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Ubiquitous abundance distribution of non-dominant plankton across the global ocean

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Abstract

Marine plankton populate 70% of Earth's surface, providing the energy that fuels ocean food webs and contributing to global biogeochemical cycles. Plankton communities are extremely diverse and geographically variable, and are overwhelmingly composed of low-abundance species. The role of this rare biosphere and its ecological underpinnings are however still unclear. Here, we analyse the extensive dataset generated by the Tara Oceans expedition for marine microbial eukaryotes (protists) and use an adaptive algorithm to explore how metabarcoding-based abundance distributions vary across plankton communities in the global ocean. We show that the decay in abundance of non-dominant operational taxonomic units, which comprise over 99% of local richness, is commonly governed by a power-law. Despite the high spatial turnover in species composition, the power-law exponent varies by less than 10% across locations and shows no biogeographical signature, but is weakly modulated by cell size. Such striking regularity suggests that the assembly of plankton communities in the dynamic and highly variable ocean environment is governed by large-scale ubiquitous processes. Understanding their origin and impact on plankton ecology will be important for evaluating the resilience of marine biodiversity in a changing ocean.

Main text

Introduction

Marine plankton communities are composed of an enormous number of cohabiting species^{1 2 3}, in spite of the potentially strong selective pressures imposed by the abiotic environment⁴. Plankton blooms at temperate latitudes – where a few dominant species become hugely abundant in just a few days – spectacularly illustrate the existence of spatio-temporally restrained niches⁵. Heterogeneity in the physico-chemical environment thus affects local species composition and underpins plankton biogeography⁶.

Adaptation to idiosyncratic environmental conditions and competitive exclusion are however mitigated by the strong spatio-temporal variability of ocean dynamics⁷. Therefore, a fraction of plankton communities is found in sub-optimal growth conditions, with a resulting low abundance. In microbial assemblages, this non-dominant component is referred to as 'the rare biosphere'^{8 9 10 11 12}, and is largely responsible for their enormous diversity. Since the species composing the rare biosphere are for the most part unculturable and lack precise morphological and ecological characterization, the investigation of plankton communities and their ecological patterns relies more and more on the measure of their genetic diversity. On the one hand, these observations have revealed plankton biogeography, showing that local species composition reflects the distribution of environmental drivers^{13 1}. On the other hand, plankton assemblages have been included in the rapidly growing number of microbial communities used as benchmarks for testing general macroecological theories and supporting the existence of universal biodiversity patterns^{14 15 8 16}. Here, we examine the quantitative variation in the rate of decay of metabarcoding-derived abundances across communities that are ecologically uniform (marine plankton), but differ both in taxonomic composition and in geographical location in the global ocean.

One primary feature of ecological communities, on which classical indicators of diversity and evenness are based, is how many individuals belong to each of the taxa observed in a local sample⁷. This information is typically represented in two forms. In rank-abundance plots, species are arranged in decreasing order of abundance, whereas Species Abundance Distributions (SADs) represent the frequency histogram of species abundances. The shape of these plots is invariably characterized by a small number of abundant species and a larger number of rare ones, motivating the search for general principles able to account for the functional form of the abundance decay^{17 18 19 20 21}. Attempts to derive SADs from ecological mechanisms or statistical laws has had to address the problem of the deviations in empirical distributions from the theoretically-postulated laws, which has spurred the development of increasingly sophisticated statistical methods^{22 23 24}. Whether observed distributions can be described by a same functional form, and if so what are its underpinnings, is however still debated^{22 23 25 26 27}, being hampered by the limited discriminating power of qualitative fits and by the sparse spatiotemporal and/or morphological resolution typical of empirical datasets.

Describing empirical SADs by fitting a specific model moreover implies that the ecological processes or statistical principles generating such a theoretical distribution apply uniformly to all taxa in the community. Whereas this might hold true if species assemblies were essentially shaped by stochastic processes constrained at the system level, it would be natural to expect that different components of the community may respond to different ecological processes. In the latter case, empirical SADs would be the overlap of multiple theoretical distributions, and fitting the whole community with a single law

would introduce irreducible discrepancies. Magurran & Henderson²⁸ and Ulrich & Ollik²⁹ have indeed shown that 'occasional' and 'frequent' (in a time series) species in animal communities follow different SADs, with the former obeying a highly skewed distribution.

In our analysis, we restrict our focus to taxa that are non-dominant and which, in plankton communities subjected to a high degree of dispersal, are arguably akin to 'occasional' species. In order to reduce the possible bias introduced by choosing a specific family of fitting distributions, we use several laws considered in the literature, including a general neutral model that encompasses generic shapes of abundance decay (exponential and power-law). Comparison of the distributions that best fit non-dominant taxa decay in 372 samples reveals an unexpected quantitative regularity, which suggests that the statistical structure of the low-abundance component is shaped by common processes shared by marine plankton communities.

Results

We exploited the extensive molecular dataset generated from the *Tara* Oceans expedition, which comprises millions of protist metabarcode sequences from 121 different locations worldwide³⁰, constituting a comprehensive picture of planktonic protist communities. By using different proxies for protist 'taxa', as defined by swarm³¹ (hereafter swarms or species) and UCLUST for 95% and 97% sequence identities (hereafter OTUs), we aimed to minimize possible intraspecific variability and PCR/sequencing errors. We analyzed abundances of pelagic protist taxa spanning more than three orders of magnitude in cell size (from 0.8 μm - 2 mm, subdivided in 4 size classes: pico-nano, nano, micro, meso; Methods), hence assessing communities that are subjected, to different physiological and ecological constraints in terms of their metabolic rates, population densities, dispersal and diversification potential^{32 33 34}. The depth of sequencing² and consistency of sampling protocols (Methods) allowed us to address not only the way that relative species abundance decays in every local community, but also its geographical variation³⁵.

As expected, considering that they are sampled in different locations and environmental contexts, the overlap in composition of any couple of the 121 communities examined was small. The average Jaccard index is 0.14 ± 0.07 for pico-nano, 0.08 ± 0.06 for nano, 0.08 ± 0.07 for micro and 0.03 ± 0.06 for the meso size class. Correspondingly, the rank-abundance plots of planktonic protists displayed sample-to-sample heterogeneity, as illustrated in Fig. 1a. However, the tail of non-dominant species – responsible for most of the community diversity – appears to follow an analogous scaling in all samples. This regularity may indicate that species in the range of lowest abundances can be considered separately from the most abundant plankton types. If local communities are the composition of groups of species that are driven by distinct ecological and/or statistical processes, we can try to isolate a single group based on its adherence to the same scaling law. We thus decided to use the homogeneity of the abundance decay as a proxy for automatically identifying, sample-by-sample, the community component of non-dominant taxa. We adapted the method introduced in Clauset et al.³⁶ (Methods) to single out the largest community component that is described by a family of distributions within a given level of statistical confidence (Methods). We applied such an adaptive algorithm to several theoretical models, including classical distributions^{18 21 37} (exponential, log-series, log-normal, Poisson log-normal and zero-sum multinomial) and to a general model, described below, with density-

dependent species-neutral demography, which includes both exponential and power-law decay^{38 39}. Models having a probability lower than 10% of generating a distance equal or larger than the observed distance between empirical and best fitting distributions were rejected as being not statistically significant (corresponding to $p < 0.1$; see Methods). The largest range of abundance of statistically significant fits (the extension of the fit) singles out the non-dominant component of the community that is comprehensively described by the chosen family of distributions. We refer to the distribution that has the maximum likelihood over the extension as the best-fitting distribution of a given sample (e.g., in Fig. 1b). Importantly, since fitting distributions belong to the same functional family, the parameters of the best fit are quantitatively comparable across organism size and geographical location.

Examination of the empirical abundance distributions indicates a dominant power-law trend in the abundance decay, with no multimodality. We hence chose to fit the data with a model that reproduces this distribution and can moreover accommodate deviations from the power-law regime, which are common for the rarest abundance classes of empirical SADs (Methods). This model (equation (3), Methods) has been derived by He³⁸ under the neutral hypothesis that demographic events (birth and death) occur for every species at the same constant per capita rates b and d , corrected by nonlinear terms χ and μ ^{38 27 39} that depend on the number of individuals of the focal species. Such nonlinearities can be interpreted as describing frequency-dependent demography and/or immigration/emigration. By deriving analytically the asymptotic limit of equation (3) (Supplementary Information) we find that the model distribution encompasses three regimes (illustrated in Fig. 1b inset). Intermediate abundances decay as a power-law with exponent λ , given by:

$$\lambda = 1 - \chi/b + \mu/d, \tag{1}$$

that crosses over to an exponential decay (with exponent $r = -\log(b/d)$) for large abundances. On the other hand, nonlinearities in demographic rates parametrize the finite-size deviation from the power-law, that occurs for rare species and, at first order, is proportional to $\chi/b + \mu/d$. Both the exponent λ of the associated power-law and the rare species deviations thus depend on the two parameters χ/b and μ/d , which are independently fitted to the data. Equation (1) predicts that whenever the difference between the two nonlinearity parameters is constant (therefore, $\chi/b = \text{const} + \mu/d$), the power-law exponent will be invariant, independently of how rare classes deviate from the power-law trend.

The model distribution (equation (3), Methods) fits the non-dominant component of the swarm-based SADs in 372 out of 388 samples (Methods, see Supplementary Data 1 for SADs and fits of each sample). The fits to other distributions, delivered by the adaptive algorithm with the same stringent thresholds for tolerance and fit extension, were only significant in a few samples, if at all. The Poisson-lognormal distribution provides a statistically significant test for 136 samples, whereas the exponential, log-series, log-normal, and zero-sum multinomial distributions are never significant. The 16 samples that were not fitted by the model of equation (3) possessed highly irregular trends that, at the same level of statistical significance, were not fitted by any other examined distribution either. We also tested whether the fitted parameters were affected by sequencing depth (i.e., number of reads obtained for each sample), as is common in community-level statistics¹⁸, and found no significant effect (Supplementary Information). The possibility of fitting almost all samples with the same model allowed us to compare the parameters of the best fit across geographical sites. Table 1 reports the average and Coefficient of Variation (subdivided by size class and all size classes confounded) of the parameters for all samples where the fit was significant.

On average, the fit encompasses 99.4% of species in each sample, and only fails to account for the abundance of a handful of dominant swarms. For non-dominant species, the rate of exponential decay r is very small throughout (Table 1). In the model, this occurs when the linear per capita birth and death rates b and d are comparable locally (though not necessarily identical in all locations), suggesting that the non-dominant component of the community is overall in demographic equilibrium. In the open ocean, such balance could be favoured by the strong dispersal induced by water transport, that would effectively temper the differences between demographic parameters (see Methods and Discussion). In the absence of an appreciable exponential cutoff, plankton protist SADs thus display an extensive power-law regime covering the largest part of the abundance range (up to 4 orders of magnitude). Moreover, the rarest classes generally exhibit a deviation (negative more often than positive) from a perfect power-law, as captured by the nonlinearity parameters χ/b and μ/d . The range of variation of these parameters is broader than what was found when fitting similar but more parsimonious models to macroorganism communities^{19 39 40}. Nevertheless, they present a strong correlation along a line with slope close to 1 (Fig. 2). Such a pattern results in a strikingly small variation of the exponent of the power-law trend (equation (1)) across samples (Fig. 1b, Table 1).

In terms of species composition, the dominant and non-dominant taxa of the community do not appear to be conserved across locations, as one would expect if there were species that are always rare or always common. Indeed, for each swarm we calculated the fraction of samples in which it is dominant (if present). On average, such fraction is 0.08 ± 0.15 for the pico-nano size class, 0.08 ± 0.11 for nano, 0.09 ± 0.09 for micro and 0.07 ± 0.06 for meso. Hence, there is almost no swarm that occurs systematically in the dominant component, but swarms are instead commonly found in both dominant and non-dominant components, indicating that species that are locally abundant are in most cases rare if not absent in other locations.

When displayed on a map (Fig. 3 and Supplementary Figure 1), the uniformity of the power-law exponent value pairs with a lack of geographic signatures. We then used a collection of contextual data⁴¹ – including physicochemical measures performed at each sampling site, satellite-derived diagnostics, and outputs of simulations of global-scale coupled climatic and ecological models – to assess covariation with the best fit parameters³⁵. Previously, local environmental variables have been shown to explain part of the bacterioplankton community features and their biogeography, and temperature is known to underpin classical macroecological patterns such as latitudinal diversity gradients⁴². Oceanographic parameters related to the processes of transport and mixing at the local scale are moreover expected to influence patterns of dispersal and niche arrangement, thus affecting community assembly. Although such abiotic and biotic contextual variables have considerably larger coefficients of geographic variation (CV) with respect to the power-law exponent (e.g., 30% for a particularly stable physical parameter, Mixed Layer Depth Temperature; 121% for nitrates; 50% for surface chlorophyll), we found no relationship with the power-law exponent holding consistently across size classes or across parameters. The few significant correlations (listed in Supplementary Table 1) explained only a small fraction of the variance (Supplementary Information). This result again supports the conclusion that no specific local condition shapes the SAD of non-dominant species.

Consequently, dominant species are expected to carry the most biogeographical information. Indeed, those species that achieve dominance can be considered to be those that win the competition race whose terms are set by the local abiotic niche. The repartition obtained by our algorithm allows us to test if biogeographical differences in community composition can be recapitulated by considering only

the most abundant species. To this end, we computed pairwise distances of communities of the same size fraction, making use of Jaccard and Bray-Curtis metrics. We then evaluated the same distances by keeping only those few 'dominant' species whose abundance was superior to either the threshold provided by the fitting algorithm, or to the maximal abundance that we were able to process numerically (this definition of dominance is hence conservative). As illustrated in Supplementary Figures 2 and 3, these two metrics correlate very strongly independently of how the dissimilarity is measured, hence confirming the above expectations.

In spite of the overall small variation of the exponent across samples, statistically significant differences were found among size classes, with bigger size classes having the largest power-law exponent (Table 1). Systematic variations in parameters with the size class could stem from scalings in physiology, demography, or speciation rate, as the metabolic theory of ecology would predict³², or to size class-dependent water filtration modulating the scale of the sampled community. Alternatively, it is possible that these changes reflect the different degrees to which a neutral model is able to account for the actual process of community assembly. Due to the higher likelihood of niche overlap, it has indeed been suggested that communities with high species richness are more likely to obey the tenets of neutral theories⁴³. This explanation is consistent with the observation that when size decreases (and correspondingly, richness increases), the agreement of the nonlinearity parameters to the scaling defined by equation (1) improves (Fig. 2). Moreover, plotting the exponent λ against swarm richness (Supplementary Figure 4) suggests a possible convergence of the power-law exponent to a theoretical value of 1.5 in samples displaying the highest swarm richness values.

Similar widespread power-law regimes with limited geographic variation in their exponents could be retrieved when the same analysis was repeated with OTUs (both 95% and 97%) rather than swarms. The most notable difference is an expected dependence of the power-law exponent on the level of metabarcoding sequence aggregation: its average value increases slightly but significantly as the taxonomic resolution decreases (Supplementary Table 2 and 3), indicating that abundances decay at a slower rate (and diversity increases) when the community is described at a finer taxonomic level. We therefore conclude that the consistency of the observed patterns is unlikely to be a consequence of molecular/clustering artifacts.

Discussion

Our results demonstrate that the abundance distributions of non-dominant plankton are overwhelmingly characterized by a power-law decay. Analogies with previous work^{28 29} suggest that the non-dominant component of the community could be composed of 'transient' or 'occasional' taxa. For plankton assemblages that live in an environment with strong spatio-temporal variation and a high degree of transport-induced mixing, however, it is not obvious to distinguish the endemic and occasional component. For occasional species, we can nevertheless argue that dispersal, and not competition at the sampling location, is likely to be the main driver of the demographic dynamics⁴⁴.

By separating each community into a dominant and non-dominant part, we have found that the biogeographical information is essentially carried by dominant species, likely the most adapted to idiosyncratic environmental conditions. The non-dominant component instead follows a power-law

abundance decay whose exponent varies much less than any other locally measured parameter, and that appears to carry no geographic signature.

The fact that a density-/dispersal-dependent neutral demographical model predicts the observed shape of the abundance decay may appear to contradict the observation that – locally – huge differences exist in plankton growth rates, leading to blooms visible even from space. However, following the removal of the dominant species, such differences in growth rate may have secondary effects on the abundance distribution. Two species that bloomed in regions distant from the sampling location, and were transported by ocean currents across more or less hostile environments, will likely have similar average demographic histories. As long as they find a niche they can thrive in, thus avoiding extinction, their abundance in other regions of the ocean should be largely independent of their specific adaptations. Moreover, competitive ability in favourable conditions might be irrelevant if the non-dominant part of the community is essentially composed of slow-growing organisms (for instance, in the form of resting stages), as hypothesized for the rare biosphere^{10 9}. The similarity of the SADs power-law exponent to $3/2$, a value obtained, for instance, in temporal spectra of intermittently varying ecosystems⁴⁵, might indicate that local abundances bear a signature of spatio-temporal variability²⁷.

All in all, understanding the interplay between ocean transport and community structure would require a resolution in space and time that is still unattained at a broad geographical scale. However, the combination of different observation platforms⁴⁶, and the genomic characterization of samples in a given – usually coastal – location^{3 47 48} opens new perspectives for a dynamic characterization of drifting communities, which is not possible with the dataset we used.

Our interpretation of the observed ubiquitous trends in the plankton protist SADs, is based on features that characterize the plankton lifestyle. It should thus not be expected that communities experiencing other ecological contexts and diverse assembly processes display the same regular pattern as evidenced in this work. Indeed, SADs reported for other microbial communities, in particular the gut microbiota³⁷, have been shown to obey different laws, possibly indicating different degrees of dispersal or experienced environmental variability. The current boost in molecular biodiversity surveys will undoubtedly help to clarify the universality of the observed pattern, and its likely relation with the peculiar interaction between ecology and physical forcing in the open ocean.

Methods

Sequence data

Seawater samples were collected from 121 sites distributed worldwide. Each sample was filtered using different mesh sizes so as to isolate different classes of the planktonic community: the picoplankton (0.8-5 μm), the nanoplankton (5-20 μm), the microplankton (20-180 μm), and the mesoplankton (180-2000 μm). Total DNA was extracted from each size class and the V9 region of the 18S rRNA gene⁵⁰ was PCR-amplified and subjected to Illumina sequencing in order to describe eukaryotic planktonic communities. The retrieved paired-end sequencing reads were assembled using the fastx software (http://hannonlab.cshl.edu/fastx_toolkit/index.html) and dereplicated. To remove potential artefacts, we excluded sequences (i) that did not contain both forward and reverse primers, and (ii) identified as chimeras by the usearch programme (version 4.2; Edgar et al.⁵¹), using either the V9_PR2 reference database as reference (database W2; Guillou et al.⁵²), or the *de novo* approach. The resulting sequences were clustered based on their similarity. First, the swarm algorithm²⁶ was used to minimize the amount of PCR/sequencing errors, as well as intraspecific variability. Because we used it to cluster sequences distant from one mismatch, swarms represent the Operational Taxonomic Units (OTUs) at the finest taxonomic resolution. Second, swarms were clustered at 97% and 95% similarity using the UCLUST algorithm⁵³ so as to obtain descriptions of the community structure at coarser taxonomic levels. All OTUs were then assigned to a taxon using the ggsearch program (Fasta package, <http://faculty.virginia.edu/wrpearson/fasta/CURRENT/>) against the V9_PR2 and the SILVA databases (<http://www.arb-silva.de/projects/living-tree/>; release LTPs111, February 2013). Finally, we excluded any swarm or OTU assigned to Bacteria, Archaea, Metazoa, Fungi or that were unassigned so as to focus only on the protist component of the dataset, thus allowing a consistent analysis of eukaryotic microbial communities in different samples. Sequence data are available at EMBL-EBI with accession number PRJEB16766.

Species Abundance Distribution Model

Community assembly models allow to predict abundance distributions. Here we use the abundances of swarms or OTUs as a proxy for species abundances and do so in any particular sampling location and size class, from simple demographical hypothesis. Following He³⁸, we assume that all K species in a local community undergo birth and death at rates that depend only on the species abundance (and not on its identity). For $n \geq 1$, the birth and death rates of a species of n individuals are:

$$\begin{cases} b_n = bn + \chi, \\ d_n = dn + \mu, \end{cases} \quad (2)$$

where b and d represent the linear per-capita birth and death rates while χ and μ are their non-linear corrections, whose effect is especially important for species of low abundance. When $n=0$, for consistency, $d_0=0$ and $b_0=v+\chi$ is the immigration/speciation rate (expressed as a sum for calculation convenience).

The solution of the master equation describing the ecological stochastic dynamics of such a modeled community provides the expected species abundance density distribution $\langle \phi_n \rangle$, that reads^{54 19 38 39}:

$$\langle \phi_n \rangle = \theta \frac{\Gamma(n+\alpha)\Gamma(1+\beta)}{\Gamma(\alpha)\Gamma(n+\beta+1)} e^{-rn}, \quad (3)$$

where:

$$\begin{cases} \alpha = \chi/b & , & r = -\log(b/d), \\ \beta = \mu/d & , & \theta = K \phi_0 (v/\chi + 1). \end{cases} \quad (4)$$

Note that the distribution, once normalized, depends on only three independent parameters (r, α, β); as in demographic terms linear birth and death rates compensate each other, so that only their relative value matters.

We found an asymptotic approximation ($n \gg 1$) of equation (3) (see Supplementary Information for the derivation) in the form:

$$\langle \phi_n \rangle = H n^{-\lambda} e^{-rn}, \quad (5)$$

where H is a constant and $\lambda = 1 - \alpha + \beta$. Equation (5) is an *exponentially truncated power-law*^{20 55 56 57} and for abundances of the order of a few tens of individuals and above, it approximates very well to the exact model distribution defined in equation (3). However, for low abundances, i.e., rare species, non-trivial combinations of the α and β parameters can cause detectable deviations from a pure power-law (see Fig. 1b). At first order, such deviations are controlled by a factor $\lambda(\alpha + \beta)$ (see Supplementary Information). Note finally that from equation (5) one can retrieve both the *exponential* (when $\alpha = \beta + 1$) and the *logseries* (when $\alpha = \beta$) distribution in particular cases.

It is important to stress that for the general case in which the non-linear terms account for both dispersal and density dependent effects, their respective contributions to equations (2) can not be disentangled. Therefore, no univocal conclusion can be drawn about the relative effect of local ecological dynamics versus dispersal from fitting the model to the observational data. Nevertheless we can consider that, in the oceanic environment, dispersal has related effects on both d_n and b_n . Indeed, the demographic parameters at the local scale are affected by the water flux through the boundary of the (supposedly well-mixed) sampling region. Because the movement of oceanic surface waters can be considered as an approximately incompressible planar flow, the inflow equals the outflow. For planktonic species whose abundance is sufficiently large (for which density-dependent terms can be neglected) and uniform at a scale bigger than that where the local community is sampled, the effect of transport-induced dispersal on the demography can be represented by a same rate t . In a linear approximation, we can write $b = \bar{b} + t$ and $d = \bar{d} + t$, where the coefficients \bar{b} and \bar{d} are the per capita local rates of cells division and death. If dispersal dominates local population dynamics, hence $t \gg \bar{b}, \bar{d}$, then the community will be effectively close to equilibrium. Such situation would result in a vanishing exponential cutoff (i.e. $r \sim 0$) and, correspondingly, in an extended power-law regime for the Species Abundance Distribution (equations (3) and (5)).

Model fitting and testing

We developed an algorithm to adaptively fit the theoretical model to the empirical distributions, which allows us to automatically distinguish between two components of the community: a part that is described by the model within a fixed confidence level, and a part of dominant species whose abundance cannot be described by the same model within the same confidence level. A definition of the rare component based on setting an arbitrary (and sufficiently small) threshold in abundance¹³ would provide similar best-fit parameters, but underestimate the extension of the non-dominant component, thus also decreasing the statistical power of the fit. We fitted the data by maximum likelihood. Indeed, alternative methods – such as least-squares minimization – can produce substantially inaccurate estimates^{36–58}. To assess the significance of the obtained fits we rely on p-value calculation and not on the fraction r^2 of variance accounted for by the fits, as the latter has been criticized as having little power as a hypothesis test indicator^{36–59}. We applied the same adaptive algorithm to the previously introduced model (equation (3)) and to other theoretical models commonly used in SAD model selection studies: the exponential, log-series, log-normal, Poisson log-normal and zero-sum multinomial distributions.

The fits, whose parameters are summarized in Table 1, are obtained for each sample by iteration of four steps: 1) maximize the likelihood of the distribution of a subset of species whose abundance is smaller than a given threshold, thus obtaining the best fitting parameters; 2) compute a measure of the distance between the fit and the data; 3) evaluate, by bootstrapping, the statistical significance of the fit and generate numerical p-values; 4) repeat the above steps for increasing values of the abundance threshold and select the largest subset of species such that the p-value associated with its fit is larger than a given confidence.

Observed abundances of swarms/OTUs in a specific sample, from now on denoted for simplicity 'species', are arranged in order of increasing abundance in the vector $\mathbf{n}=(n_1, \dots, n_k, \dots, n_K)$, such that $n_k \leq n_{k+1}$. Hence n_k is the number of individuals (abundance) of species k , $N = \sum n_k$ is the total number of individuals, and K is the number of species observed in the local community. The typical representation of such observations is obtained by counting the number of species whose abundance belongs to fixed intervals of abundances (the empirical SAD). Fig. 1b represents such a histogram in logarithmic binning, that is most adapted for visualizing the SAD in double logarithmic scale. In our study, we focus on subset of $\tilde{K} < K$ species, whose abundances $\tilde{\mathbf{n}}=(n_1, \dots, n_k, \dots, n_{\tilde{K}})$ are smaller than a cutoff $n_{cut} = n_{\tilde{K}}$, which we denote sub-community. For statistical purposes, we are interested in the associated cumulative distribution function \tilde{S} defined as:

$$\tilde{S}(i) = \frac{\sum \text{number of species with abundance} = n}{\tilde{K}} \quad (7)$$

The *discrete upper-bounded model distribution* $p(n)$ is defined from equation (3), by imposing an upper limit to the abundances, as:

$$p(n) = \frac{\Gamma(n+\alpha)}{\Gamma(n+\beta+1)} \frac{e^{-m}}{A(r, \alpha, \beta, n_{cut})}, \quad (8)$$

where $A(r, \alpha, \beta, n_{cut})$ is the normalization constant. In the limit of $n_{max} \rightarrow \infty$, we find $p(n) \rightarrow \langle \phi_n \rangle$. The correspondent cumulative distribution is denoted as $P(i) = \sum p(n)$.

Step 1 of the adaptive loop allows to obtain the parameters for the best fit to any given sub-community data by *likelihood maximization*. We define the log-likelihood of the data given the model distribution in equation (8) as:

$$\log L(r, \alpha, \beta, n_{cut} | \tilde{n}) = -r \sum n_j - \tilde{K} \log A(r, \alpha, \beta, n_{cut}) + \sum \log \Gamma(n_j + \alpha) - \log \Gamma(n_j + \beta + 1). \quad (9)$$

Equation (9) is maximized using a *generalized simulated annealing* algorithm⁶⁰ to retrieve the best estimates of the model parameters (r, α, β) for a fixed n_{cut} . This approach improves the optimization process by minimizing the risk of remaining trapped in a local minimum.

In order to evaluate the goodness of the fit, we need to introduce a metric of the distance between the empirical and the theoretical distributions (step 2). To this aim, we chose the *Anderson-Darling distance*⁶¹, best adapted to detect differences in low-abundance classes than the more commonly used Kolmogorov-Smirnov statistics. The Anderson-Darling metric D between the cumulative distributions reads:

$$D = \max_i \frac{|\tilde{S}(i) - P(i)|}{\sqrt{P(i)(1 - P(i))}}. \quad (10)$$

The distance between distributions, however, does not provide the probability that the observed data are obtained as a random sample from the theoretical distribution. Indeed, the intrinsically discrete structure of the distributions does not allow the use of critical values tables for statistical tests, so that a p-value cannot be directly assigned from the Anderson-Darling test.

We adopt thus the bootstrapping approach followed by Clauset et al.³⁶ (step 3). The rationale is that that best fits to the data obtained in step 1 shall be discarded if their distance from the empirical data is unlikely due to random fluctuations. Such random deviations are quantified by the statistics of the distances between random samples of the best fitting model distribution and their relative maximum likelihood fits. For each fit, we generated 200 synthetic datasets, whose \tilde{K} abundances match the length of the vector \tilde{n} , by sampling the model distribution $p(n)$ for the best fitting parameters (r, α, β) . We then measure the Anderson-Darling distance of each such synthetic dataset from the distribution that fits them with highest likelihood. Finally, we assign a *p-value* to the original fit as the fraction of those distances that are larger than the Anderson-Darling distance between the original data and its best fitting distribution. Hence, fits are considered significant if the empirical distance falls within 'typical' values that we would expect to obtain by random sampling. In this case, the fraction p is large. Instead, p is small if the samples are systematically less distant from their fit than the empirical distribution is from its own fit. By setting a minimum threshold on p (in our analysis, 0.1), we aim to exclude the latter case.

We repeated the maximum-likelihood fit and p-value calculation for sub-communities of growing size (step 4), by progressively increasing n_{cut} (starting from $n_{cut} = 100$). We select then the largest sub-community compatible with the p-value threshold and we call n_{max} its associated n_{cut} . The p-value and n_{max} of this sub-community is displayed for every sample in Supplementary Data 1. Our method allows the identification of n_{max} even when the Anderson-Darling statistics do not present a marked

minimum in such interval. However, it is computationally more intensive than the method proposed by Clauset et al.³⁶, where the p-value was only computed for the sub-community that minimizes the Kolmogorov-Smirnov distance. For this reason, the adaptive fit was bounded to a maximum abundance n_{cut} of 10100, and still numerical calculations were only possible on a computer cluster. Correspondingly, the extension of the fits reported in Table 1 underestimate the real maximal abundance that could be accommodated by the model, thus the size of the non-dominant component of the community.

In the adaptive algorithm, the level of confidence for statistical significance affects the range of abundances that fall within the non-dominant component of the community. If the confidence level is too high (so that the statistical test is too stringent), the fit will not accommodate for the inevitable noise induced by measurement errors, fitting will be poor for any theoretical distribution, and the identification of the non-dominant component inefficient. If it is too low, the adaptive fit will always succeed, and the whole distribution will likely be described by one single law, whose statistical significance will however be poor. We chose a confidence level of $p=0.1$, which is more stringent than what was used in previous analyses. We checked that small changes in the confidence level did not affect the results: relaxing the tolerance by decreasing the threshold p-value to 0.05 led to a few more stations to be fitted by equation (3), and slightly larger non-dominant components, but only a negligible enhancement of the variability in the distributions of the power-law exponent.

Data availability

Sequence data are available at EMBL-EBI with accession number PRJEB16766 and the R code used to produce the fits is available at <https://github.com/serjaaa/adapta-fit-sads>. The whole set of fitted parameters are available from the corresponding authors [E.S-G. and S.D.M.] upon reasonable request. All plots of RADs, SADs and best fitting distributions are included in the Supplementary Data file.

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Author Contributions

S.D.M. conceived and directed the study. E.S-G. obtained the analytical results, designed the adaptive algorithm and produced the fits. S.M. carried out the preliminary analysis on protist RADs. L.Z. performed statistical analysis on fitted parameters. S.D.M., E.S-G., L.Z. and C.B. interpreted the results and wrote the manuscript. C.d.V. and E. K. provided access to the *Tara* Oceans dataset and commented on early versions of the manuscript.

Author Information

Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Correspondence and requests for materials should be addressed to Enrico Ser-Giacomi or Silvia De Monte.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature

Main text Figures

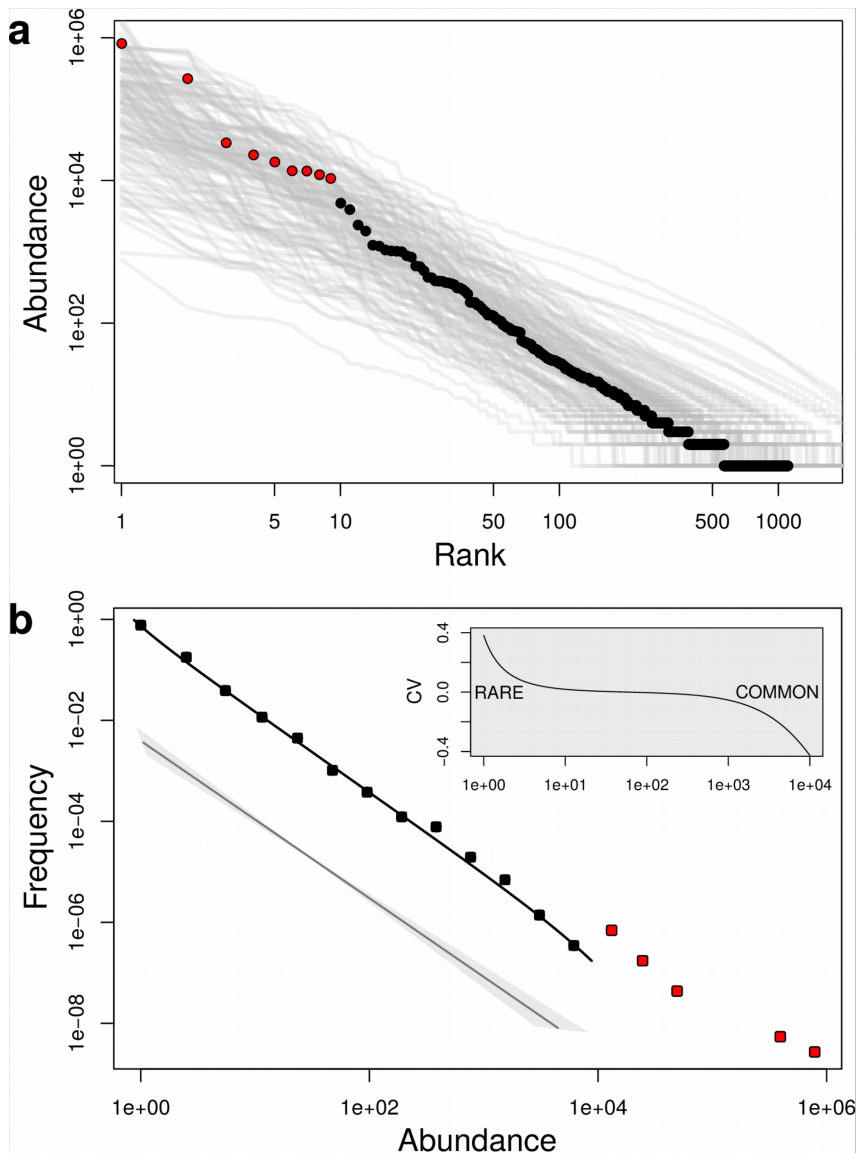


Figure 1 | Abundance distributions of protist swarms. a, rank-abundance plots for all local communities (grey) reveal that the abundance decay for non-dominant species is consistent across samples. Circles illustrate how dominant and non-dominant species get partitioned in one local community (same colours as in panel b). **b,** The corresponding empirical SAD (squares) is the histogram of swarms of similar abundance (logarithmic binning). The frequency of non-dominant species displays a different regime (black), than dominant ones (red). The distribution obtained by adaptively fitting the model equation (3) (black curve) describing the non-dominant component of the community, has a leading associated power-law trend whose exponent λ is given by equation (1). The limited range of variability across locations and sizes of this trend is illustrated below in grey. The straight gray line is a power-law with exponent corresponding to the average of λ

across all samples. The gray shaded region represents the extent of the power-law variation when the exponent varies within one standard deviation around such mean value. The inset displays the coefficient of variation between the best-fitting distribution given by equation (3) and its associated power-law, showing that the model can capture deviations from the power-law scaling for both abundant and rare species. The distribution used for this illustration has been chosen among those which display deviations from a power-law regime for both low and high abundances, and have a sizable dominant component. The fits for all samples are displayed in Supplementary Data 1.

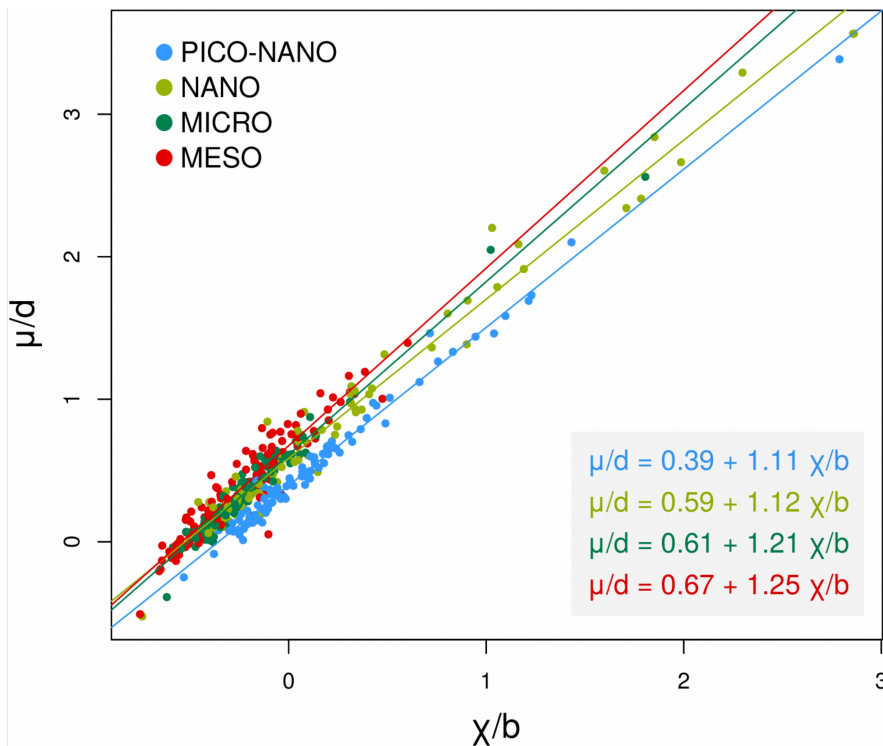


Figure 2 | Relationship between fitted nonlinear parameters. The independently fitted relative nonlinear rates μ/d and χ/b show a very strong linear covariation, best fitted by the equations in the inset. Such linear relations (solid lines) underpin the invariance of the power-law exponent (equation (1)) within a size class: the difference of the nonlinearity parameters is almost constant even though their sum, thus the deviation from the perfect power-law regime for low abundances, has a high variability. The decrease in the slope of the regression line with

size class corresponds moreover to the size-dependence of the power-law exponent, and illustrates that small size classes seem to follow more closely the relation among parameters (a line with unitary slope) predicted when the exponent λ is constant.

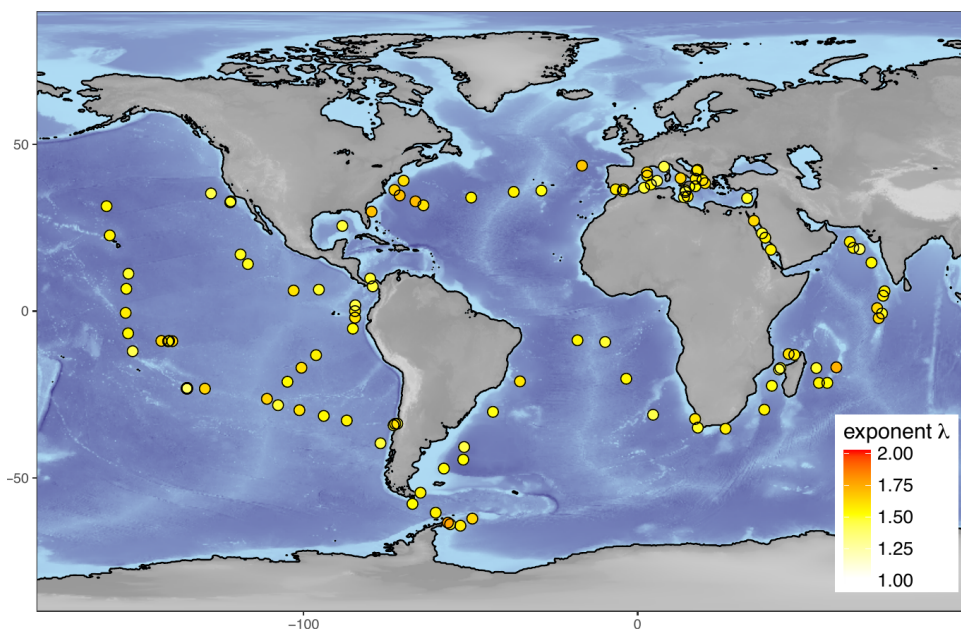


Figure 3 | Sample locations and their associated average power-law exponent. Global distribution of the power-law exponents associated to the best fitting distributions, averaged over size classes. The color of the dots indicates the value of such exponent in a given sampling location, and displays a remarkably small geographic variat

Main text table

	Fitted/total samples	Extension of the fit		% Swarms in the fit		r		χ/b		μ/d		λ	
		mean	CV	mean	CV	mean	CV	mean	CV	mean	CV	mean	CV
Pico-nano	99/103	9009	0.22	99.6	0.01	2.6e-04	0.77	0.07	5.29	0.47	0.89	1.40^a	0.06
Nano	54/60	9285	0.19	99.7	0.002	6.4e-05	1.72	-0.01	39.0	0.56	0.77	1.57^b	0.06
Micro	111/114	9523	0.17	99.6	0.003	5.7e-05	2.28	-0.27	0.89	0.28	1.00	1.55^b	0.05
Meso	108/111	8778	0.30	99.4	0.008	6.5e-05	2.92	-0.29	0.86	0.32	1.06	1.61^c	0.08
All sizes	372/388	9135	0.23	99.6	0.007	1.1e-04	1.73	-0.15	2.27	0.39	0.97	1.53	0.08

Table 1 | Parameters of the best fitting model. Results of the adaptive fit of the swarm-based SADs with equation (8) (Methods) and corresponding parameter statistics (mean and coefficients of variation across samples), separated by size fraction (pico-nano 0.8-5 μm , nano 5-20 μm , micro 20-180 μm , meso 180-2000 μm). The vast majority of samples can be fitted by the model to the confidence level of 0.1. The extension of the fit indicates that the model is followed for nearly 4 orders of magnitude in abundance, encompassing a broad non-dominant community. Despite variations in sampling location of the fit parameters (r , χ/b , μ/d), the associated power-law exponent λ has a coefficient of variation (< 8%) much smaller than any other contextual parameter (Methods), suggesting that rareness in plankton communities follows a ubiquitous scaling law. Superscripts behind λ values indicate groups assigned by the post-hoc Tukey's test (corrected $p < 0.05$) for differences between size fractions.