community assembly causes higher biodiversity in more productive environ-  
678 ments.” In: *Science* 328.5984 (2010), pp. 1388–91.
- 679 [99] Fukami Tadashi. “Historical Contingency in Community Assembly: Integrating Niches, Species Pools, and  
680 Priority Effects”. In: *Annual Review of Ecology, Evolution, and Systematics* 46.1 (2015), pp. 1–23.
- 681 [100] Daniel Sprockett, Tadashi Fukami, and David A. Relman. “Role of priority effects in the early-life assembly  
682 of the gut microbiota”. In: *Nature Reviews Gastroenterology and Hepatology* (2018), pp. 1–9.
- 683 [101] Teresa Nogueira et al. “Horizontal Gene Transfer of the Secretome Drives the Evolution of Bacterial Cooper-  
684 ation and Virulence”. In: *Current Biology* 19.20 (2009), pp. 1683–1691.

- 685 [102] Luke McNally, Mafalda Viana, and Sam P. Brown. “Cooperative secretions facilitate host range expansion in  
686 bacteria.” In: *Nature communications* 5 (2014), p. 4594.
- 687 [103] A. Li et al. “The fundamental advantages of temporal networks”. In: *Science* 358.6366 (2017), pp. 1042–1046.  
688 DOI: [10.1126/science.aai7488](https://doi.org/10.1126/science.aai7488)
- 689 [104] Gregory J. Caporaso et al. “Global patterns of 16S rRNA diversity at a depth of millions of sequences per  
690 sample.” In: *Proceedings of the National Academy of Sciences of the United States of America* 108 (2011),  
691 pp. 4516–22. eprint: [arXiv:1408.1149](https://arxiv.org/abs/1408.1149).
- 692 [105] Fredrik Backhed et al. “Dynamics and stabilization of the human gut microbiome during the first year of life”.  
693 In: *Cell Host and Microbe* 17.5 (2015), pp. 690–703.
- 694 [106] D. W. Pitta et al. “Temporal dynamics in the ruminal microbiome of dairy cows during the transition period”.  
695 In: *Journal of Animal Science* 92.9 (2014), pp. 4014–4022.
- 696 [107] Tiantian Ren et al. “Seasonal, spatial, and maternal effects on gut microbiome in wild red squirrels”. In:  
697 *Microbiome* 5.1 (2017), p. 163. DOI: [10.1186/s40168-017-0382-3](https://doi.org/10.1186/s40168-017-0382-3).
- 698 [108] Peter J Turnbaugh et al. “The human microbiome project: exploring the microbial part of ourselves in a chang-  
699 ing world”. In: *Nature* 449.7164 (2007), pp. 804–810. DOI: [10.1038/nature06244](https://doi.org/10.1038/nature06244).
- 700 [109] Helmut Hillebrand et al. “Decomposing multiple dimensions of stability in global change experiments”. In:  
701 *Ecology Letters* 21.1 (2018), pp. 21–30. ISSN: 1461-0248. DOI: [10.1111/ele.12867](https://doi.org/10.1111/ele.12867).
- 702 [110] Sean D. Connell and Giulia Ghedini. “Resisting regime-shifts: the stabilising effect of compensatory pro-  
703 cesses”. In: *Trends in Ecology & Evolution* 30.9 (2015), pp. 513–515. DOI: [https://doi.org/10.](https://doi.org/10.1016/j.tree.2015.06.014)  
704 [1016/j.tree.2015.06.014](https://doi.org/10.1016/j.tree.2015.06.014).
- 705 [111] Patrick D. Schloss et al. “Introducing mothur: Open-source, platform-independent, community-supported soft-  
706 ware for describing and comparing microbial communities”. In: *Applied and Environmental Microbiology*  
707 75.23 (2009), pp. 7537–7541.
- 708 [112] Crispin M. Mutshinda, Robert B. O’Hara, and Ian P. Woiwod. “What drives community dynamics?” In: *Pro-*  
709 *ceedings of the Royal Society B* 276.1669 (2009), pp. 2923–2929.
- 710 [113] Richard R. Stein et al. “Ecological Modeling from Time-Series Inference: Insight into Dynamics and Stability  
711 of Intestinal Microbiota”. In: *PLoS Computational Biology* 9.12 (2013), pp. 31–36.

- 712 [114] Robert B. O’Hara and Mikko J. Sillanpää. “A review of bayesian variable selection methods: What, how and  
713 which”. In: *Bayesian Analysis* 4.1 (2009), pp. 85–118.
- 714 [115] David I. Warton et al. “So Many Variables: Joint Modeling in Community Ecology”. In: *Trends in Ecology  
715 and Evolution* 30 (2015), pp. 1–14.
- 716 [116] Hongzhe Li. “Microbiome, Metagenomics, and High-Dimensional Compositional Data Analysis”. In: *Annual  
717 Review of Statistics and Its Application* 2.1 (2015), pp. 73–94. DOI: [10.1146/annurev-statistics-  
718 010814-020351](https://doi.org/10.1146/annurev-statistics-010814-020351).
- 719 [117] Matthew C.B. Tsilimigras and Anthony A. Fodor. “Compositional data analysis of the microbiome: funda-  
720 mentals, tools, and challenges”. In: *Annals of Epidemiology* 26.5 (2016), pp. 330–335. DOI: [https://doi.  
721 org/10.1016/j.annepidem.2016.03.002](https://doi.org/10.1016/j.annepidem.2016.03.002).
- 722 [118] Gregory B. Gloor et al. “Microbiome Datasets Are Compositional: And This Is Not Optional”. In: *Frontiers  
723 in Microbiology* 8 (2017), p. 2224. DOI: [10.3389/fmicb.2017.02224](https://doi.org/10.3389/fmicb.2017.02224).
- 724 [119] Stuart G. Baker. “The Multinomial-Poisson Transformation”. In: 43.4 (1994), pp. 495–504. DOI: [10.2307/  
725 2348134](https://doi.org/10.2307/2348134). URL: <http://www.jstor.org/stable/2348134>.
- 726 [120] A. Skrondal and S. Rabe-Hesketh. *Generalized Latent Variable Modeling: Multilevel, Longitudinal, and Struc-  
727 tural Equation Models*. Chapman & Hall/CRC Interdisciplinary Statistics. CRC Press, 2004. ISBN: 9780203489437.  
728 URL: <https://books.google.com/books?id=YUpDqCzb-WMC>.
- 729 [121] Martyn Plummer. *JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling*. 2003.
- 730 [122] R Core Team. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Com-  
731 puting. Vienna, Austria, 2016. URL: <https://www.R-project.org/>.
- 732 [123] M. J. Denwood. “runjags: An R package providing interface utilities, model templates, parallel computing  
733 methods and additional distributions for MCMC models in JAGS”. In: *Journal of Statistical Software* (in  
734 press). URL: <http://runjags.sourceforge.net>.
- 735 [124] Martyn Plummer et al. “CODA: Convergence Diagnosis and Output Analysis for MCMC”. In: *R News* 6.1  
736 (2006), pp. 7–11.
- 737 [125] Curtis S. McKay. “Create Plots from MCMC Output”. In: *R News* (2015).
- 738 [126] John F. Geweke. *Evaluating the accuracy of sampling-based approaches to the calculation of posterior mo-  
739 ments*. Clarendon Press, Oxford, UK, 1991.

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

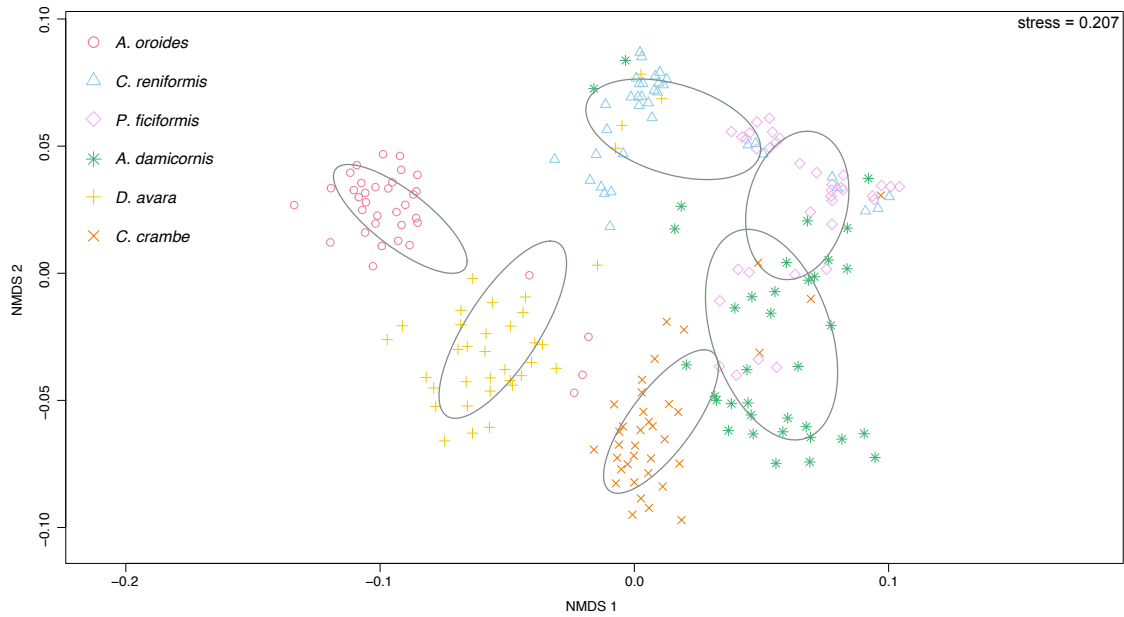


Figure 1: Microbiome compositional similarity across host species. Non-metric multidimensional scaling (NMDS) calculated on Jaccard distances among all 36 monthly samples for each host species ( $n=36 \times 6=216$ ). Colors and shapes denote all monthly samples from a given host species surrounded by 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 (x) *C. crambe*. ANOSIM:  $R=0.767$ ,  $P<0.001$



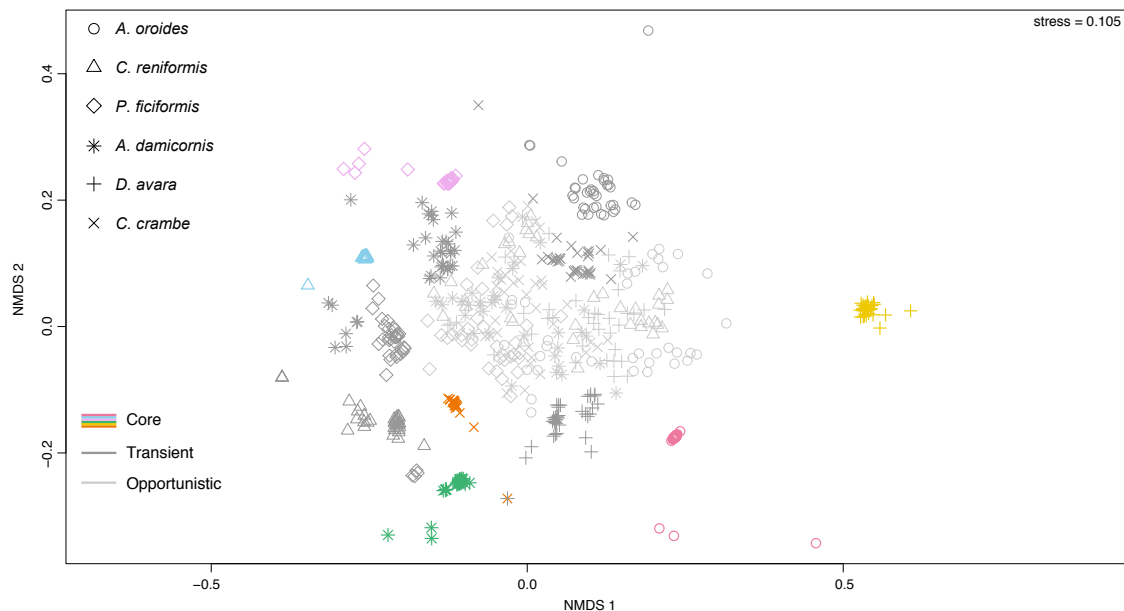


Figure 2: Microbiome compositional similarity across assemblages and host species. Non-metric multidimensional scaling (NMDS) calculated on Jaccard distances among all 36 monthly samples for each host and assemblage ( $n=36 \times 6 \times 3=648$ ). Colors and shapes denote all monthly samples from a 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.

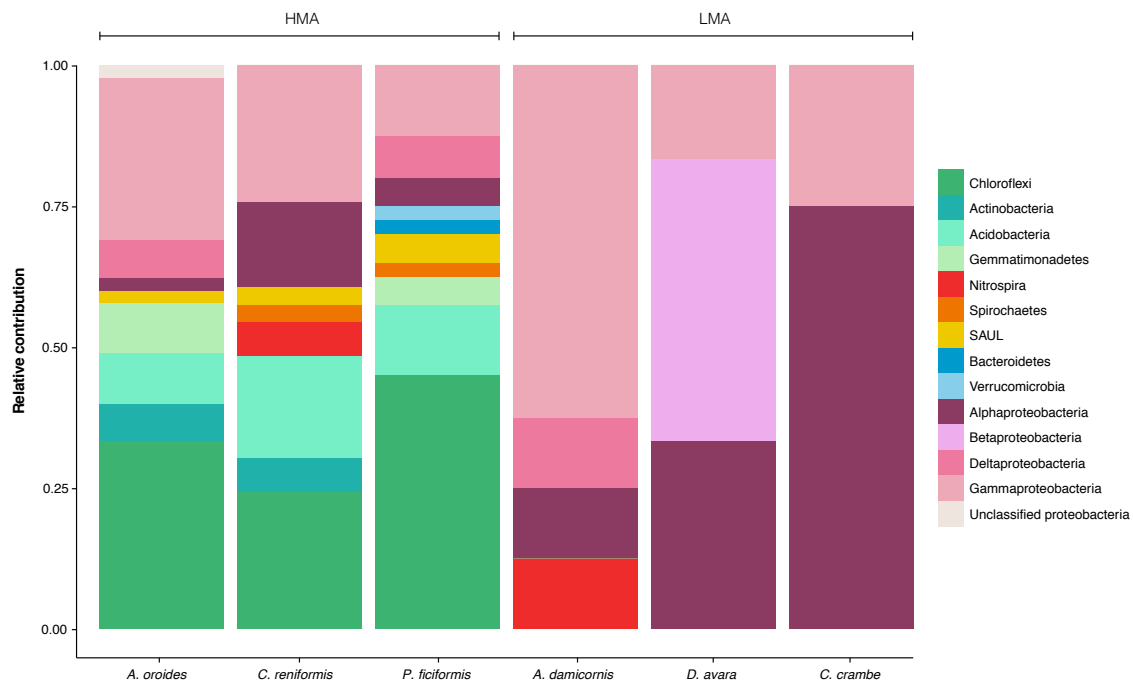


Figure 3: Taxonomic profiles of core microbiomes across host species and lifestyles (HMA vs. LMA). Taxonomic classification at the phylum level of core taxa and their relative contribution to diversity (species richness) for each core microbiome. The core microbiomes of HMA hosts harbored a larger taxonomic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

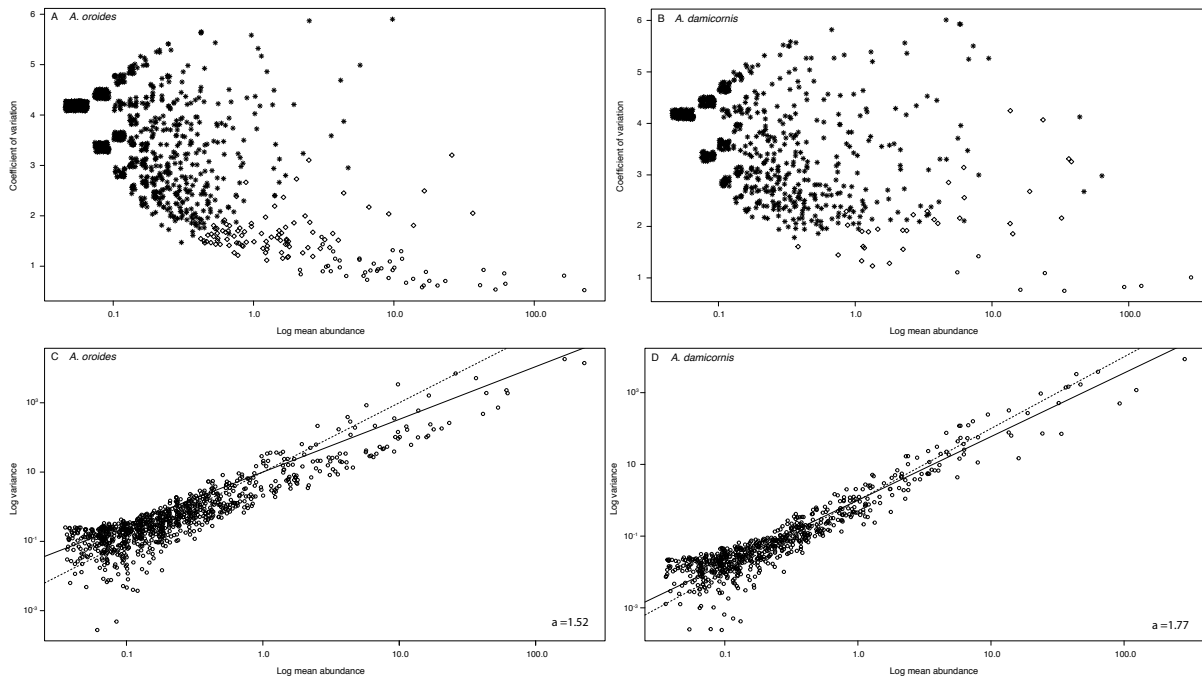


Figure 4: The top panel shows the relationship between temporal variability (CV) and mean log abundance for each taxon's abundance trajectory over time, for host (A) *A. oroides* and (B) *A. damicornis*. Overlaying points have been separated jitter (random noise). Opportunistic, transient and core taxa 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*.

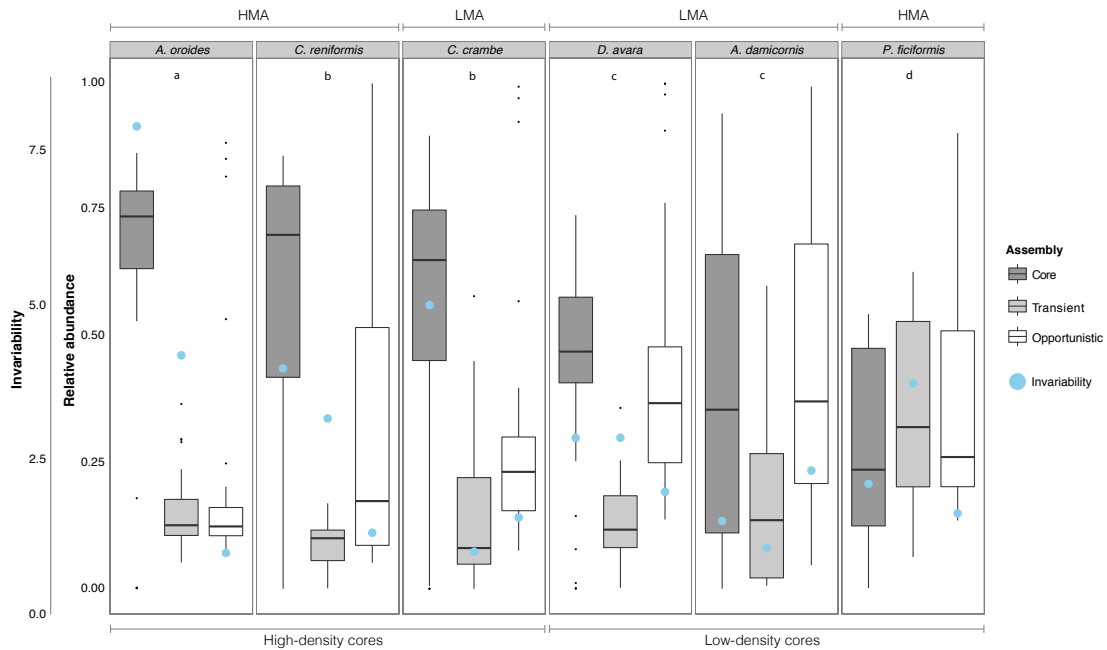


Figure 5: The contribution of each assemblage to microbiome abundance and its aggregated stability across hosts. The inner y-axis shows the contribution to microbiome relative abundance by each assemblage across host species. Each box shows the median including the first and third quartiles (the 25<sup>th</sup> and 75<sup>th</sup> 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.

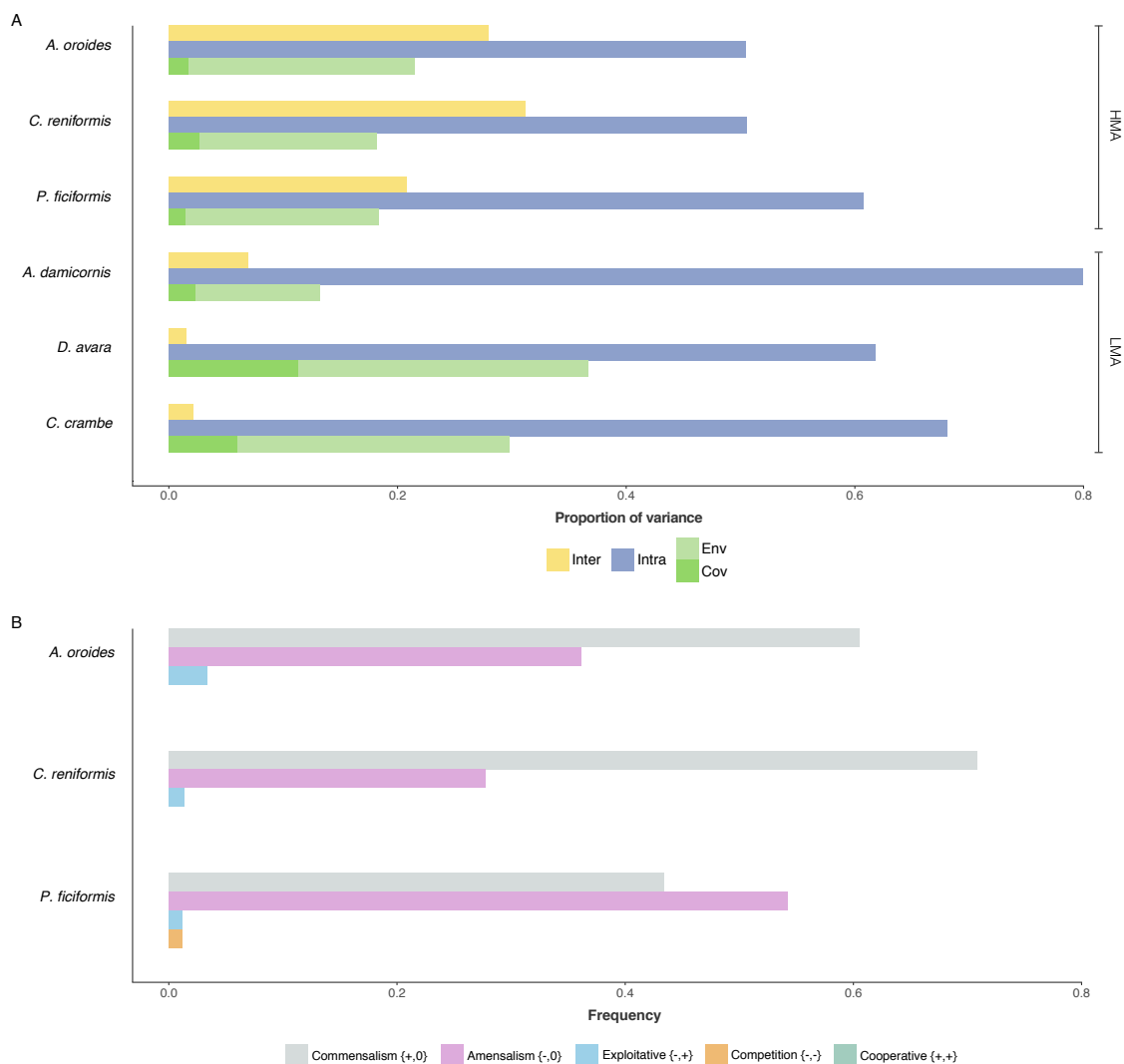


Figure 6: Processes explaining core microbiome dynamics and the frequency of all possible interaction types within HMA core microbiomes. Panel A shows the relative contribution of interspecific (yellow) and intraspecific (blue) interactions and environmental variability (greens) to temporal variation 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.

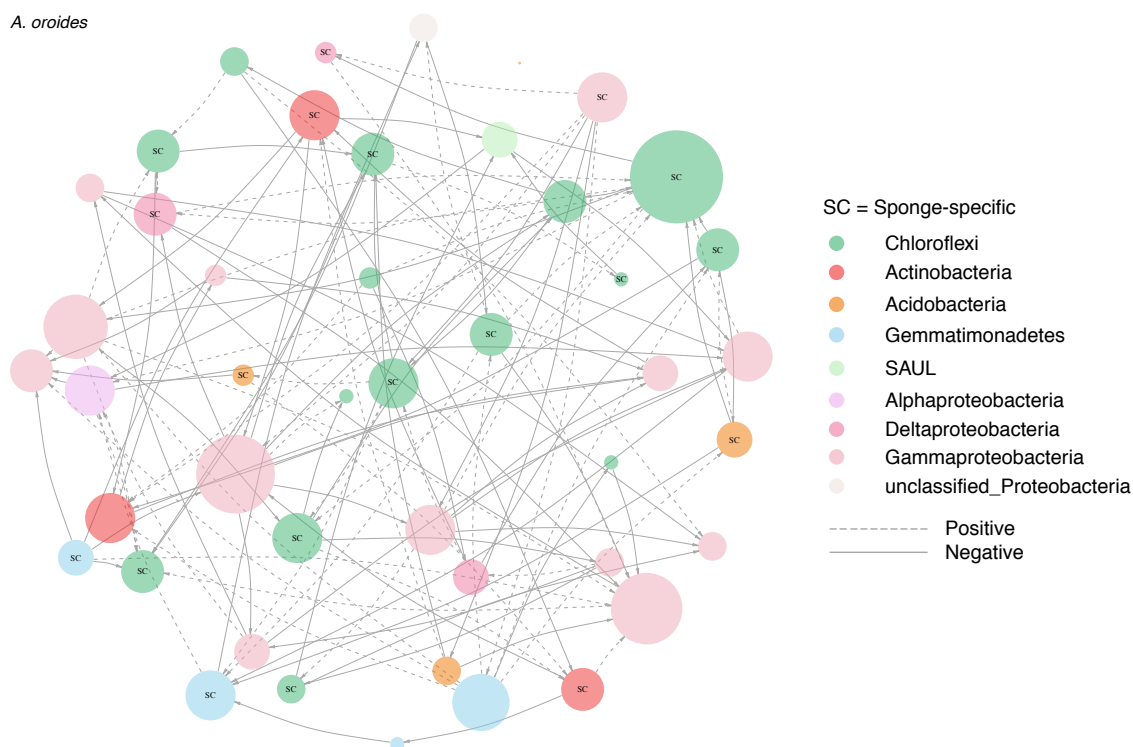


Figure 7: The most credible network structure for HMA host *A. oroides*'s core microbiome. Nodes represent core taxa and links their inferred ecological interactions. Node size is scaled to their degree (i.e. in and out-going links). Colors correspond to different bacterial phyla and dash and solid lines 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.