Microbial interactions lead to rapid micro-scale successions on model marine particles

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In the ocean, organic particles harbour diverse bacterial communities, which collectively digest and recycle essential nutrients. Traits like motility and exo-enzyme production allow individual taxa to colonize and exploit particle resources, but it remains unclear how community dynamics emerge from these individual traits. Here we track the taxon and trait dynamics of bacteria attached to model marine particles and demonstrate that particle-attached communities undergo rapid, reproducible successions driven by ecological interactions. Motile, particle-degrading taxa are selected for during early successional stages. However, this selective pressure is later relaxed when secondary consumers invade, which are unable to use the particle resource but, instead, rely on carbon from primary degraders. This creates a trophic chain that shifts community metabolism away from the particle substrate. These results suggest that primary successions may shape particle-attached bacterial communities in the ocean and that rapid community-wide metabolic shifts could limit rates of marine particle degradation.

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Bacterial colonization of particulate organic matter (POM) in the ocean is a well-known example of microbial community assembly with important implications for global carbon cycling\(^2\). On global scales, POM mediates the transfer of nearly two billion tons of carbon from the surface to the deep ocean\(^3\). However, at micrometre scales, marine particulates serve as spatially isolated, nutrient-rich microhabitats in an otherwise nutrient-poor environment\(^4\). Microbes from the surrounding seawater, representing a complex colonization pool of bacteria, archaea, eukaryotes and viruses, attach to these particles, eventually forming dense multi-species communities\(^5\). Within these communities, local interactions between neighbouring cells are predicted to play an important role in shaping community-level structure and function\(^6\). These interactions include exploitation of public goods\(^7\) (for instance, broadcasted degradation products of carbohydrate-active enzymes\(^8\)), antagonistic interactions via antibiotics\(^9\) and quorum sensing\(^10,11\). Moreover, at regional scales, the efficiency with which bacteria move through a particle ‘landscape’ via active or passive dispersal is likely to influence their ecological success\(^12\). These processes combine to give rise to dynamics at the level of the community, particularly in the context of a diverse natural microbial assembly, is still not well understood.

In this work, we investigate the dynamical process by which marine bacteria self-assemble into dense, diverse communities on organic particulates. In the wild, it is often difficult to characterize these community assembly processes and their corresponding drivers, since naturally occurring particles can vary widely in age, size and chemical composition. Here we take an alternative approach, in which we immerse chemically defined, nutrient-rich microparticles in coastal seawater. Using this hybrid approach—maintaining high levels of microbial diversity, while reducing substrate heterogeneity—we track the dynamics of particle colonization with high temporal resolution and explore the underlying drivers of these dynamics. We find that marine bacterial communities assembled on model particles undergo rapid turnover, shifting from a community capable of degrading the particle substrate to one that cannot in a matter of hours. The timescale of this transition could influence the balance between organic matter consumption and biomass build-up in the ocean, potentially a key factor shaping particle remineralization rates in the ocean.

### Results

**Model system.** To enable studies of microbial community dynamics, we developed a model system inspired by bacterial colonization of POM in the ocean. We simulated POM with paramagnetic micro-particles (Supplementary Fig. 1: median diameter 40.7 \(\mu\)m) made of chitin—a highly abundant biopolymer in the ocean\(^19\). We incubated these particles in a sample of coastal seawater (Fig. 1a), which contained a diverse microbial assemblage of nearly one million bacteria per millilitre, as well as myriad viruses and small eukaryotes\(^4\). Over nearly 6 days, bacteria from the surrounding seawater (Supplementary Discussion) self-assembled into communities on the chitin particle microhabitats (Fig. 1b,c; Supplementary Fig. 2). At discrete time intervals, we harvested pools of particles (roughly 1,000 per sample), thus allowing us to reconstruct the average community assembly dynamics occurring over many spatially distinct, but temporally synchronized, particles. To assess the reproducibility of these dynamics, we performed three replicates of the colonization process from a single, well-mixed seawater sample.

**Successions in particle-attached bacterial communities.** Despite the extreme diversity of the surrounding microbial assemblage, we found that the overall growth dynamics of particle-attached bacterial communities were surprisingly simple. To characterize these combined growth dynamics, we quantified the number of copies of the V4 hypervariable region of the 16S rRNA gene—a rough proxy for the number of bacteria—present per particle on average over time. Across three colonization replicates, the dynamics were well described by a logistic growth model (Fig. 1c). In particular, bacterial communities initially underwent rapid exponential growth, in which the number of 16S rRNA gene V4 copies doubled every 3.3 h. However, the total abundance saturated at nearly \(10^5\) 16S rRNA gene V4 copies per particle after only 40 h of colonization.

Although the total abundance curve saturated early, the underlying colonization dynamics of individual taxa revealed a rapid ecological succession, with wholesale community turnover not only during exponential growth, but also long after the total bacterial abundance had saturated (Fig. 2a). In particular, many...
taxa experienced a sharp drop in absolute abundance, often by orders of magnitude, soon after reaching their peak absolute abundance levels (for example, operational taxonomic unit 1 (OTU 1) in Fig. 2c). As they dwindled, these taxa were replaced by others, which reached maximum levels that often matched (or exceeded) the earlier colonizers (Fig. 2b), but that declined in turn as still others supplanted them. In total, this dynamic process of community turnover brought 53 highly abundant taxa—present at >1% relative abundance in at least one time point—that each peaked in abundance at times ranging from 16 to 140 h of incubation (Fig. 2a). While microbial successions are widely documented (for example, in the human gut\textsuperscript{20,21}, the soil\textsuperscript{22} and the marine environment\textsuperscript{23,24}), such dramatic community turnover has not, to our knowledge, been observed on the spatial (microns) or temporal (hourly) scales documented here.

Given that these dynamics originated from the migration, growth and interactions of many diverse bacteria, we predicted that chance events might give rise to divergent community dynamics, even from the nearly identical starting conditions of our three colonization replicates.\textsuperscript{25} However, across these replicates, individual taxon trajectories were highly reproducible (Fig. 2d; Supplementary Fig. 3). For abundant taxa—present at >1% relative abundance at any time point and in any replicate—the median Spearman correlation between individual taxon trajectories from different replicates was >0.8 (Fig. 2d). This high level of reproducibility indicates that technical variation across samples was minimal. However, it also suggests that the average process of community self-assembly is robust to ecological drift, particularly historical contingencies that can arise in a complex microbial milieu.

Importantly, while community turnover occurred continuously, we identified three discrete phases of colonization based upon changes in the community-wide diversity over time (Fig. 2e). In the first phase of colonization (\(t = 8–20\) h), the communities were at their most diverse (effective number of species, \(N_{\text{eff}} \approx 180\) OTUs; Supplementary Methods). The second phase was characterized by a significant decline in community-wide diversity, which reached a minimum (\(N_{\text{eff}} \approx 20–30\) OTUs) after 36–44 h. However, in the third phase, the community-wide diversity rose again, eventually plateauing (\(N_{\text{eff}} \approx 50–70\) OTUs) after 72 h. Notably, this non-monotonic trend in community diversity held for several diversity metrics (Supplementary Fig. 4).

**Mechanisms underlying successional dynamics.** What drives the community shifts that define these three phases of particle colonization? As is often true in plant communities, we hypothesized that temporal changes in the behaviour and metabolism of particle-attached communities may shape the successional patterns that we observed.\textsuperscript{26,27} To test this hypothesis, we took two complementary approaches. First, we performed metagenomic sequencing of the time series to gain a holistic view of how the metabolic potential of the community changed with time. Second, we amassed and phenotypically characterized a collection of bacterial strains (Supplementary Data 1) isolated from different phases of colonization. Using their

### Figure 2 | Bacterial communities undergo rapid, highly reproducible successions.

- **(a)** Absolute abundance trajectories for individual taxa from a single colonization replicate (Replicate 2). Individual trajectories are normalized to the maximum value. Colour bar indicates order-level taxonomic identities. Line plot above the heat map shows the logistic fit to the total bacterial abundance trajectory. **(b)** Maximum abundance per particle attained by each taxon. Error bars are s.d.’s (\(n = 3\)). **(c)** Absolute abundance trajectories for three representative taxa across colonization replicates (\(\triangle, \bigstar, \bigcirc\)). Grey lines indicate the median trajectories. **(d)** Histogram of cross-replicate correlations for individual taxa (Methods). *Shannon diversity* (\(\sum_{p>0} p \ln p\)) over time for the three colonization replicates (\(\triangle, \bigstar, \bigcirc\)). Samples for which sequencing coverage was insufficient for the Shannon diversity to saturate have been omitted. The solid grey line (\(\cdot\)) indicates the initial Shannon diversity of the seawater.

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16S rRNA gene sequences, we mapped these isolates to the OTUs originally observed via 16S sequencing (Supplementary Methods; Supplementary Fig. 5). This allowed us to link the phenotypic traits of individual isolates to their taxon’s colonization dynamics.

Overall, our data suggest that the three phases of colonization were governed by distinct ecological processes: (i) phase I, attachment, (ii) phase II, selection and (iii) phase III, replacement by secondary consumers. In phase I, particle-attached bacterial communities were as diverse as the seawater from which the colonizers originated (Fig. 2e; Supplementary Fig. 4), despite low total bacterial abundance (Fig. 1c). Moreover, the frequencies of gene families associated with chitin metabolism (e.g., GH18 family chitinases) were low (Fig. 3a). This suggests that, at early stages of colonization, the composition of particle-attached communities is not determined by growth on the particle substrate, but instead, may be governed by particle attachment ability. In general, particle attachment is a complex trait influenced by bacteria-particle encounter rates, chemotaxis, biofilm production, and the expression of chitin-binding proteins. Nonetheless, given the diversity of taxa able to colonize particles in phase I, this suggests that particle attachment is a weak selective filter.

By contrast, the dramatic decline in community-wide diversity that defined phase II (t = 20–44 h) was likely driven by strong ecological selection for chitin metabolism and rapid dispersal ability. In particular, gene families associated with chitin metabolism peaked in relative abundance in phase II (Fig. 3a). Moreover, the frequencies of gene families associated with chitin metabolism were associated with multiple stages of colonization, including extracellular chitin degradation (with GH18 family chitinases), chitin-specific substrate attachment (via chitin-binding proteins), chemotaxis towards chitin monomers, and catabolism of chitin oligomers (Fig. 3a). Indeed, among taxa with isolate representatives, four of the five taxa that were highly abundant in phase II could grow in culture with chitin as the sole carbon source (Fig. 3b; Supplementary Fig. 7a). Interestingly, all four of these chitin-metabolizing taxa were also able to (i) broadcast extracellular chitinases into the surrounding environment (Fig. 3b; Supplementary Fig. 7e) and (ii) to consume two common chitinase degradation products, chitin monomers (N-acetylglucosamine or GlcNAc) and dimers (N,N-diacylchitobiose or (GlcNAc)₂) (Fig. 3b; Supplementary Fig. 7b,c). Moreover, all taxa that gained prominence in phase II were motile under laboratory conditions (Fig. 3b; Supplementary Fig. 7d), highlighting that rapid dispersal via active swimming may influence colonization order.

As particle-attached communities entered phase III (t = 44–140 h), the community-wide diversity rose again from its phase II minimum as, simultaneously, the ecological selection for chitin metabolism and rapid dispersal that defined phase II was relaxed. Community-wide, the relative levels of gene families associated with chitin metabolism and chemotaxis towards chitin degradation products declined in phase III, sometimes by orders of magnitude (for example, GH18 chitinases, Fig. 3a). Similarly, among taxa with isolate representatives that reached prominence in phase III, none were motile under laboratory conditions (Fig. 3b), and the majority (8 out of 11) were unable to grow in culture with chitin as the sole carbon source (Fig. 3b; Supplementary Fig. 7a). Incidentally, the minority that could metabolize chitin did not broadcast extracellular chitinases, nor could they typically consume chitin monomers or dimers.

Figure 3 | Differences in functional traits between phase II- and phase III-dominant taxa. In both subpanels, phases of colonization (I, II and III) are indicated with the grey colour bar. (a) The fraction of read annotations mapped to a given functional category over time. DNA Pol I, DNA polymerase I (EC 2.7.7.7); GH18 family, glycoside hydrolase family 18; CBP, chitin-binding protein (auxiliary activity family 10); Chemotaxis, N-acetylglucosamine-regulated methyl-accepting chemotaxis protein; DeAc, N-acetylglucosamine-6-phosphate deactylase (EC 3.5.1.25); DeAm, glucosamine-6-phosphate deaminase (EC 3.5.99.6); Chitobiose catabolism, (GlcNAc)₂ Catabolic Operon (SEED Subsystem). (b) Left heat map: absolute abundance trajectories of isolated taxa. Leftmost letter identifiers show order-level taxonomic identities. Right heat map: whether isolates do (blue) or do not (black) display a functional trait (assays described in Methods; Supplementary Methods). Grey: within-taxon isolates differ in their phenotype. The number of isolates surveyed per taxon ranged from 1 to 3.
quite dramatic; in some cases, isolates grew 1,000-fold (out of 12 co-cultured pairs, despite their inability to grow in monoculture). Interestingly, the degree of growth enhancement (doublings) over 7 days in co-culture, with little or no growth in their monoculture counterparts (Supplementary Discussion). Altogether, despite their widespread inability to consume chitin, the primary particle resource, phase III-dominant taxa often grew to the levels that rivalled those from phase II (Fig. 2b). Thus, phase III marked a community-wide shift in metabolism away from chitin towards other nutrient sources.

Given their inability to metabolize chitin directly, we hypothesized that phase III-dominant taxa instead consumed nutrient byproducts produced by chitin metabolizers. To test this hypothesis, 106 co-cultured isolates from two phase III-dominant taxa (from distinct bacterial phyla, Proteobacteria and Bacteroidetes) with each of six chitin metabolizing isolates (representing three orders within Gammaproteobacteria). Of the six chitin metabolizers, three could broadcast extracellular chitinases, while three did not (Figs 3b and 4), suggesting potential differences in their ability to sustain a non-chitin-metabolizing subpopulation. Altogether, we found that isolates of phase III-dominant taxa grew robustly on chitin particles in 10 out of 12 co-cultured pairs, despite their inability to grow in monoculture. Indeed, the enhancement of their growth was often quite dramatic; in some cases, isolates grew 1,000-fold (~10 doublings) over 7 days in co-culture, with little or no growth in monoculture. Interestingly, the degree of growth enhancement did not depend on whether the chitin metabolizing co-culture partner could broadcast extracellular chitinases (Fig. 4).

How do chitin metabolizers facilitate the growth of phase III-dominant taxa? Previous studies have documented 'cheater' strains—specialized for consumption of GlcNAC and (GlcNAC)2—that do not produce chitinases themselves, but can exploit chitin-degrading taxa by scavenging for their degradation products29,30. However, the taxa that dominated phase III were unlikely to be canonical cheaters. In particular, gene families involved in GlcNAC and (GlcNAC)2 catabolism decreased in relative abundance from phase II to phase III (Fig. 3a), suggesting that phase III was not enriched in taxa that specialized in the consumption of these products. Similarly, only 1 out of the 11 isolated taxa that were highly abundant in phase III was able to grow in culture with GlcNAC or (GlcNAC)2 as the sole carbon source (Fig. 3b; Supplementary Fig. 7b,c). However, in the same minimal medium, these isolates could grow on many other carbon sources (Supplementary Fig. 8), indicating that growth deficits stemmed from a lack of a suitable carbon source, rather than auxotrophies or missing co-factors. More broadly, this implies that chitin metabolizers facilitate the invasion of phase III-dominant taxa by providing them with alternative carbon sources. Possible sources include, but are not limited to, cell debris, biofilm-associated exopolysaccharides, or small metabolic byproducts (for example, organic acids).

**Discussion**

Overall, we have demonstrated that bacterial communities colonizing nutrient-rich microhabitats undergo successional dynamics driven by two factors—dispersal limitation and facilitative interactions—that, together, drive primary successions at the scale of tens of microns. Together, our results suggest that the existing theory of successions that has been developed for plants and animals may be applied to complex natural microbial communities, thereby providing a basis for linking microbial community structure to their population dynamics and activity.

Our work also illustrates that micro-scale ecological dynamics may have important consequences for global ecosystem processes. In particular, the rapid successional transition from primary particle degraders (in phase II) to secondary consumers (in phase III) that we observed in our system suggests that the bacteria commonly found on naturally occurring particles may not be the primary particle degraders. Instead, most particle-attached bacteria may be secondary consumers that recycle waste products from primary degraders. These secondary consumers could increase the biomass yield of the particle-attached community, while decreasing particle degradation rate, as they compete with primary degraders for essential resources like space or oxygen. Therefore, the timescale of this transition could influence the balance between organic matter consumption and biomass build-up in the ocean, potentially a key factor shaping particle remineralization rates in the ocean. Further work should be aimed at understanding the impact of particle-attached community dynamics from microscopic to global scales.

**Methods**

**Sampling of seawater.** Coastal ocean surface water samples were collected on 7 October 2013 from a sampling site located near Northeastern University’s Marine Science Center (Canoe Beach, Nahant, MA, USA; 42°25'11.57" N, 70°54'26.60" W). At the time of sample collection (roughly 15:00 UTC), the water temperature was 16.5°C, while the ambient air temperature was 18.1°C. Salinity was measured to be 29.7 p.p.t. using a handheld refractometer (VWR #89970-226).

**Colonization of chitin particles in seawater.** Two millilitres of chitin magnetic beads (New England Biolabs #E8036L; roughly 2.5 × 107 beads per ml) stored in 20% ethanol were washed three times with 50 ml of artificial seawater. Beads were resuspended in 100 ml of artificial seawater, resulting in a bead stock at 5,000 beads per ml. In each of three 1-l screw-cap high-density polyethylene bottles, 16 ml of the bead stock were added to 800 ml of unfiltered seawater, yielding a final bead concentration of 100 beads per ml. Bottles were rotated end-over-end at four rotations per minute on a homemade bottle rotator under ambient lighting and temperature conditions. At each time point, 1 ml was filtered onto a 0.2-μm-pore-size filter. Filters were stored at −80°C until further analysis.
Quantification of total particle-attached bacteria over time. As described above, 1,000 beads were prepared from each incubation bottle at each time point. Total bacterial DNA was quantified for each of these samples using a quantitative PCR (qPCR) assay (Supplementary Methods). For each sample, the total amount of genomic DNA present in each sample was calculated from the Ct by plotting absolute abundance trajectories. The number of 16S V4 copies present in a sample was calculated from the Ct by the following equation:

\[ N = 10^{(C_{t} - C_{0}) \times 10} \]

where \( N \) is the number of 16S V4 copies present in a sample, \( C_{t} \) is the Ct value, and \( C_{0} \) is the Ct value of a 16S rRNA standard.

Chitinase broadcasting assay. A plate-based chitin clearing assay was used to assess chitinase broadcasting activity. Chitinous beads were prepared from marine Broth 2216 medium supplemented with 1,000 chitin beads per ml. A standard agar stab assay was used to assess the potential for Motility assay. A standard agar stab assay was used to assess the potential for motility among isolates. Motility test agar medium was prepared with Marine Broth 2216 (Di introducing) as described above. Total double-stranded DNA was quantified for each sample with a Quant-it Picogreen dsDNA Assay Kit (Life Technologies #P7899).

Isolate co-culture experiments. To characterize interactions between community members, we performed co-culture experiments with pairs of strain isolates. In each experiment, one strain was mixed with a nutrient-rich, chitin-degrading strain, with the degrader in large excess (degrader:non-degrader = 90:10). Combinations of strains, as well as monocultures of each strain, were grown in Tibbles–Rawling medium with chitin beads (1,000 beads per ml) at a starting cell density of 10^6 cells per ml. Cultures were grown for 7 days at room temperature and rotated end-over-end at six revolutions per minute. For each culture, samples were harvested at the beginning (t = 0 days) and end (t = 7 days) of the growth period and frozen at –80 °C for subsequent analyses.

Quantifying the total number of cells in each sample is experimentally challenging. Therefore, the total amount of genomic DNA present in each sample was estimated by using a modified version of the Illumina 16S library preparation. This was used to map isolates to OTUs identified via culture-independent methods (Supplementary Methods). The information was used to map isolates to OTUs identified via culture-independent methods (Supplementary Methods).
quantified for each sample with a Quant-iT PicoGreen dsDNA Assay Kit (Life Technologies #P7589).

To estimate the relative abundance of each strain within the co-cultures, amplicon libraries (16S rRNA gene V4 hypervariable region) were prepared according to a previously described protocol31. Sequences were sequenced on an Illumina MiSeq (paired-end, 250-bp reads) at the BioMicro Center (Massachusetts Institute of Technology, Cambridge, MA). The absolute abundance of each strain in each sample was calculated by multiplying the strain's relative abundance in a given sample by the total amount of genomic DNA present in that sample.

Data availability. Sequence data that support the findings of this study have been deposited in the NCBI databases BioProject (with accession code PRJNA319196) and BioSample (with accession codes SAMN04886652 to SAMN04886699). Isolate 16S sequence and phenotype data can be found in Supplementary Data 1. The authors declare that all other data supporting the findings of this study are available within the article and its Supplementary Information files, or from the corresponding author upon request. Scripts for processing data can be found at https://github.com/mdatta8788/chitinParticlesSuccession. All scripts are also available from the corresponding author upon request.

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Author contributions
M.S.D. and O.X.C. designed the experiments. M.S.D. and O.X.C. analysed the data and wrote the paper. J.G., M.F.P. and O.X.C. provided technical support and conceptual advice. All authors discussed the results and commented on the manuscript.

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