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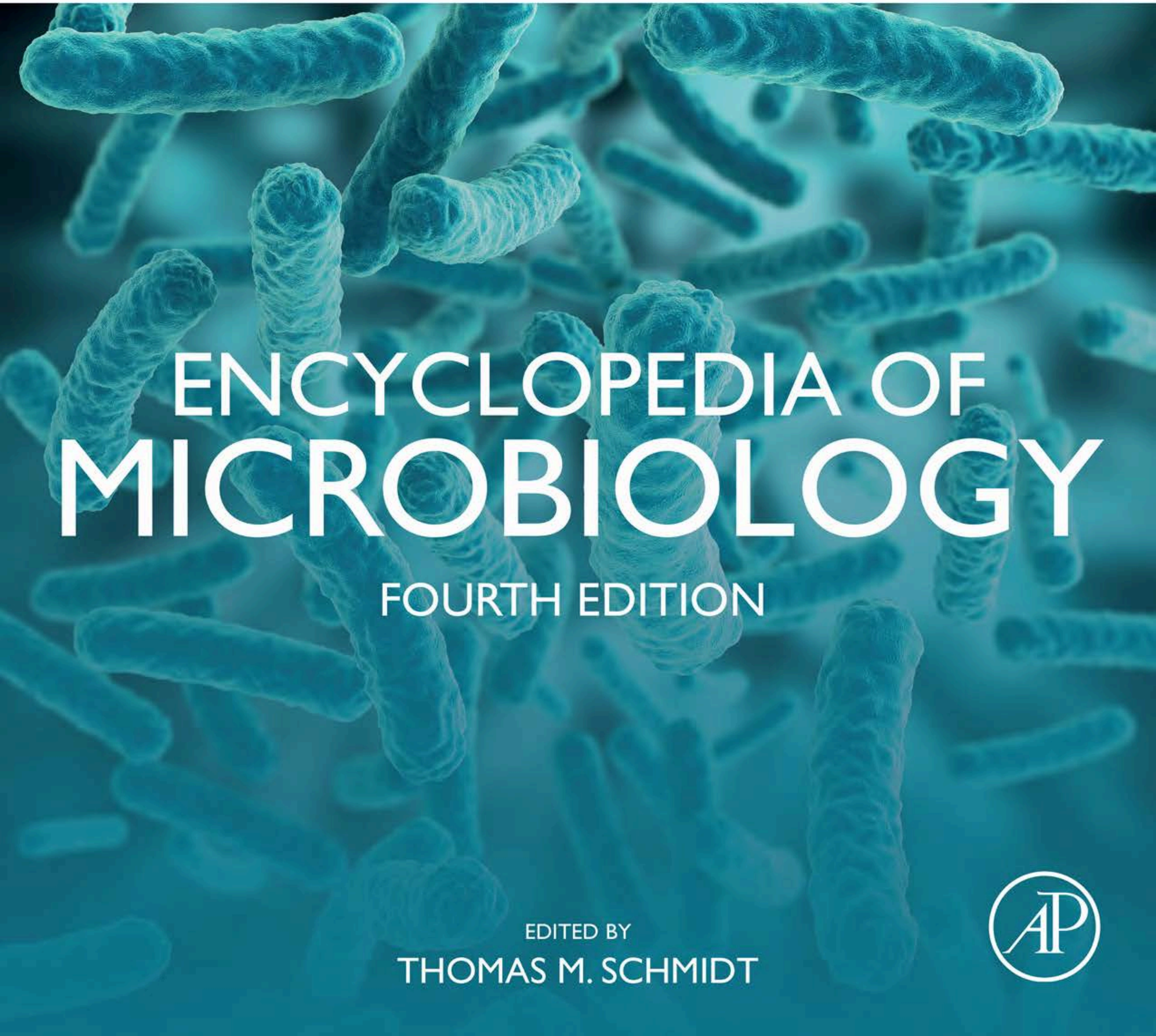

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Models in Microbial Ecology @ Encyclopedia of Microbiology

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Abstract

Mathematical modelling is nowadays a central tool in microbial ecology. Ecological theory and numerical modelling are essential for developing a deeper understanding of the mechanisms that shape the assembly and evolution of microbial communities. Microbes interact among themselves and with their environment in complex ways, and can display a very rich set of spatio-temporal dynamics. Modelling these processes is thus a challenging enterprise that needs to be subject to experimental validation. This chapter provides a review of the state-of-the-art of models in microbial ecology, ranging from the microscopic level (e.g. resource uptake) to the macroscopic level (e.g. spatial organisation). Special emphasis is given to the modelling of i) uptake kinetics, elemental stoichiometry and functional trade-offs; ii) food web and eco-evolutionary dynamics; iii) micro-scale variability and social behavior in microbes. The overarching point of view is the use of theoretical models to improve our understanding of how microbial communities operate and affect ecosystem functioning.

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Models in Microbial Ecology

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Introduction

The term *microorganism* or *microbe* refers to all unicellular organisms, which are microscopic in size ($< 1000\ \mu$m), including prokaryotes (bacteria and archaea) and unicellular eukaryotes (protists). Microbes are possibly the earliest evidence of life on Earth, approximately 3.700 million years ago (Dodd et al., 2017). Today, the vast majority of microbial prokaryotes (bacteria and archaea) on Earth are found in the open ocean (10^{29} cells), soils (10^{29} cells), deep oceanic and terrestrial subsurfaces (10^{30} cells). Bacteria are the largest contributor to global microbial biomass, followed by archaea, protists, and unicellular eukaryotes (Bar-On et al., 2018). The global biomass of bacteria on Earth is estimated to be 70 Gt Carbon, which constitutes 15% of global carbon biomass of all living organisms on Earth. This figure is dominated by terrestrial deep subsurface environments (60 Gt C) and marine deep subsurface environments (9 Gt C). The global biomass of archaea is estimated to be 7 Gt C, a figure dominated by terrestrial (4 Gt C) and marine deep subsurface (3 Gt C) environments. In open ocean environments, for instance, the abundance of bacteria is four times the abundance of archaeal cells (Bar-On et al., 2018), and the entire microbial food web, including protozoan microzooplankton, is generally from five to ten times the mass of all multicellular marine organisms (Pomeroy et al., 2007). The human gut is also a large reservoir of microbial prokaryotes, with the number of bacterial cells residing in the human body being of the same order as the number of human cells (i.e. close to a 1:1 ratio) (Sender et al., 2016), although is not as species rich (on the order of 10^2 bacterial ecotypes) compared to soils or oceans (Faith et al., 2013). Freshwater microbial eukaryotic richness is estimated to be on the order of $2{\cdot}10^4$ species (Debroas et al., 2017).

Microbes can live as single-cells or form colonies. In addition to their ubiquity and important contribution to the global pool of carbon, microorganisms play fundamental roles in several biochemical processes and their ecological importance is, nowadays, unquestionable (Prosser et al., 2007b). Marine microbial communities are at the bottom of the trophic food webs that ultimately feed global fisheries, and about one half of Earth's primary production occurs in the ocean (Field et al., 1998). Microbes control many processes that sustain life on Earth: they are crucial for virtually all biogeochemical processes, perform photosynthesis, and decompose inert organic matter into simpler compounds that are the basis of many food chains (Falkowski et al., 2008, Thompson et al., 2017). Moreover, they frequently constitute the basis of food webs themselves, both in marine and terrestrial ecosystems (Field et al., 1998). Microbial communities often live in association with host organisms, both plants and animals, including humans, where they have a very profound impact in controlling host's health and several aspects of their life cycles, such as flowering time in plants or reproductive behavior in animals (Wagner et al., 2014, Leitão-Gonçalves et al., 2017). From a biotechnological perspective, microorganism consortia are used to purify wastewater, control catalytic reactions, including those involved with biofuels, and increase crop yields (Halan et al., 2012, Mueller and Sachs, 2015). Finally, even though most microbes are harmless, some species are responsible for diseases that affect multicellular organisms, including humans (Costerton et al., 1999).

The aim of this chapter is to provide a summary of the state-of-the-art regarding the use of mathematical models in microbial ecology and plankton dynamics. Unveiling the means by which microbial communities assemble, stabilize, and operate is essential to predicting and manipulating their functions, and thus likely to be among the most important questions modern ecology faces. Such relevance arises not only from the intellectual merit of the question *per se*, but also from its utility for coping with many of the challenges that will confront human society in the coming years, such as the management of natural resources and ecosystems or the palliation of the effects of climate change (Prosser et al., 2007a). Despite this well-founded importance, there are large gaps of knowledge about the rules governing the assembly of microbial communities. Such gaps partly stem from the difficulty of studying microbes in their natural ecological context, which has biased the development of microbiology towards studies in which populations are treated in lab-created setups that do not capture the complexities of the natural environments. In this scenario, the development of ecological models, as shown in this chapter, and recent experimental efforts aiming to quantify species interactions in increasingly complex communities, can improve our understanding of how microbial communities operate and affect ecosystem functioning.

Uptake machinery

One of the main ways in which microbes interact with their environment is through their uptake machineries, which enable the harvesting of key resources that they require to grow. Autotrophic microbes, for example, harvest sunlight through their photosynthetic apparatus. Both autotrophs and heterotrophs capture key inorganic and/or organic nutrients using membrane transport proteins, also

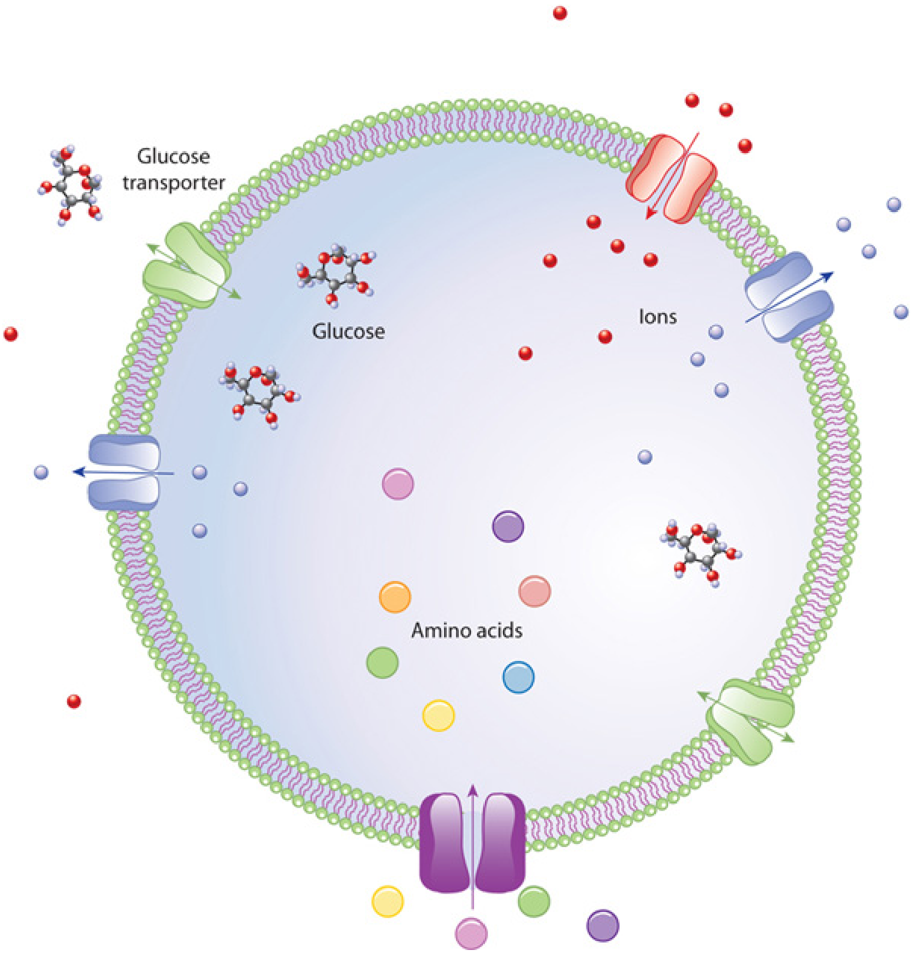

Fig. 1: Specialized proteins in the cell membrane regulate the concentration of specific molecules inside the cell. Picture credits: © 2010 Nature Education

called transporters (see Figure 1) (J, 1967). Models have considered uptake machineries in many different ways. The uptake of light by autotrophic microbes, for example, was initially approached simply as if it were one more nutrient (Jassby and Platt, 1976), although current models take into account the dynamics of cellular chlorophyll and the photosynthesis apparatus (Cullen, 1990). The classical representation for nutrient uptake, on the other hand, centers on the « Michaelis-Menten » (MM) functional form (Michaelis and Menten, 1913). This equation is based on theoretical considerations (see chapter "Enzyme Kinetics" of Lehninger's book (Nelson et al., 2008)) and has been supported by empirical observations leading to the « Monod model » of microbial growth (Monod, 1949).

If we call $U(R)$ to the uptake rate (mmol cell^{-1} day^{-1}) for a particular nutrient or resource R (mmol m^{-3}), the *canonical* MM equation is usually written as:

$$
\begin{aligned}
U(R) &= \frac{U_{max}\, R}{(U_{max}/A) + R} \\
&= \frac{U_{max}\, R}{K_R + R} \qquad (1)
\end{aligned}
$$

where U_{max} represents the maximum possible uptake rate (mmol cell^{-1} day^{-1}) of the cell; and A is the nutrient uptake affinity (m^3 cell^{-1} day^{-1}) of the cell. The ratio $K_R = U_{max}/A$ is called the half-saturation constant (mmol m^{-3}) because it represents the concentration of resources at which the uptake rate is half of its maximum ($U_{max}/2$). See BOX 1 for a step-by-step derivation of the MM equation and its use in resource uptake kinetics. See also (Aksnes and Egge, 1991, Nelson et al., 2008, Bonachela et al., 2011, Vallina et al., 2014b) for alternative derivations of the MM equation.

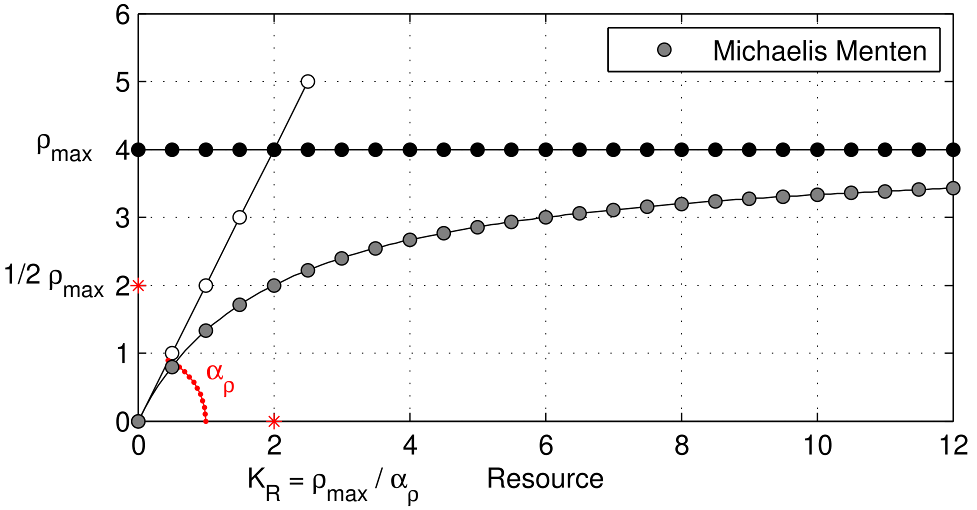

Fig. 2: Michaelis-Menten function (gray dots) that relates the specific uptake rate $\rho(R)$ (day^{-1}) to the external concentration of resources (mmol m^{-3}). The specific affinity α_ρ (m^3 mmol^{-1} day^{-1}) represents the initial slope of the curve at zero resource conentration (white dots). The specific maximum uptake rate ρ_{max} (day^{-1}) represents the horizontal asymptote (black dots) of the curve that is reached at infinite resource conentration. The lines for specific affinity and maximum uptake rate intersect at the half-saturation constant K_R. The specific affinity quantifies the competitive ability of microbes at low resource concentration, and specific maximum uptake rate quantifies the competitive ability of microbes at high resource concentration. Formally speaking, the specific affinity and specific maximum uptake rate are primary traits, while the half-saturation constant is a composite trait of these two primary traits ($K_R = \rho_{max} \ / \ \alpha_\rho$).

Sometimes it may be convenient to use instead biomass-normalized traits by defining $\alpha_\rho = A \ B^{-1}$ as the specific uptake affinity (m^3 mmol^{-1} day^{-1}) and $\rho_{max} = U_{max} \ B^{-1}$ as the specific maximum uptake rate (day^{-1}), where B is the cell's biomass (mmol cell^{-1}). Thus, if we call $\rho(R)$ to the biomass-specific uptake rate (day^{-1}) for resource R (mmol m^{-3}), the *biomass-specific* MM equation becomes:

$$\rho(R) = \frac{\rho_{max} \ R}{(\rho_{max}/\alpha_\rho) + R} = \frac{\rho_{max} \ R}{K_R + R} \tag{2}$$

The Michaelis-Menten model for resource acquisition described in Eq. (2) effectively summarizes the main features of the nutrient uptake apparatus using just two primary traits: specific affinity α_ρ and specific maximum uptake rate ρ_{max}. Graphically, the specific affinity α_ρ represents the initial slope of the curve that relates the specific uptake rate $\rho(R)$ to the external concentration of resources (Button et al., 2004), while the specific maximum uptake rate ρ_{max} represents the horizontal asymptote of the uptake curve that is reached at infinite resource conentration (see Figure 2). Ecologically, the specific affinity quantifies the competitive ability of microbes at low resource concentration, and the specific maximum uptake rate quantifies the competitive ability of microbes at high resource concentration. Formally speaking, the half-saturation constant is a composite trait of these two primary traits ($K_R = \rho_{max} \ / \ \alpha_\rho$). Extensions of Eq. (2) can be used to model the uptake of several substitutable forms of the same elemental nutrient (e.g. nitrate, nitrite, and ammonium forms of nitrogen), and can be combined with other expressions (e.g. Liebig's law of the minimum (de Baar, 1994)) to model the uptake of several non-substitutable nutrients (e.g. phosphorous, nitrogen, iron, etc).

The specific Michaelis-Menten equation for resource uptake can also be expressed as a function of the number n of transporters specific to the focal nutrient (sites cell^{-1}); the handling h rate of the nutrient ions per transporter (mmol site^{-1} day^{-1}); and the affinity a constant per transporter (m^3 site^{-1} day^{-1}), which results from considering the area of the transporter (m^2 site^{-1}) times its mass transfer efficiency (m day^{-1}) for the nutrient. Lets now define $\rho_{max} = nhB^{-1}$, $\alpha_\rho = naB^{-1}$, and $K_R = (\rho_{max}/\alpha_\rho) = (h/a)$, where B is the biomass of the cell (mmol cell^{-1}). That represents the MM uptake rate as a function of three major physiological traits of the cell, normalized by its biomass (B), providing further biological context to the MM uptake kinetics parameters. Then Eq. (2) becomes:

$$\rho(R) = \frac{(h \, n \, B^{-1}) \, R}{(h/a) + R} = \frac{(h \, n \, B^{-1}) \, R}{K_R + R} \tag{3}$$

BOX 1. Michaelis-Menten kinetics

- Enzyme-substrate reaction

The cannonical Michaelis-Menten equation was originally derived to describe enzyme-substrate kinetics (Michaelis and Menten, 1913, Briggs and Haldane, 1925). The MM equation describes the formation of a product (P) from a substrate (S), mediated by the binding interaction with an enzime (E) to form a complex enzime-substrate (ES) that finally releases the product. This two-step sequence of reactions (binding + catalysis) can be described by the following diagram:

$$[\mathrm{E}] + [\mathrm{S}] \quad \underset{\mathrm{k_d}}{\overset{\mathrm{k_a}}{\rightleftarrows}} \quad [\mathrm{ES}] \quad \overset{\mathrm{k_h}}{\rightarrow} \quad [\mathrm{E}] + [\mathrm{P}] \tag{4}$$

where $[\mathrm{S}]$ is the concentration (mmol m^{-3}) of substrate; $[\mathrm{E}]$ is the concentration (mmol m^{-3}) of free enzymes; $[\mathrm{ES}]$ is the concentration (mmol m^{-3}) of enzymes forming the enzyme-substrate complex (i.e. non-free enzymes); $[\mathrm{P}]$ is the concentration (mmol m^{-3}) of the product; $\mathrm{k_a}$ is the forward reaction rate constant (m^{3} mmol^{-1} d^{-1}) to form complex ES; $\mathrm{k_h}$ is the forward dissociation rate constant (mmol mmol^{-1} d^{-1}) of complex ES to form product P; and $\mathrm{k_d}$ is the reverse dissociation rate constant (mmol mmol^{-1} d^{-1}) of complex ES back to free enzimes and substrate. The law of mass action enables writing the reactions as a set of differential equations:

$$\frac{\mathrm{d[S]}}{\mathrm{dt}} = -\mathrm{F_a} \qquad + \mathrm{F_d} \tag{5}$$

$$\frac{\mathrm{d[E]}}{\mathrm{dt}} = -\mathrm{F_a} + \mathrm{F_h} + \mathrm{F_d} \tag{6}$$

$$\frac{\mathrm{d[ES]}}{\mathrm{dt}} = \mathrm{F_a} - \mathrm{F_h} - \mathrm{F_d} \tag{7}$$

$$\frac{\mathrm{d[P]}}{\mathrm{dt}} = \qquad \mathrm{F_h} \tag{8}$$

$$\mathrm{F_a} = \mathrm{k_a}\,[\mathrm{E}]\,[\mathrm{S}] \tag{9}$$

$$\mathrm{F_h} = \mathrm{k_h}\,[\mathrm{ES}] \tag{10}$$

$$\mathrm{F_d} = \mathrm{k_d}\,[\mathrm{ES}] \tag{11}$$

where $\mathrm{F_i}$ represents the fluxes (mmol m^{-3} d^{-1}) among state-variables in the system, each of them governed by a rate constant $\mathrm{k_i}$ (see arrows in equation Eq. (4)). The MM kinetics assumes a single binding site per enzyme, thus 1 mole of enzyme binds to 1 mole of substrate to form 1 mole of enzyme-substrate complex. The total concentration of enzymes $[\mathrm{E_T}]$ is assumed to be constant (i.e. conservation constrain) and is given by the sum of the free enzymes [E] plus the non-free enzymes forming the complex [ES]:

$$[\mathrm{E_T}] = [\mathrm{E}] + [\mathrm{ES}] \tag{12}$$

Assuming steady-sate of the complex $[\mathrm{ES}]$, solve for $[\mathrm{E}]$ using Eq. (7):

$$\mathrm{F_a} = \mathrm{F_h} + \mathrm{F_d} \tag{13}$$

$$[\mathrm{E}]\,[\mathrm{S}]\,\mathrm{k_a} = [\mathrm{ES}]\,(\mathrm{k_h} + \mathrm{k_d}) \tag{14}$$

$$\frac{[\mathrm{E}]\,[\mathrm{S}]}{[\mathrm{ES}]} = \frac{\mathrm{k_h} + \mathrm{k_d}}{\mathrm{k_a}} \equiv \mathrm{k_m} \tag{15}$$

$$[\mathrm{E}] = \mathrm{k_m}\,\frac{[\mathrm{ES}]}{[\mathrm{S}]} \tag{16}$$

where the parameter $\mathrm{k_m}$ is known as the Michaelis constant (mmol m^{-3}), a.k.a. half-saturation constant. Substituting Eq. (16) into Eq. (12) and solving for [ES]:

$$[\mathrm{E_T}] = \mathrm{k_m}\,\frac{[\mathrm{ES}]}{[\mathrm{S}]} + [\mathrm{ES}] = \frac{\mathrm{k_m} + [\mathrm{S}]}{[\mathrm{S}]}\,[\mathrm{ES}] \tag{17}$$

$$[\mathrm{ES}] = [\mathrm{E_T}]\,\frac{[\mathrm{S}]}{\mathrm{k_m} + [\mathrm{S}]} = \frac{[\mathrm{E_T}]\,[\mathrm{S}]}{((\mathrm{k_h} + \mathrm{k_d})/\mathrm{k_a}) + [\mathrm{S}]} \tag{18}$$

Substituting Eq. (18) into Eq. (8) and solving for the production rate of P:

$$\mathrm{V(S)} \equiv \frac{\mathrm{d[P]}}{\mathrm{dt}} = \frac{\mathrm{k_h\,[E_T]\,[S]}}{\mathrm{((k_h + k_d)/k_a) + [S]}} \tag{19}$$

The maximum production rate (mmol m^{-3} d^{-1}) occurs when all enzymes are tied to a substrate (i.e. saturating conditions), which means that there are no free enzymes ($\mathrm{[E]} = 0$) since they are all bound as enzyme-substrate complex ($\mathrm{[ES]} = \mathrm{[E_T]}$). Thus:

$$\mathrm{V_{max}} = \mathrm{k_h\,[E_T]} \tag{20}$$

Substituting Eq. (20) into Eq. (19) we obtain the final expression for the production rate V (mmol m^{-3} d^{-1}) of product P from substrate S:

$$\mathrm{V(S)} = \frac{\mathrm{k_h\,[E_T]\,[S]}}{\mathrm{((k_h + k_d)/k_a) + [S]}} = \frac{\mathrm{V_{max}\,[S]}}{\mathrm{k_m + [S]}} \tag{21}$$

- Resource uptake analogy

  By direct analogy, we can translate the canonical MM equation to model the uptake rate of resources by microbes using the following change of variables:

$$\mathrm{[S]} = \mathrm{[R]} \tag{22}$$

$$\mathrm{[E_T]} = n\,\mathrm{[N]} \tag{23}$$

$$\mathrm{k_a} = a \tag{24}$$

$$\mathrm{k_h} = h \tag{25}$$

$$\mathrm{k_d} \ll \mathrm{k_h} \tag{26}$$

$$\mathrm{k_m} = \mathrm{K_R} \tag{27}$$

  where $\mathrm{[R]}$ is the molar concentration of resource (mmol m^{-3}); $\mathrm{[N]}$ is the abundance of microbes (cells m^{-3}) in the population; n is the number of transporters per cell (sites cell^{-1}); a is the binding affinity per transporter (m^{3} site^{-1} d^{-1}) for the resource; and h is the handling rate per transporter (mmol site^{-1} d^{-1}) for the resource. Substituting Eqs.(22)–(27) into Eq. (21) gives the uptake rate of resource by the microbial population (mmol m^{-3} d^{-1})

$$\mathrm{V(R)} = \frac{h\,n\,\mathrm{[N]\,[R]}}{(h/a) + \mathrm{[R]}} \tag{28}$$

  Dividing equation Eq. (28) by the biomass concentration (mmol m^{-3}) of the microbial population $\mathrm{[C]} = B \times \mathrm{[N]}$, where B is the biomass per cell (mmol cell^{-1}), then leads to the MM equation for specific uptake rate (d^{-1}) of resource R by the microbial population, which was also previously defined in the main text (see equation Eq. (2)):

$$\begin{aligned} \rho(\mathrm{R}) \equiv \frac{\mathrm{V(R)}}{\mathrm{[C]}} &= \frac{h\,n\,B^{-1}\,\mathrm{[R]}}{(h/a) + \mathrm{[R]}} \\ &= \frac{\rho_{max}\,\mathrm{[R]}}{K_R + \mathrm{[R]}} \end{aligned} \tag{29}$$

Variations of Eq. 3 have been used to model the uptake of several nutrients by different transporters (see Section) or even the uptake of the same nutrient by several types of transporter (Button, 1998). Furthermore, Eq. (3) can be used to relate a « gleaner -- opportunist » trade-off to the three physiological traits that the cell can manipulate (number of transporters, their affinity, and their handling rate) by imposing that $\alpha_\rho \times \rho_{max} = (n/B)^2\;(h\;a) =$ constant (see Figure 4). See Section for more details.

The examples above, however, neglect the possibility for the cell to regulate the uptake apparatuses as a response to changes in the environment. This phenotypic plasticity has been documented in the past in a diversity of microbes and for a wide range of resources, including light as well as nutrients (Smith et al., 2009). Because they affect microbial growth, understanding these acclimation responses is essential to predicting reliably the role of microbes in ecosystem functioning (e.g. global biogeochemistry). In the case of light acclimation, modelled responses range from changes in pigments that optimize light uptake to photo-protective mechanisms limiting damages caused by excess of light to the photosynthetic apparatus (Armstrong, 2006, Geider et al., 1998, Litchman and Klausmeier, 2008). In the case of nutrient uptake, cells can for example alter the number and handling rate of transporters used to take up the focal nutrient. Most models focus on the commonly observed negative correlation between nutrient availability and maximum uptake rate ρ_{max} by means of phenomenological expressions (Morel, 1987). More mechanistic models include interactions between different ecophysiological processes and cellular nutrient pools by assuming instantaneous acclimation time (Geider et al., 1998, Smith et al., 2009, Pahlow and Oschlies, 2009), or including explicitly a dynamic equation for transporter regulation (Bonachela et al., 2011, 2013). Such models have been employed to reproduce successfully laboratory and field patterns that were not explained by non-plastic models (Smith et al., 2015, Lomas et al., 2014, Arteaga et al., 2016). Including a dynamic number of transporters allows equation Eq. (3) to account for another important feature that this MM equations neglect: the so-called boundary layer for the cell (see (Bonachela et al., 2011) and references therein for details). Mixing high- and low-affinity transport systems, where at least one system is inducible (i.e. whose expression is genetically regulated), is an alternative way of implementing plasticity of nutrient uptake. Under nutrient-replete conditions, there is a low affinity transporter that is always expressed; but under nutrient starvation, the synthesis of a high affinity transporter is switched on. This leads to a varying mix of two different uptake curves, in different proportions depending on the numbers of each transporter type (Lin et al., 2016, Caceres et al., (under review). However, phenomenologically this mix of the high and low affinity transporters can look like a single Michaelis-Menten uptake curve with phenotypic plasticity. Because in some well studied cases the genes of these regulatory systems are known (Martiny et al., 2006), this opens the venue for linking mechanistic modelling of uptake kinetics to ecological and evolutionary processes of microbes (see Sections and).

Although more experimental information is becoming available, our understanding of the wide diversity of microbial acclimation processes remains limited. One aspect that remains unknown, for example, is the metabolic cost of plasticity in the uptake apparatus which, as models have shown, potentially plays an important role in whether responding to environmental changes is beneficial or detrimental to the microbial organism (Menge et al., 2011); also, the evolutionary cost and trade-offs that emerge from the use of, e.g. the nutrient uptake apparatus as a gateway for viral infections by bacterio- and phyto-phages (Menge and Weitz, 2009). Finally, more and more models are now exploring the eco-evolutionary interactions that emerge from the overlap between acclimation in the uptake apparatus and microbial rapid evolution (Lomas et al., 2014, C.T. and C.A., 2013), interactions that are key to predict reliably microbial dynamics and their role in their environment.

Elemental stoichiometry

Understanding microbial elemental composition is essential to understanding the role that microbes play in local and global biogeochemistry (Geider and La Roche, 2002, Bonachela et al., 2016). Microbes require a wide range of micro- and macro- nutrients to grow and reproduce. Models for microbial growth typically rely on the Liebig's law of the minimum and focus only on the nutrient that limits most such growth (de Baar, 1994). However, the identity of this nutrient is highly species- and environment-specific. For example, whereas carbon is typically considered the limiting resource for bacteria such as *Escherichia coli* in terrestrial ecosystems, phosphorus typically limits microbes in fresh water, and nitrogen is limiting in marine environments (Sterner and Elser, 2002, Proctor and Karl, 2007, Moore et al., 2013). Iron is essential for all autotrophic microbes, whereas silica is only limiting for diatoms. Furthermore, in the absence of other mechanisms or competitive interactions, the number of elemental nutrients (i.e. that cannot be substituted one for another) imposes an upper limit in the number of microbial populations that can coexist at equilibrium in a single homogeneous habitat. In other words, the maximum number of microbial ecotypes coexisting at steady-state cannot exceed the number of essential resources, in the absence of environmental heterogeneity (either spatial and/or temporal) and/or stabilizing interactions (Grover, 1997) (see Section).

Based on the observation that several parts of the ocean show a remarkably constant ratio of key nutrients such as carbon, nitrogen, and phosphorus (Redfield, 1934, 1958), models have classically approached microbial elemental composition by focusing on the most limiting nutrient and calculating cell content and uptake of the rest of nutrients using the so-called Redfield ratios. Such approach has been used in aquatic ecosystem models, both at the local and the global level (e.g. (Follows et al., 2007)). However, more recent theoretical and field observations have shown that microbial elemental ratios are highly variable in the short and long term (Galbraith and Martiny, 2015), and that different microbial species manage such ratios in different ways in response to their environment (Martiny et al., 2013, Klausmeier et al., 2004a). Early models introduced the possibility of a dynamic ratio of, e.g. nitrogen to phosphorus assuming total independence between the two (Legovic and Cruzado, 1997, Klausmeier et al., 2004b, Smith and Yamanaka, 2007). Cells in these models show limitation by either one or the other nutrient, which provides arguments for coexistence between species that, for the same environmental conditions, are limited by different nutrients. Under this situation, a sufficient condition of stable coexistence is that each microbial ecotype must be a stronger competitor for the nutrient limiting its own growth than for the nutrients limiting its competitors' growth (Tilman, 1982, Grover, 1997). Except for extreme conditions such as high mortality rates, in these models the cellular elemental ratio matches that of the nutrients introduced in the environment, which is an homeostatic response that has been observed experimentally (e.g. (Rhee, 1978)). These models also replicate early laboratory observations regarding the existence of one single input ratio for which growth is limited by the two nutrients, which represents an optimum as it is the point with the least limitation by either resource (Rhee and Gotham, 1980).

For microbes, however, nutrients such as phosphorus and nitrogen are not completely independent from each other; for example, phosphorus is essential for protein synthesis (e.g. in the form of ATP), and proteins are mostly composed of nitrogen (Geider and La Roche, 2002). Models that have introduced interactions between the different cellular nutrient pools predict a much wider set of environmental conditions for which co-limitation is possible (Klausmeier et al., 2007, Pahlow and Oschlies, 2009, Bonachela et al., 2013, Agren, 2004, Arteaga et al., 2016) . As a consequence, the patterns of coexistence predicted by these more realistic models change significantly with respect to those of early models, which in turn affects their predictions regarding microbial community composition. Modelling such nutrient interactions is, nonetheless, a highly non-trivial task due to the multiple layers at which they occur and how the dynamics of microbial stoichiometry are intertwined with other resources (e.g. light, temperature (Moreno et al., 2018)) or cellular plastic responses to resource changes (e.g. regulation of nutrient uptake proteins; see Section). For the same reasons, essential aspects of such dynamics and their overall emergent results remain unknown. For example, the extent to which the correlation between microbial maximum growth rate and phosphorus content (the so-called growth rate hypothesis (Elser et al., 1996)) holds across organisms and different environmental conditions is still a matter of debate (Moody et al., 2017). There is also very little empirical and theoretical information regarding the interactions between the dynamics of elemental stoichiometry and that of nitrogen fixation (Pahlow et al., 2013), the latter affecting not only the focal organism's stoichiometry but also that of the rest of its community. Although current laboratory work aims to fill the knowledge gap regarding species-specific responses to different environmental conditions (e.g. (Mouginot et al., 2015, Edwards et al., 2015)), additional multidisciplinary efforts combining field, laboratory, and models are needed in order to unravel the dynamics of microbial stoichiometry.

Functional trade-offs

The efficiency of resource acquisition and utilization determines species competitive ability, and therefore contributes to its fitness. Several models have been proposed to mathematically encode nutrient uptake and its investment in population growth. One of the first attempts is the so-called Michaelis-Menten equation, in which cell growth is a saturating function of the concentration of external resources (Monod, 1949). The MM model assumes that resource uptake leads to growth *instantaneously*. Therefore, in this model there is no difference between both processes (uptake and growth) and they are perfectly coupled. However, even though this assumption provides a moderately accurate picture for constant or low-frequency fluctuating environments (Grover, 1990), the MM model may fail under high-frequency fluctuating conditions because it does not consider cell storage effects. A more detailed description is provided by the so-called Droop model of internal store (Grover, 1991), in which the level of nutrients stored in the cell (i.e., the cell quota) is described explicitly.

Internal store models consider that resource uptake and cell growth are two sequential processes that are decoupled. Resource uptake rate (mmol cell^{-1} day^{-1}) is represented by a saturating function $U(R)$ of the concentration of external resources R (mmol m^{-3}), such as the cannonical MM model (see Equation 1). Once absorbed, resources accumulate in the cell and determine the specific growth rate (d^{-1}) as a saturating function $\mu(Q)$ of the internal quota of resources Q (mmol cell^{-1}). In a seminal work (Droop, 1973), Droop proposed the following saturating dependence between growth rate and cell quota that has been widely used since:

$$\mu(Q) = \mu_\infty \left(1 - \frac{Q_{min}}{Q}\right) \tag{30}$$

where Q is the concentration of intracellular resources, μ_∞ the specific growth rate at infinite quota, and Q_{min} the minimum quota required for growth (Figure 3b). The parameters in Eq. (1) and Eq. (30) define a spectrum of resource acquisition and utilization strategies, and thus impact the species fitness. Therefore, they can be understood as functional traits (Violle and et al., 2007). Alternative forms of the Droop model can take into account the maximum storage capacity of the cell (Q_{max}) by replacing the constant μ_∞ by $\mu_\infty = \mu_{max}/(1 - Q_{min}/Q_{max})$, where $\mu_{\max}$ is the maximum specific growth rate at full storage of resources (Grover, 1997).

If parameters A, U_{max}, Q_{min}, Q_{max} and μ_{max}, in Eqs. (1) and (30) were independent from each other, it would be possible to evolve a super-species with the strongest competitive abilities regardless of the environmental conditions, often termed « Darwinian demon » . However, due to physiological constrains, functional traits very often correlate with each other in a way that one trait cannot increase indefinitely without the decrease of another (Figure 3c). These correlations lead to **trade-offs**, i.e. situations in which improving in one task weakens the performance in another task, and thus to the evolution of ecological strategies that are only selected for in a narrow range of environmental conditions.

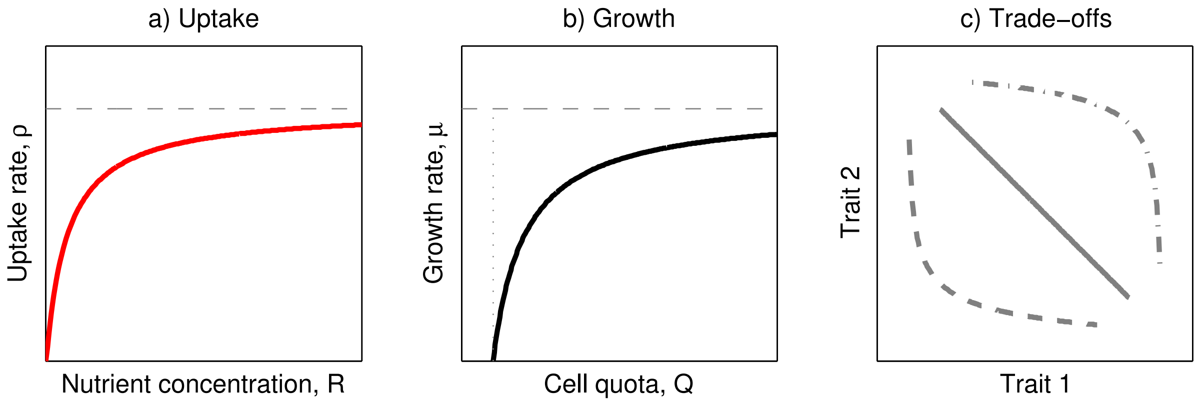

Fig. 3: a) Uptake rate as a function of the external nutrient concentration as defined in Eq. (2) -- the gray dashed line represents ρ_{max}; b) Growth rate as a function of cell quota -- the gray dashed line represents μ_{max} and the dotted line represents Q_{min}; c) Three possible shapes for two-trait trade-offs depending on how changes in one of the traits impact the other.

One of such trade-offs, experimentally measured in bacteria and phytoplankton (Healey and Hendzel, 1980, Button et al., 2004, Elbing et al., 2004), appears to exist between specific affinity α_ρ and specific maximum uptake rate ρ_{max} (Litchman et al., 2015b, Vallina et al., 2017) such that $\rho_{max} \times \alpha_\rho =$ constant, although the thermodynamic basis of this trade-off are yet unclear (Wirtz, 2002). This « affinity vs. handling-rate » trade-off defines a spectrum of resource uptake strategies from gleaners to opportunists, each of them adapted to different resource concentrations (see Figure 4). High affinities (and hence low ρ_{max}) constitute gleaner strategies that are favored at low concentrations of resources, while low affinities (and hence high ρ_{max}) constitute opportunistic strategies that are better competitors at high concentrations of resources (see Figure 4) (Grover, 1997, Fiksen et al., 2013). The root of this trade-off is the way uptake sites are packed in the finite cell surface (Aksnes and Egge, 1991) (see Eq. (3)). Assuming a fixed cell size: 1) for a constant handling rate per transporter (h), decreasing the number of transporters (n) while increasing their affinity (a) will lead to a gleaner strategy (and vice-versa); 2) for a constant affinity per transporter, decreasing the number of transporters while increasing their handling rate will lead to an opportunist strategy (and vice-versa); and 3) for a constant number of transporters per cell, increasing their handling rate while decreasing their affinity rate will lead to an opportunist strategy (and vice-versa); this last case provides the fastest transition from one strategy to the other (e.g. from blue to red in Figure 4). Finally, decreasing the number of transporters while increasing both their affinity and handling rates will lead to basically no change in the uptake strategy (see Figure 4). The affinity of a transporter increases with its active area, and the handling rate of a transporter increases with the speed at which the carrier protein change its shape when it moves molecules across the membrane (see Figure 1) although the exact mechanism is not well understood.

A variable cell size with a constant per-surface density of transporters (i.e. the proportion of the cell's surface covered by uptake sites) can also affect biomass-specific uptake rates. For a constant per-transporter affinity (a) and handling rate (h), both the specific affinity (α_ρ) and maximup uptake rate (ρ_{max}) should in theory decrease with cell size due to a concomitant decrease in the surface-to-volume ratio (Aksnes and Egge, 1991). There is strong experimental support for these allometric relationships for marine phytoplankton (Edwards et al., 2012) and the ecological implication is that the ability to compete for limiting nutrients should tend to decline with increasing cell volume in microbes (Chisholm, 1992). However other physiological limitations and trade-offs can appear with cell size, complicating this picture (Lindemann et al., 2016). For example, small cells (< 10 μm) have several physiological constrains (e.g. nonscalable components) that lead to low ρ_{max} (Marañon et al., 2013, Marañón, 2015). These limitations are less acute for larger cells because there is more internal space for catalytic and biosynthetic units, although other physiological constrains such as intracellular distances arise for much larger cells (Marañón, 2015). Large phytoplankton cells, such as diatoms, also have vacuoles that provide a high storage capacity for nutrients. These processes may help attenuate the negative effect of cell size on their biomass-specific effective growth rate and explain why relatively large cells (10 - 40 μm) usually have a dominant contribution (> 50 %) to total biomass under blooming conditions of opportunist phytoplankton (Marañón, 2015).

Since cell metabolism and functional traits are strongly linked to the microorganisms' size (Kempes et al., 2012, Marañón, 2015), they may also correlate with other traits, such as susceptibility to viral attacks or predation risk, that are influenced by cell size (Litchman and Klausmeier, 2008). Furthermore, due to the differences in species competitive ability at different external nutrient concentrations of the affinity -- handling-rate (or gleaner -- opportunist) trade-off defined earlier, if resources are provided in pulses rather than with a constant supply, the optimal uptake strategy changes as resources are depleted, leading to the formation of temporal niches that may favor the coexistence of competitors (Cermeno et al., 2011, Vallina et al., 2017). Functional traits and trade-offs are thus not

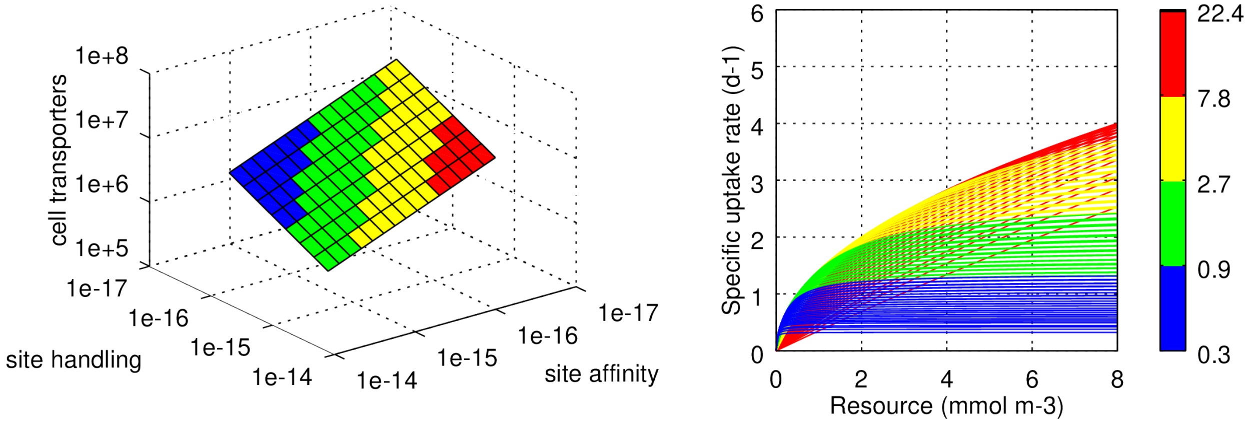

Fig. 4: A « gleaner *versus* opportunist » trade-off of the type $\rho_{max} \times \alpha_\rho = constant$ leads to: (Left panel) a plane in a 3D space that relates three cell traits, specifically: affinity rate per transporter (m^3 site^{-1} day^{-1}), handling rate per transporter (mmol site^{-1} day^{-1}), and number of transporters per cell (sites cell^{-1}), none of which can be maximized without minimizing another. (Right panel) an array of uptake strategies that gradually go from gleaner ecotypes (blue color) to opportunist ecotypes (red color) as measured from their biomass-specific uptake rate $\rho(R)$ (day^{-1}). Under fluctuating conditions of resource concentration, each of these strategies will dominate the community at their opimal nutrient concentration that is given by $N_{opt} = \rho_{max}/\alpha_\rho = K_R$ (half-saturation constant -- mmol m^3), where α_ρ is the specific affinity (m^3 mmol^{-1} day^{-1}) and ρ_{max} is the specific maximum uptake rate (day^{-1}) of each microbial ecotype. Under steady-state conditions, the uptake strategy with lowest Rstar (see Eq. 43) will tend to outcompete all other strategies asymptotically in time.

only important at the level of the individual, determined by physiological constrains and controlling individual performance; they also have fundamental implications in species competitive ability and ultimately impact population dynamics and community composition (Tilman et al., 1982, Litchman and Klausmeier, 2008, Litchman et al., 2015b). Additional processes, such as spatial heterogeneities in nutrient availability or in population density also foster species coexistence and contribute to explaining global patterns of species distributions (Vallina et al., 2014b, Tarnita et al., 2015, Martínez-García and Tarnita, 2017)

In addition to the trade-off in resource acquisition discussed above, other trade-offs linking nutrient acquisition and utilization have been quantified in microbes. For instance, three major strategies have been defined for phosphorus acquisition in phytoplankton (Litchman and Klausmeier, 2008): (i) rate-adapted species, represented by high uptake rate (ρ_{max}) and high growth rate (μ_{max}); (ii) storage specialist, represented by high ρ_{max} but low μ_{max}; and (iii) affinity-adapted species, represented by low ρ_{max} and high affinity α_ρ (Crowley, 1975). Related trade-offs have been also found between resource use efficiency and growth rate or between the use of different resources (nitrogen vs. phosphorous) in phytoplankton (Grover, 1997). Moreover, even though we have placed the focus here in competition for a shared resource as a fundamental driver of community composition, trade-offs have been also studied, both experimentally and theoretically, between different resource utilization abilities (Posfai et al., 2017). Finally, trade-offs also emerge in many other aspects of microbial lives, such as biofilm production (Nadell and Bassler, 2011), sporulation (Martínez-García and Tarnita, 2016, Wolf and et al., 2015) or chemotaxis (Yi and Dean, 2016). They also control various ecological processes that underlie the composition, dynamics and stability of microbial communities, such as dispersal to new environments, dormancy or foraging (see also Section).

Food web dynamics

Models of microbial food webs focus on simulating the flux of mass among species at different trophic levels (Mostajir et al., 2015). The structure of such interactions is usually represented with a network in which each node represents a species and links represent the existence of interactions between them. Food webs are a subclass of ecological networks (Montoya et al., 2006, Xiao et al., 2017) in which species are connected by prey-predator interactions (Allesina et al., 2008, Allesina and Pascual, 2008, Thompson et al., 2012). Planktonic communities of unicellular organisms, dominated by protists (unicellular algae and protozoa), bacteria, and viruses (Smetacek, 2002) constitute one of the best studied examples of microbial food webs. They were traditionally seen as linear food chains (Steele, 1974) until the discovery of feedbacks between the species in higher and lower trophic levels, termed the *microbial loop*, emphasized the complexity of their structure (Azam, 1998, Pomeroy et al., 2007) (Figure 5). Another example of microbial food webs are soil microbial communities, whose dynamics may shed light on the flows of energy that govern below-ground decomposition

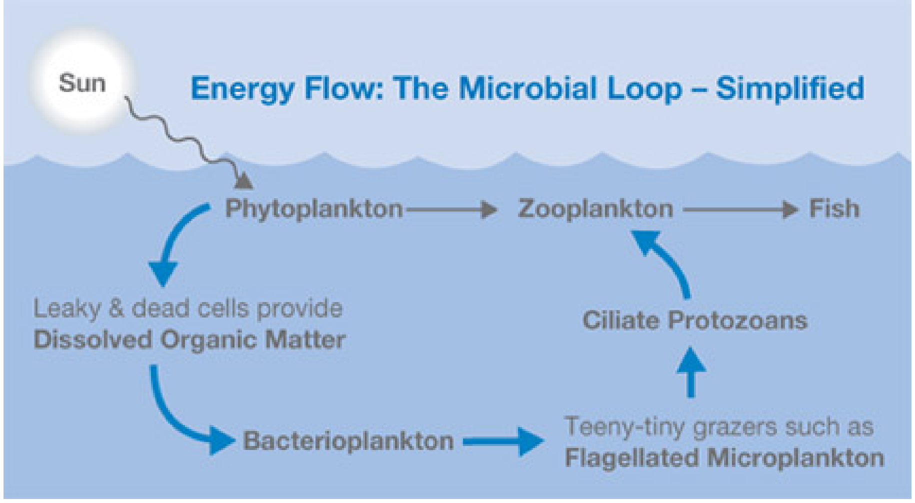

Fig. 5: Simplified marine food web incoporating both a food chain between different types of plankton (black arrows) and the microbial loop (blue arrows), mediated by the decomposed organic matter. Picture credits: 🅭 Sharon Moen (2005) (Moen, 2005)

processes and nutrient cycling (Scheu, 2002). The existence of prey-predator interactions leads to negative correlations among predator and prey populations (i.e. an increase in the abundance of predators leads to a decrease of their prey) (Wangersky, 1978). Population dynamics in food web models is remarkably rich and complex, ranging from equilibrium to oscillations and chaos (Murray, 2002b, Fussmann and Heber, 2002, Huisman and Weissing, 1999).

The general equation describing the dynamics of a food web, assuming linear Lotka-Volterra (LV) interactions, is:

$$\dot{x_j} = x_j \left(\sum_i \alpha_{ji}\, x_i - m_j \right) = x_j \;\, g_j(\mathbf{x}) \tag{31}$$

where $\dot{x_j}$ (mmol m^{-3} d^{-1}) represents the rate of change in the concentration of focal species j (mmol m^{-3}); α_{ji} (m^3 mmol^{-1} d^{-1}) is the strength of the interaction of species i upon species j (which is positive when i is a prey of j and negative when i is a predator of j); and m_j (d^{-1}) gives the background mortality rate of species j (see BOX 2). LV equations assume that the predator-prey (i.e. resource-consumer) interactions do not saturate at high prey concentration because the biomass-specific handling rate of the predators is much higher than their biomass-specific affinity ($\rho_{ji}^{max} \gg \alpha_{ji}$). Hence, the interaction is mainly governed by the affinity (see Eq. (2) after assuming that $\alpha_\rho / \rho_{max} \approx 0$). Furthermore, even if we relax this constrain, the assumption of a linear functional response between predator may still be valid when prey concentration is relatively low. For example, for prey i concentration values lower than the 25% of the predators j half-saturation constant $K_{ji} = \rho_{ji}^{max} \,/\, \alpha_{ji}$ (mmol m^{-3}) the linear approximation and the non-linear saturating curve are quite similar (see Figure 2). This implies that the LV model assumes that the food web interactions are essentially limited by the encounter rate between predator and prey, either because of the fast handling rate of predators and/or because of the low concentration of prey.

The α_{ji} values are the elements of the Interaction matrix ($\mathbf{A}$) of the LV food web. Element $\alpha_{ji} = \partial(\dot{x_j}/x_j) \,/\, \partial x_i$ (m^3 mmol^{-1} d^{-1}) provides the linear effect that a small change in the concentration of species i has on the *biomass-specific* rate of change ($\dot{x_j}/x_j$) of species j (Novak et al., 2016). From a mathematical point of view, the Interaction matrix is related to the Jacobian matrix ($\mathbf{J}$) of the LV model linearized around the steady-state equilibrium x^*, because $\mathbf{J} = \mathrm{diag}(\mathbf{x}^*)\,\mathbf{A}$ (see BOX 3). The elements $\mu_{ji} = \partial\dot{x_j} \,/\, \partial x_i$ (d^{-1}) of the Jacobian matrix provide the linear effect of a small change in the concentration of species i on the *absolute* rate of change ($\dot{x_j}$) of species j at equilibrium (Berlow et al., 2004). That is, if a change in the concentration of a given species i does not affect the rate of change of another species j, then they are not linked (either directly or indirectly) in the food web (Novak et al., 2016). When predator i and prey j are connected, then $\alpha_{ji} > e_i\, \alpha_{ij}$, where $0 < e_i < 1$ is the assimilation efficiency of predator i. Therefore, the Interaction matrix is said to be "skew-symmetric" because the negative effect of predator i on prey j is larger (in absolute magnitude) than the positive effect of prey j on predator i by a constant factor. For the Jacobian matrix this is not necessarily the case because its elements are proportional to the concentration of the species at equilibrium, and inverted biomass pyramids (i.e. top heavy) are possible (Barbier and Loreau, 2019). The Jacobian matrix is important when modelling microbial communities because its eigenvalues inform about the asymptotic stability (Allesina and Tang, 2012, Coyte et al., 2015) of the network to small perturbations of the steady state (i.e. food web resilience – see BOX 3). The diagonal elements of the Jacobian (μ_{jj}) represent the strength of the interaction of a species j with itself, and are usually considered to be negative (e.g. intra-specific competition). Negative interactions in these diagonal elements of the Jacobian mimic the existence of a carrying capacity (e.g. through quadratic mortality or self-regulation) for each species, leading to the *logistic equation* (Murray, 2002a). This promotes asymptotic stability of the network at equilibrium by preventing excessive growth of any microbial species (Haydon, 1994). While negative diagonal elements μ_{jj} are stabilizing, the off-diagonal elements μ_{ji} are destabilizing (Neutel et al., 2002). The Jacobian matrix ($\mathbf{J} = \mu_{ji}$) is said to be *negative diagonally dominant* and thus stable (Hofbauer and Sigmund, 1988, Logofet, 1993) if there is a set of positive numbers $\pi_1, \pi_2, ...\pi_n$, such that $\pi_j\,\mu_{jj} + \sum_{i \neq j} \pi_i\,|\mu_{ji}| < 0$. In other words, if for each species j in the network the intra-specific competition ($\mu_{jj} < 0$) is stronger than the sum of all the inter-specific interactions μ_{ji} affecting species j.

BOX 2. Lotka-Volterra food webs -- Steady states

Resource-ratio (R^* rule)

$$\frac{\mathrm{d}x_j}{\mathrm{d}t} = \text{NetGrowth} - \text{NaturalMort}$$

$$\left.\frac{\mathrm{d}x_j}{\mathrm{d}t}\right|_{x^*} = (\alpha_j R - m_j)\,x_j = 0$$

$$(\alpha_j R - m_j)\,x_j = 0$$

$$R^* = \frac{m_j}{\alpha_j} = \left(\frac{\text{Mortality rate of consumer } x_j \text{ upon resource } R}{\text{Affinity rate of consumer } x_j \text{ upon resource } R}\right) \tag{32}$$

Food Chain $(\ h = j-1\ <\ j\ <\ k = j+1\ )$

$$\frac{\mathrm{d}x_j}{\mathrm{d}t} = \text{NetGrowth} - \text{GrazingMort} - \text{NaturalMort}$$

$$\left.\frac{\mathrm{d}x_j}{\mathrm{d}t}\right|_{x^*} = (\ \ \alpha_j\,x_h \ \ - \alpha_k\,x_k \ \ - m_j)\,x_j = 0$$

$$(\ \ \alpha_j\,x_h \ \ - \alpha_k\,x_k \ \ - m_j)\,x_j = 0$$

$$x_h^* = \frac{m_j + (\alpha_k\,x_k^*)}{\alpha_j} = \left(\frac{\text{Mortality rate of predator } x_j \text{ upon prey } x_h}{\text{Affinity rate of predator } x_j \text{ upon prey } x_h}\right) \tag{33}$$

Food Web ($h =$ **prey** $<\ j\ <\ k =$ **predator**)

$$\frac{\mathrm{d}x_j}{\mathrm{d}t} = \text{NetGrowth} - \text{GrazingMort} - \text{SelfMort} - \text{NaturalMort}$$

$$\left.\frac{\mathrm{d}x_j}{\mathrm{d}t}\right|_{x^*} = (\sum_h \ \ \alpha_{jh}\,x_h \ \ - \sum_k \alpha_{jk}\,x_k \ \ - \alpha_{jj}\,x_j \ \ - m_j)\,x_j = 0$$

$$(\sum_i \alpha_{ji}\,x_i \ \ - m_j)\,x_j = 0$$

$$\sum_i \alpha_{ji}\,x_i^* \ \ = m_j \tag{34}$$

Matrix notation

$$\dot{x_j} = x_j\,(\sum_i \alpha_{ji}\,x_i - m_j) = 0$$

$$\dot{\mathbf{x}} = \mathrm{diag}(\mathbf{x})(\mathbf{A}\,\mathbf{x} - \mathbf{m}) = \mathbf{0}$$

$$\mathbf{x}^* = \mathrm{inv}(\mathbf{A})\ \mathbf{m} \approx \left(\frac{\text{Mortality rate of all predators } j > i \text{ upon prey } x_i}{\text{Affinity rate of all predators } j > i \text{ upon prey } x_i}\right) \tag{35}$$

BOX 3. Lotka-Volterra food webs -- Stability analysis

The general form a multi-species food web ecosystem model is:

$$\frac{\mathrm{d}x_j}{\mathrm{d}t} \equiv \dot{x_j} = g_j(x_1, x_2, ..., x_N)\, x_j = g_j(\mathbf{x})\, x_j = f_j(\mathbf{x}) \tag{36}$$

where x_j (mol m^{-3}) refers to a given state-variable j in the ecosystem that can change with time ($x_j \equiv x_j(t)$), such as the concentration of one species when it refers to a biotic variable or the concentration of abiotic nutrients if they are explicitly resolved in the model. The integer value N gives the total number of variables in the ecosystem; and $g_j(\mathbf{x})$ gives the specific rate of change (d^{-1}) of x_j as a non-linear function g_j of the concentration of the relevant interacting variables specified as a vector $\mathbf{x} = x_1, x_2, ..., x_N$. When $g_j(\mathbf{x}) > 0$ the population x_j grows, and when $g_j(\mathbf{x}) < 0$ the population x_j decreases. Therefore $\dot{x_j} = f_j(\mathbf{x})$ gives the absolute rate of change (mol m^{-3} d^{-1}) of variable x_j at any time as a function of its non-linear interactions with the other variables in the food web. Solving (integrating in time) this system of differential equations gives the time series of each variable x_j. The species concentration in the steady-state (x_j^*) are the *fixed points* of Eqs. (36), which are obtained by setting all the rates of change $\dot{x_j}$ for all j equal to zero:

$$\dot{x_j} = f_j(\mathbf{x}^*) = 0 \tag{37}$$

A fixed point is defined as any vector $\mathbf{x}^*$ with coordinates $(x_1^*, x_2^*, ..., x_N^*)$ in the phase space in which the concentration of the variables do not change with time (i.e. the time series are flat). It is possible that a system has more than one feasible (i.e. with positive concentrations) fixed point and therefore multiple steady-states. A steady state can be locally stable, neutrally stable, or unstable; depending on the dynamics of the system in the vicinity of the fixed point (see Figure 6). Thus in order to study that dynamics, we add an infinitesimal perturbation to each steady-state concentration:

$$\mathbf{x}(t) = \mathbf{x}^* + \Delta\mathbf{x}(t) \tag{38}$$

where $\Delta\mathbf{x}(t=0) = \epsilon\, \mathbf{x}^*$ with $\epsilon \ll 1$, and calculate the change of the perturbation $\Delta\mathbf{x}(t) = \mathbf{x}(t) - \mathbf{x}^*$ over time. When $\Delta\mathbf{x}(t) > 0$ the perturbed community departs from its fixed point (which is thus unstable), and when $\Delta\mathbf{x}(t) < 0$ the perturbed community returns to its fixed point (which is thus stable). To study the change with time of this perturbed community $\Delta\mathbf{x}(t)$ by means of Eq. (36) we need to *linearise* the original non-linear system around the fixed point. This will give a linear approximation of the original non-linear system only valid for small departures from the steady-state. For larger perturbations, the behavior of the linear system can be significantly different to that of the original non-linear one, and the approximation may no longer be valid. To linearise Eqs. (36), we obtain its Taylor expansion around the fixed point and neglect terms of second order (i.e. $\mathcal{O}(\epsilon^2)$) and higher (May, 1974, Novak et al., 2016):

$$\Delta\dot{x_j} \approx \sum_{i=1}^{N} \frac{\partial f_j(\mathbf{x}^*)}{\partial x_i}\, \Delta x_i = \sum_{i=1}^{N} (\alpha_{ji}\, x_j^*)\, \Delta x_i = \sum_{i=1}^{N} (\mu_{ji}\, \Delta x_i) \tag{39}$$

$$\alpha_{ji} = \left.\frac{\partial(\dot{x_j}/x_j)}{\partial x_i}\right|_{\mathbf{x}^*} \qquad \mu_{ji} = \left.\frac{\partial \dot{x_j}}{\partial x_i}\right|_{\mathbf{x}^*} \tag{40}$$

where α_{ji} (m^3 mol^{-1} d^{-1}) measures the effect of population i on the *biomass-specific* growth of population j, and $\mu_{ji} = \alpha_{ji}\, x_j^*$ (d^{-1}) measures the effect of population i on the *absolute* growth of population j; both at fixed point $\mathbf{x}^*$ in the linearised system. For example, the value $\mu_{jh} = \alpha_{jh}\, x_j^*$ defines the (linearised) interaction of prey at lower trophic level h on predator j (growth of j due to ingesting h); the value $\mu_{jk} = -\alpha_{jk}\, x_j^*$ defines the interaction of predator k on prey at lower trophic level j (mortality of j due to predation by k); and the value $\mu_{jj} = -\alpha_{jj}\, x_j^*$ defines the interaction of population j on itself (quadratic mortality of j due to intra-specific competition), if any. Note that $\alpha_{jh} = e_j\, \alpha_{hj}$, where $0 < e_j < 1$ is the assimilation efficiency of population j, which means that predator j has stronger negative effect on the growth rate of prey i than the positive effect that prey i has on the growth rate of predator j. This is because only a fraction of the prey ingested will be assimilated into predators' biomass, which leads to the skewed symmetry of the food web interactions.

An equivalent but more compact matrix notation can be used for Eq. (39):

$$\Delta\dot{\mathbf{x}}(t) \;=\; \mathbf{J}\;\Delta\mathbf{x}(t) \tag{41}$$

where $\mathbf{x}$ is the $(N$ x $1)$ column vector of x_j (mol m^{-3}), $\dot{\mathbf{x}}$ is their absolute rate of change (mol m^{-3} d^{-1}) and $\mathbf{J} = \partial\dot{\mathbf{x}} \,/\, \partial\mathbf{x}$ is the $(N$ x $N)$ *Jacobian matrix* whose elements μ_{ji} (d^{-1}) are defined in Eq. (40). The off-diagonal elements μ_{ji} of $\mathbf{J}$ measure the inter-specific interactions, while the diagonal elements μ_{jj} measure the intra-specific interactions. Note that linearising a non-linear ecosystem leads to assuming linear Lotka-Volterra (LV) dynamics around its fixed point(s). The analytical solution of this linear ecosystem gives the change with time of the perturbed food web:

$$x_j(t) = x_j^* + \Delta x_j(t) = x_j^* + \sum_{i=1}^{N}(c_i\, \boldsymbol{v_i}\, e^{\lambda_i t}) \tag{42}$$

where c_i are constants, and λ_i are the *eigenvalues* corresponding to the *eigenvectors* $\boldsymbol{v_i}$ of the Jacobian matrix such as $\mathbf{J}\,\upsilon_i = \lambda_i\,\upsilon_i$. This simply means that a linear transformation $\mathbf{J}$ applied to υ_i (eigenvector i) may change is its length by a factor λ_i (eigenvalue i). Thus the eigenvectors of $\mathbf{J}$ can be stretched (unstable) or contracted (stable) by their eigenvalues, but they do not change direction because they are linearly independent among them. The eigenvalues may be complex numbers, but the system's resilience is given by their real part. For the system to be *stable* in the vicinity of a given steady-state, (the real part of) all eigenvalues of $\mathbf{J}$ must be negative. This can be easily understood by inspecting Eq. (42): if one (or more) eigenvalues is positive, the perturbation grows exponentially with time and thus that particular fixed point would be unstable. If we define the *dominant* eigenvalue (λ_d) as the largest eigenvalue, a necessary and sufficient condition for stability is that $\lambda_d < 0$. For non-positive eigenvalues if the real part of (at least) the dominant eigenvalue is zero, the steady-state is *neutrally stable* (the perturbation does not move along at least one eigenvector). The eigenvectors with negative eigenvalues form the stable eigenspace (*stable manifold*); the eigenvectors with positive eigenvalues form the unstable eigenspace (*unstable manifold*); the eigenvectors with zero eigenvalues form the neutrally stable eigenspace (*center manifold*). A summary of the several stability regimes of fixed points (e.g. stable or unstable nodes, stable or unstable spirals, unstable saddle points, neutrally stable centers) and their relationship to the two major properties of the Jacobian matrix (its trace and determinant) can be found in Figures 6 and 7. This asymptotic stability analysis must be performed around all the feasible steady-states of the system (there might be more than one) to obtain the whole picture of the stability properties of the food web ecosystem in its N-dimensional phase-space.

When essential nutrients are not explicitly included in the simulated food web, the nutrient competition among basal species must be implicitly assumed by imposing negative α_{ji} elements in the Interaction matrix. This is probably one of the major criticisms of classical food web models (see Eq. 36), because this simple approach lacks mechanistical foundations. Thus, it is usually advisable to add (at least) one essential abiotic nutrient N to the system by imposing a mass conservation constrain (that is, the total mass N_{tot} must be constant) such that $N = N_{tot} - \sum_j x_j$ (Grover, 1997). This basically means closing the system in terms of mass circulation and thus that the sum of all the differential equations is zero ($\dot{N} + \sum_j \dot{x_j} = 0$). When this constraint is explicitly included in the simulated food web, introduces a carrying capacity for the *whole* food web (i.e. all nodes) because there is an upper limit to the whole community density given by the total mass N_{tot} in the system. Furthermore, the interaction of consumers that are not connected by predator-prey links but share the same resource(s), may be indirectly channeled through *resource competition* for the same pool of essential nutrients or common prey. That means that there is no need to impose non-zero elements in the Interaction matrix for their interaction. Another interesting feature of any food web (simulated or real) is the presence of indirect interactions among the species comprising the food web: even species that are not linked by direct predator-prey interactions (they don't prey upon each other) can be connected if they share a common predator, leading to *apparent competition* (Holt, 1977, Holt and Bonsall, 2017).

The temporal dynamics of food webs depends, therefore, on both bottom-up and top-down controls (de Ruiter et al., 1995). Resource supply acts as bottom-up control, while predator (or virus) induced mortality acts as top-down control. This mesh of interactions is usually composed by many weak and few strong linkages between species (Neutel et al., 2002). Top-down controls can be either stabilizing or destabilzing of food web dynamics depending on the functional form of the predatory response (Abrams and Allison, 1982, Haydon, 1994). While the LV equations assume linear functional relationships, more mechanistically driven models of microbial food webs use non-linear functional forms ((Ward et al., 2012)). In addition, food web models can include killing-the-winner (KTW) mortality of microbial communities, either by viral infection (Thingstad, 2000, Winter et al., 2010) or by preferential grazing (Vallina et al., 2014b). KTW is known to stabilize food web dynamics because it is an equalizing mechanism that « down-regulate the winners and up-regulate the losers » through density-dependent mortality (i.e. predator-mediated coexistence). KTW has a similar effect as density-dependent (e.g. quadratic) self-mortality because it also makes the diagonal elements of the Jacobian to be more negative (Haydon, 1994). Since trophic relationships add potential interactions among species, both directly and indirectly, microbial food webs bring together population-, trophic-, and ecosystem-level processes. The existence of these connections across and within different levels opens the possibility for trophic cascades (Duffy et al., 2007) and positions species interactions as biological filters that can propagate environmentally-driven fluctuations in species densities throughout the community (Ives et al., 2000, 2003). Although food webs have thus been suggested to amplify environmental fluctuations (Ives et al., 2003, Barbier and Loreau, 2019), this theoretical prediction assumes linear interactions between species for mathematical simplicity and analytical tractability. More realistic interactions are known to be highly non-linear (e.g. density-dependent interactions). Thus, due to non-linearities, food webs could be biological filters that actually dampen environmental perturbations throughout the community.

Loop length and loop weight analyses (LLA, LWA) are mathematical tools for exploring the structure and organization of trophic food webs by studying how the strength of feeding interactions affects the stability of the system. Loop length is defined as the number of different species visited through a closed pathway of interactions (i.e. ending back to the starting species) without visiting other species more than once. Loop weight is defined as the geometric mean of the absolute values of the interaction strengths in a loop (Neutel et al., 2002). The skewed combination of many weak and few strong links of predator-prey interactions within long network loops has been suggested to increase the stability of food webs (Neutel et al., 2002). However, this prediction is based on rigid non-selective predator-prey interactions, which are known to lead to ecosystem instability if they are too strong (Neutel et al., 2007). The relative contribution of weak and strong links in microbial communities may be affected by more flexible KTW interactions. In addition to loop length and loop weight, other topological properties of networks related to stability are connectivity, interaction strength, centrality, modularity and nestedness (Berlow et al., 2004, Landi et al., 2018). Connectivity measures the density of links in the network; interaction strength measures how strong these links are; centrality measures how important a node is in the network (e.g. keystone species), either because it is highly connected (to many other nodes), does so strongly (channels large flows of mass energy), or because it governs many indirect interactions and/or can trigger many secondary extinctions if the node is removed (Dunne et al., 2002); modularity implies that the network is composed of distinct and densely connected subsystems (Grilli et al., 2016); nestedness means that the diet of the most specialized species is a subset of the diet of the next more generalized species, and its diet a subset of the next more generalized, and so on (Montoya et al., 2006). These properties define the patterns of ecological networks and are used to evaluate their stability and robustness (Montoya et al., 2006, Grilli et al., 2016)

Despite the extensive research and the many models developed during the last four decades, the exact mechanisms that stabilize food webs are yet not fully understood. Early work focused on measures of stability at equilibrium (see BOX 3) and predicted that more complex food webs should lead to more unstable ecosystems (May, 1974, Harrison, 1979, Pimm, 1984). However, these predictions are challenged by field observations in both terrestrial and aquatic systems, and thus newer theories have moved the focus to aggregated community-level properties under non-equilibrium conditions (Loreau, 2010a). Yet, the analysis of microbial food web models in the steady-state is a powerful tool to predict the outcome of competition in microbial communities (i.e. species persistence) subject to lab-controlled conditions such as chemostat bioreactors (Grover, 1997, Tilman, 1982). Assuming LV interactions (Lotka, 1920, Volterra, 1928), we can predict the steady-state abundance of the different populations that form the food web. For the simplest case of a trophic interaction composed of one abiotic resource shared by several consumers, the « R-star » rule applies. The concentration of the resource at equilibrium (R^*) in a mono-culture of the consumer is given by the ratio between the mortality rate (m_j) and the uptake affinity (α_j) of the consumer j (see Eq. (32) in BOX 2). The consumer that is able to subsist at the lowest resource concentration after reaching equilibrium (i.e. lowest R^*) will eventually outcompete all other consumers (Tilman, 1982). However, this theoretical prediction only holds in the absence of stabilizing mechanisms (e.g. self-regulation), which can lead to some degree of species coexistence at steady-state (see above). The same rule applies to food webs, considering that the consumers j at lower trophic levels are the resources of consumers k at higher trophic levels. In the simplest scenario of linear food chains there is only one species per trophic level, and the concentration at equilibrium of the species at trophic level $(j-1)$ is given by the ratio between the mortality rate and the grazing affinity of its consumer at trophic level j (see Eq. (33) in BOX 2). Note that the equilibrium of each species does not depend on their own physiological traits but on those of their predators. Food chains based on linear predator-prey interactions have been very influencial in the development of ecological theory and understanding their dynamics serves as the cornerstone for studying more complex food webs and functional responses (see (Barbier and Loreau, 2019) for a review). For the most complex case of a multi-species and multi-trophic level food web, considering that species in a given trophic level j may serve as resource of the consumers at several trophic levels above it ($k > j$), the steady-state of x_j will depend on the ratio between a combination of the mortality rates and grazing affinities of those higher-trophic level consumers feeding on him (see Eq. (35) in BOX 2).

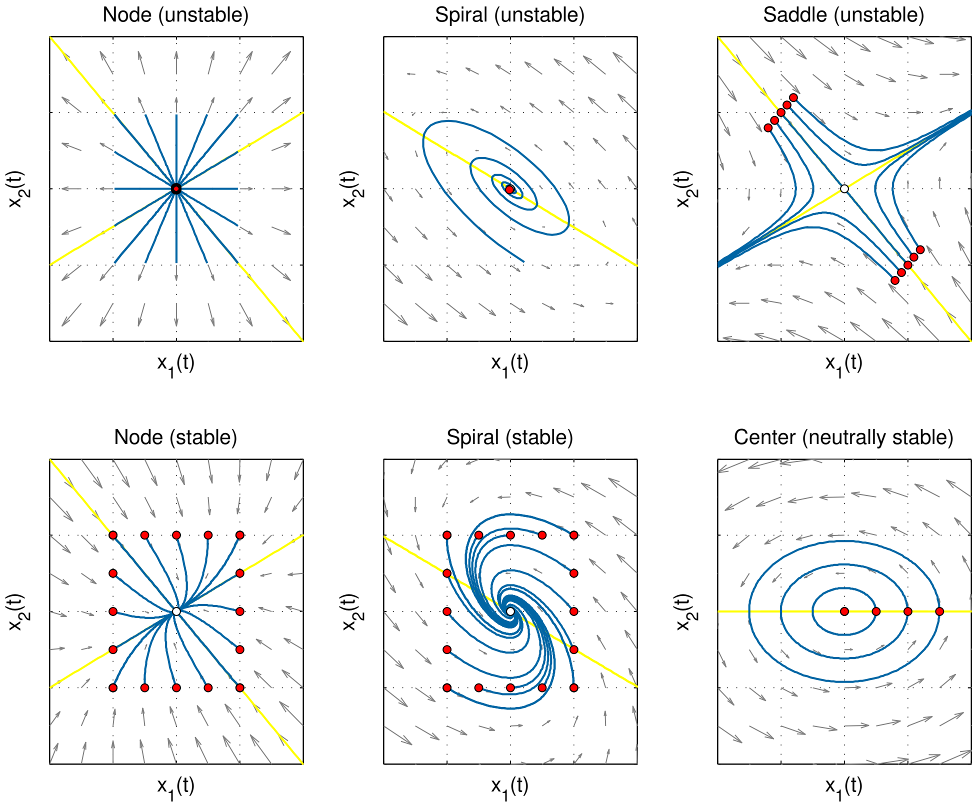

Fig. 6: Examples of the most common trajectory behaviors near fixed point singularities in the phase plane solutions of a two-dimensional continuous-time linear dynamical food web ecosystem (e.g. one predator – one prey) where the red dots are the initial conditions: [Upper left] Unstable node; [Upper middle] Unstable spiral; [Upper right] Saddle point (these are always unstable); [Lower left] Stable node; [Lower middle] Stable spiral; [Lower right] Center (these are neutrally stable)

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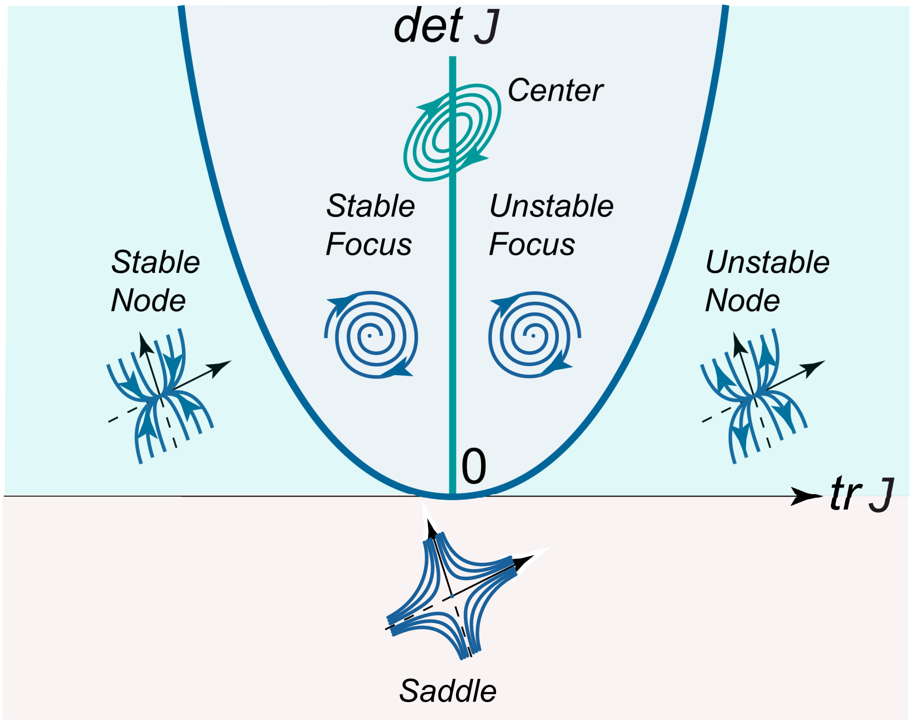

Fig. 7: Summary diagram showing how the trace **tr(J)** and determinant **det(J)** of the **Jacobian matrix (J)** define the stability types of fixed points in the phase plane of a two-dimensional continuous-time linear dynamical food chain (e.g. one predator – one prey). Picture credits: 🄯 Math24

Assuming a more realistic Michaelis-Menten (MM) formulation for resource-consumer interactions (see Section), because it accounts for consumer saturation at high resource concentration, leads to a slightly different expression for the « R-star » expression:

$$R^{*} = \frac{m_i}{\alpha_i - m_i \left(\alpha_i / \rho_i^{max}\right)} \tag{43}$$

Most food web models are based on variants of the MM formulation for resource-consumer interactions (Gilljam et al., 2015), where the R^{*} rule still applies at equili brium. However, the R^{*} rule cannot predict the outcome of competition under non-equilibrium conditions when there is a trade-off between resource uptake affinity (α_i) and maximum uptake rate (ρ_i^{max}) (see Section). The best known example occurs when under pulsed nutrient supply, high-nutrient-adapted ecotypes (HNA – which are opportunists with high ρ_i^{max}) can outcompete low-nutrient-adapted ecotypes (LNA – which are gleaners with high α_i). This occurs even if LNA ecotypes have lower R^{*} than HNA ecotypes and would otherwise dominate the community at steady-state equilibrium (Cermeno et al., 2011). The MM formulation can simulate this trade-off, which hapens when the uptake curves of two consumers intersect at some resource concentration (see Figure 4). However, the LV formulation does not account for this trade-off because LV equations assume that $\rho_{ji}^{max} \gg \alpha_{ji}$, and thus that the resource-consumer interactions are governed by just α_{ji} (i.e. without saturation at high resource concentration). Therefore, in non-equilibrium environments it is advisable to use the MM equations to simulate resource-consumer interactions in microbial food webs, and restrict the use of the LV equations to the linear stability analysis of steady-states (see BOX 3). Thus, the R^{*} rule derived for equilibrium conditions (either using LV or MM equations) is useful but does not always apply to most natural ecosystems, in which microbial communities are subject to non-equilibrium environmental conditions and physiological trade-offs are the norm (Litchman and Klausmeier, 2008, Barton et al., 2010). Furthermore, under non-equilibrium environmental conditions, classic equilibrium theory to compute ecosystem resilience (see BOX 3) does not apply, and other metrics such as the standard deviation of the population time-series are more informative (Vallina and Le Quéré, 2011). Recognizing that most microbial ecosystems are subject to non-equilibrium environmental conditions has also opened the door to a reconciliation between earlier theoretical models, whose predictions assumed that populations are in the steady-state equilibrium, and more recent numerical models that enable predictions for non-equilibrium situations (Barton et al., 2010, Vallina et al., 2017).

Ecological selection & Community assembly

The concept of «assembly rules» was proposed almost 40 years ago and refers to the fundamental mechanisms that govern how species associate to form a community. This concept defines the theoretical conditions for species persistence depending on their trait values (Diamond, 1975, Grover, 1997) and it is thus related to what is known as «ecological selection» (see below). One of the most intriguing aspects regarding microbial community assembling is how to explain the maintenance of species and trait diversity -- what are the mechanisms that allow so many different and competing species to coexist within the same ecological niche? The *competitive exclusion principle* states that two species that occupy the same ecological niche cannot coexist indefinitely (Hardin, 1960). The rate of competitive exclusion depends on the degree of niche overlap and the particular trait values of the competing species (Vallina et al., 2017). Large niche overlap and larger differences in trait values lead to faster exclusion rates than small niche overlap and smaller differences in trait values. When such niches are defined by shared resources (maximum overlap), the competitive exclusion principle translates into the *theory of limiting nutrients*, which states that there cannot be more coexisting species than the number of *essential resources* (Tilman, 1982) (see Section -- « R-star » rule).

Ecological selection is directly related to *invasion fitness* (see BOX 4) and competitive exclusion (Gause, 1934), as it works upon a multi-species community until only the set of best adapted species (a fraction of the original pool) survive locally. Ecological selection leads to the «survival of the fittest» through competitive exclusion on ecological time-scales, i.e. before longer-term evolutionary dynamics can take place (Falkowski and Oliver, 2007). The best adapted species to a particular environment or ecological niche will dominate the local community. Thus, the system may be dynamically unstable, even in the absence of environmental changes, because species extinctions may occur locally until a stable community is reached for the current environmental conditions. When the environmental conditions change, a new and different microbial community may self-assemble de-novo through ecological selection if there is exchange of species with other communities or if there is a local pool of rare (non-dominant) ecotypes available (Follows et al., 2007, Pedros-Alio, 2012). Ecological selection can thus be defined in the context of *niche space*, which can be categorized in two classes: fundamental niche and realized niche. The *fundamental niche* of a given species defines the environmental conditions that are suitable for growth in the absence of interactions with other species, while the *realized niche* defines the environmental conditions where a given species is actually observed when it is interacting with other species (Hutchinson, 1957b). Therefore, the realized niche may be narrower than the fundamental niche, due to the exploitative competition among the interacting species.

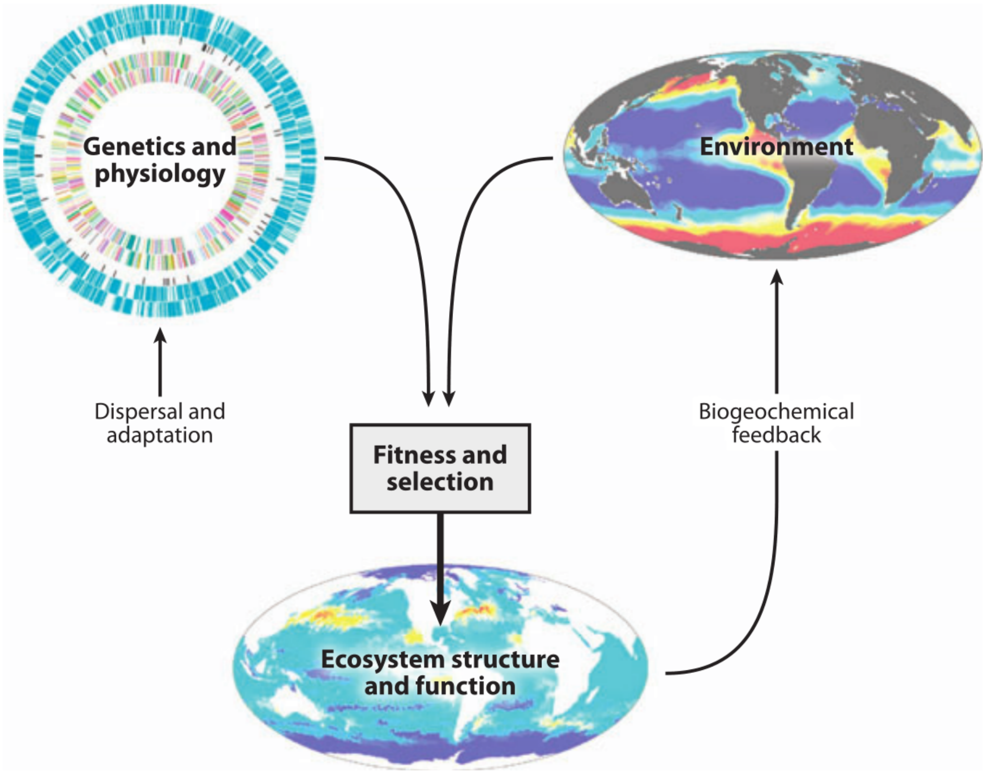

Fig. 8: The combination of different genotypes, different environmental conditions, and global ocean dispersal leads the « ecological selection » of the ecotypes with higher fitness locally, in either space or time. The resulting community assembly and species composition at each location will thus be different depending on the environmental conditions. Therefore, the ecosystem structure and functioning will vary. Furthermore, the environmental conditions will also be affected by the local community and its composition, mostly through nutrient depletion. Therefore there is a feedback between environmental conditions and the ecological selection of locally dominant ecotypes. Picture credits: © Follows and Dutkiewicz 2011 (Follows and Dutkiewicz, 2011)

Community assembly in soil ecosystems can be affected by agricultural practices and thus there is a well developed theoretical framework to simulate the observed patterns at equilibrium (de Ruiter et al., 1993, 1995, Kaunzinger et al., 1998, Neutel et al., 2002, 2007). Metabolic modelling under a reverse-ecology framework has also been used to successfully elucidate the assembly rules of the human microbiome at the community-level, suggesting that microbiome assembly is dominated by environmental filtering (Levy and Borenstein, 2013, 2014). Aquatic environments are among the best studied examples of how ecological selection may operate for the community assembly of microbial communities (see Figure 8) (Litchman and Klausmeier, 2008, Follows and Dutkiewicz, 2011). Microbial cells such as bacterioplankton and phytoplankton, are suspended in a generally well-mixed medium and compete for the same essential resources from a common and spatially fairly homogeneous pool, which implies that all individuals are potentially interacting with each other (Sommer, 2002). However, field observations contradict theoretical predictions and show that there is a much larger number of coexisting species than of non-substitutable resources (e.g. elemental nutrients) in the ocean, which has led to what is known as the «Paradox of the Plankton» (Hutchinson, 1961).

Theoretical studies have suggested several hypotheses in order to account for this discrepancy between theoretical predictions and field observations. There are several conceptual frameworks that have been explicitly invoked to explain the assembly of microbial comunities using mechanistic ecosystem models, such as niche theory for marine algae (Follows et al., 2007, Barton et al., 2010) or the human microbiome (Levy and Borenstein, 2013); neutral theory for generic host-associated microbiomes (Zeng and Rodrigo, 2018); the resource-ratio hypothesis for freshwater algae (Tilman, 1982); the killing-the-winner hypothesis for bacteria (Thingstad, 2000, Maslov and Sneppen, 2017) and phytoplankton (Vallina et al., 2014b); the nutrient-load hypothesis for cyanobacteria and phytoplankton (Brauer et al., 2012); the high-order interactions hypothesis for bacteria (Grilli et al., 2017); and even chaos theory for phytoplankton (Huisman and Weissing, 1999, 2001); among others.

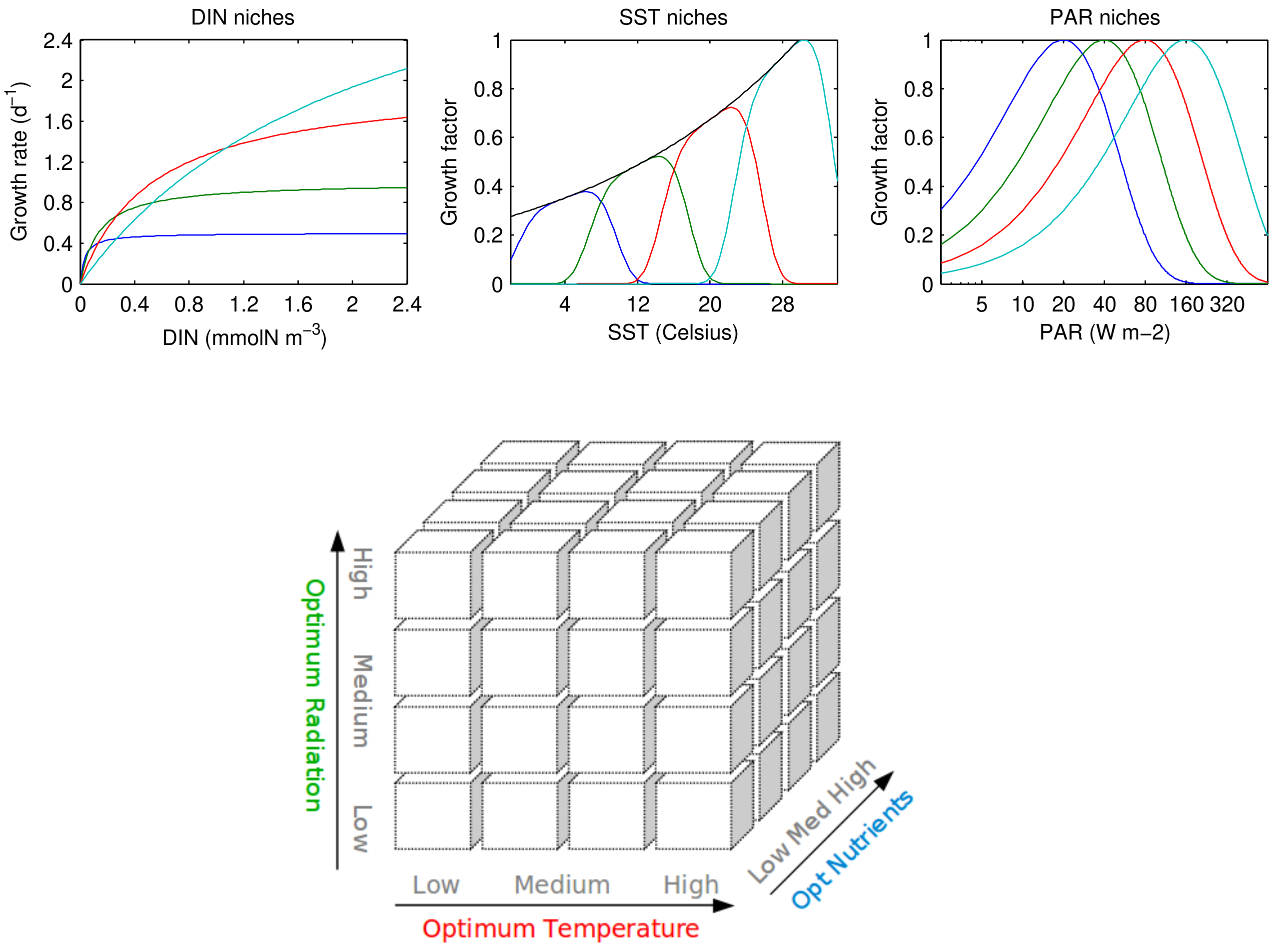

Fig. 9: Bottom: « Hypercube » setup of a model with 64 phytoplankton species each of them ocuppying a particular ecological niche given by some of their functional-traits (i.e. optimal levels) for 3 environmnetal axes: dissolved inorganic nutrients (DIN), water temperature (SST), and photosynthetically active radiation (PAR); Upper: Growth curves and optimum values ± ecological tolerances of the 64 simulated marine phytoplankton species along those 3 environmnetal axes (DIN, SST, PAR)

The *niche theory* suggests that species are ecologically unique, which implies that they occupy different environmental niches and fulfill different functional roles (MacArthur, 1968). Therefore, organisms can exploit and partition a set of resources along environmental gradients (e.g. elemental nutrients, prey-size, ambient temperature, solar radiation) by decreasing their niche overlap through specialization (Loreau, 2010a). On the other hand, *neutral theory* suggests that species are ecologically equivalent, which implies that they have a similar competitive strength, slow exclusion rates, and thus can occupy the same environmental niches or fulfill the same functional roles for long periods of time. Under this view, community assembly is governed by random demographic processes such as the rate of immigration from the regional pool (Hubbell, 2001). The *killing-the-winner* hypothesis provides a simple mechanism for stable coexistence due to the presence of a trade-off between competition ability for growth and vulnerability to mortality among the competing species. Higher-abundance species will be proportionally more susceptible to phage or predatory attack, which can eventually result in greater fitness of the lower-abundance species (i.e. the fitness of a phenotype increases as it becomes rarer) (Thingstad, 2000, Vallina et al., 2014b, Maslov and Sneppen, 2017). The resource-ratio hypothesis describes the assembly rules by which species competing for several resources can coexist at intermediate levels of nutrient supply (Tilman, 1982). Finally, high-order interactions theory suggests that the presence of a given species influences the interaction between other species (Billick and Case, 1994, Kelsic et al., 2015, Grilli et al., 2017) and shapes the relationship between ecosystem diversity and stability (Bairey et al., 2016). Recent studies, both theoretical and experimental, have shown that this higher-order interactions are often established through cross-feeding, a class of interspecific interaction in which organisms belonging to one species use metabolites produced and secreted by the other species as energy or nutrient sources (van Hoek and Merks, 2017, Goyal and Maslov, 2018, Goldford et al., 2018) (see Section).

One fundamental feature of most microbial organisms is their great capacity of passive dispersal by external agents, which affects the population dynamics and community assembly (Cermeño and Falkowski, 2009). Dispersal influences the probability of species to reach distant environments and thus their potential to interact with many other species -- hence the common say in microbial ecology «everything is everywhere, but the environment selects »(Baas-Becking, 1934, De Wit and Bouvier, 2006). For instance, aquatic microorganisms are subject to passive advection and turbulent diffusion by water currents; in terrestrial systems, wind plays a similar role. This is generally explicitly included in global ocean models (e.g. (Follows et al., 2007)). Other means by which microbes are dispersed are within the microbiome or attached to larger organisms. Community assembly theory suggests that the two main processes affecting the spatial and temporal distribution of species trait values are *species competition* and *environmental filtering*. Environmental filtering occurs when a species arrives at a focal site but fails to survive even in the absence of neighbours; competitive exclusion occurs when a species arrives and can persist in the absence of neighbours but not in their presence (Kraft et al., 2015). These processes do not act in isolation, however, and it is the interplay of competition- and filtering-driven fitness that leads to the *ecological selection* of species. Competition leads to ecological differentiation, while filtering reduces the spread of trait values and leads to similar ecological tolerances (Cornwell et al., 2006). Therefore, functional traits determine the species distribution along environmental gradients as well as the species competition for resources within a given environmental niche (Ackerly and Cornwell, 2007). Coexistence between species is thus the result of a balance between stabilizing forces (i.e. niche differences) and equalizing forces (i.e. fitness similarity) (Chesson, 2000a). Stabilizing mechanisms are those that increase the strength of intra-specific competition relative to the strength of inter-specific competition, while equalizing mechanisms are those that reduce the magnitude of the fitness difference (Loreau, 2010a). Stabilizing niche differences facilitate coexistence whereas relative fitness differences drive competitive exclusion.

BOX 4. Ecological fitness

$$\begin{aligned}\frac{\partial \mathbf{x_j}}{\partial t} &= \text{NetGrowth} - \text{NaturalMort} \\ &= \mu_j^{max}\,(\gamma_j^N\,\gamma_j^T\,\gamma_j^I)\,x_j - m_j\,x_j \\ &= \mu_j\,x_j - m_j\,x_j \\ &= (\mu_j - m_j)\,x_j \\ &= \lambda_j\,x_j \end{aligned} \tag{44}$$

where:

$$\gamma_j^N = \frac{N}{(\mu_j^{max}/\alpha_j) + N} \leq 1 \tag{45}$$

$$\gamma_j^T = \frac{\exp(-(T_j^{opt} - T)^2}{(2\,\sigma_T^2)} \leq 1 \tag{46}$$

$$\gamma_j^I = \frac{I}{I_j^{opt}}\,\exp(1 - \frac{I}{I_j^{opt}}) \leq 1 \tag{47}$$

The parameter $\lambda_j \leq \mu_j^{max}$ gives the specific rate of change of microbial ecotype j in units of inverse time (d^{-1}), and is a measure of their ecological (i.e. invasion) fitness that depends on the environmental conditions affecting their maximum growth rate μ_j^{max}. The parameters γ_j^N, γ_j^T, and γ_j^I determine the nutrient limitation, temperature limitation and irradiance limitation for microbial ecotype j, respectively. This model assumes that the effect of these three environmental factors on fitness is multiplicative, which implies that they are considered to be independent factors co-limiting growth (Fasham et al., 1990, Follows et al., 2007). The physiological traits of the different ecotypes will determine their optimal values of nutrient concentration (N_j^{opt}), optimal temperature (T_j^{opt}), and optimal irrandiance (I_j^{opt}). These three coordinates (N_j^{opt}, T_j^{opt}, I_j^{opt}) define the environmental niches where each ecotype is the best competitor (see Figure 9), and thus its location in the niche space (see Figure 9a). Note that $N_j^{opt} = K_j^{sat} = (\mu_j^{max}/\alpha_j)$ when a gleaner-opportunist trade-off is assumed (see Section). Therefore, for a given set of environmental conditions, ecological selection will lead to a community dominated by the fittest ecotypes. Changes in the environmental conditions modify the fitness of each ecotype and also the composition of the community (i.e. beta diversity; see Section).

Thus the niche space can be seen as the hypervolume of environmental conditions under which each microbial ecotype persists (Hutchinson, 1957a). Microbes in natural ecosystems have traits to cope with several environmental gradients, such as nutrient concentration, ambient temperature, solar irrandiance, etc (see Figure 9a). The patterns of functional trait similarity cannot easily be used to infer the relative contribution of environmental filtering versus competitive interaction in shaping the community assembly of microbial communities (Vallina et al., 2017). Competitive exclusion can be avoided by species that are functionally very dissimilar when the difference between the species traits are acting as stabilizing niche differences; e.g. optimal values of temperature and/or solar radiation levels (see Figure 9b). However, when differences in species traits directly translate into fitness differences, then competitive exclusion can eliminate the functionally weaker competitors within a given ecological niche (i.e. lower resource exploitation ability) (Chase and Leibold, 2003). The role of species dispersal can further blur the line separating environmental filtering and species competition. Furthermore, microbial communities in aquatic systems live in a very dynamic fluid environment, which implies that their environmental niches are neither stationary nor spatially closed. Therefore, all ecotypes can potential migrate between different niches by passive dispersal and will dominate the community where the environmental conditions match their optimal values (e.g. see Fig.S2 in (Follows et al., 2007)). A similar effect occurs by wind-mediated dispersal in terrestrial communities (Tarnita et al., 2015).

Dispersal can thus influence the microbial diversity at local and regional scales. The rate of dispersal compared to the rates of competition and/or environmental filtering will determine the actual community assembly and ecosystem structure over larger regions (Clayton et al., 2013). Spatial environmental heterogeneity, coupled to dispersal between different locations, may thus foster species diversity. Temporal heterogeneity may also promote coexistence when alternating environmental conditions within a time period favor different species, which is sometimes called the *storage effect* (Chesson, 2000b, Vallina et al., 2017). Such heterogeneity is characteristic of many real ecosystems that are subject to the effect of seasonal trends in environmental parameters. However, in order to induce a temporal niche partition and thus lead to species coexistence, time-varying environmental conditions need to satisfy two additional requirements: (i) the rate at which populations decline together with the temporal scale of the environment avoids the extinction of non-favored species and (ii) the covariance between environment and competition intensity is opposite for high density and low density species, which allows species to have positive growth rates when they become less abundant and recover larger population sizes. The temporal storage effect was initially proposed to explain coexistence in annual plants, but recent models have extended the concept to sporulating microbes and suggested its potential importance in explaining diversity in certain terrestrial communities of microbes in which dispersal can be neglected (Martínez-García and Tarnita, 2017). The theoretical frameworks and ideas discussed here are the conceptual basis for the mechanisms included in most microbial ecosystem models that are used today.

Ecological evolution & Community adaptation

Microbial organisms have the capacity to evolve over hundreds to few thousands of generations in response to environmental variability, even when mutation rates are low, because of their fast replication rates and large population sizes (Frank and Slatkin, 1990, Elena and Lenski, 2003, Huertas et al., 2011, Hellweger et al., 2014, Van den Bergh et al., 2018). Microbial communities are subject to both i) *ecological selection*, which acts through short-term competitive exclusion between species (see Section); and ii) *adaptive evolution*, which provides inheritable change of species-traits and affects the organisms' fitness after several successive events of ecological selection. Ecological evolution thus refers to the arrangement of organisms along phylogenetic lines (Bews, 1927). The relative influence and interplay of both selection and evolution on the dynamics of microbial communities is a challenging and fascinating research venue for modelers due to the overlap of temporal scales (Fussmann et al., 2007, MacColl, 2011, Ghoul and Mitri, 2016a, Doebeli et al., 2017). Formally, however, there is no difference between ecological and evolutionary dynamics because both are based on the same fundamental birth-death processes (Doebeli et al., 2017). Given the random nature of discrete genetic mutations and their effects on the phenotype, these *eco-evolutionary dynamics* can be studied with stochastic differential equations in continuous time (e.g. Focker-Planck equation) that approximate the mutation steps as infinitesimally small. Under this view, evolution can be visualized as an uphill walk on « Dynamic Fitness Landscapes » (DFL) that keep changing as a result of the evolution it engenders (Mustonen and Lassig, 2009, Metz, 2011, Richter, 2013, Richter and Engelbrecht, 2014). However DFL are *not* a driver of evolution, they are an emergent property of the underlying stochastic birth-death ecological process (Doebeli et al., 2017). Evolutionary changes in microbial communities thus respond to both local selection pressures as well as population dynamics, because ecological interactions create density-dependent selective pressures that affect gene frequencies (Cordero and Polz, 2014).

Eco-evolutionary dynamics are particularly important for microbial communities because their explicit inclusion of population dynamics into evolutionary models allows evaluation of the potential feedbacks between fitness and organisms (Dieckmann, 1999). Theoretical studies show that species will evolve to maximize their geometric mean fitness in environments that vary stochastically in time. Hence, evolutionary change is expected even if decadal-scale changes are smaller than inter-annual variability (Frank and Slatkin, 1990). An example in which eco-evo feedbacks are relevant is antibiotic-mediated interactions. Microbial evolution in a spatially structured landscape with environmental gradients of antibiotic concentration has even been shown in real time (Baym et al.,

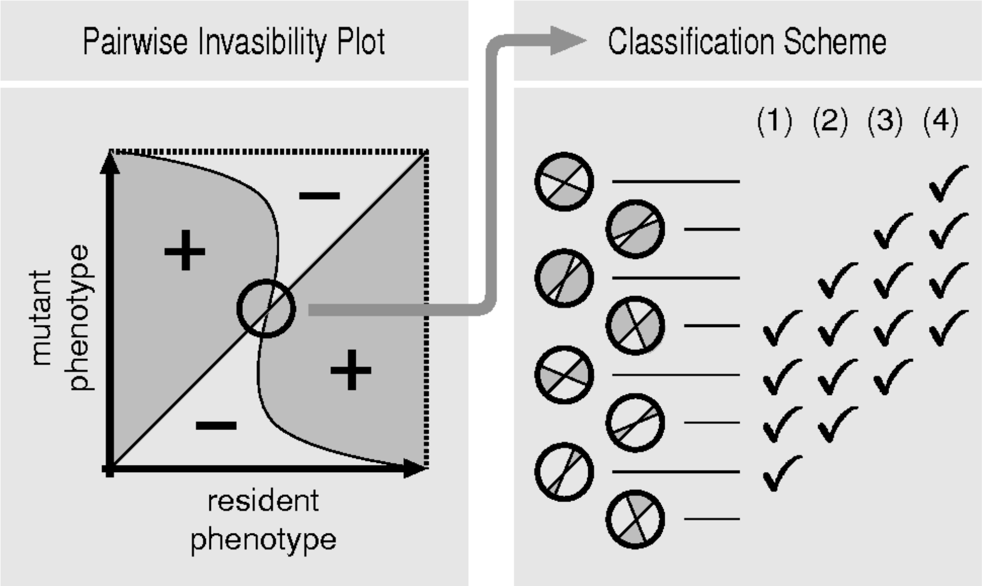

Fig. 10: Pairwise invasibility plots (PIP) and the classification of evolutionarily singular points (ESS). [left-panel] The horizontal axis defines the phenotype of the resident population given by the scalar value k_r of one trait (e.g. optimal temperature). The vertical axis defines the phenotype of a mutant population given by the scalar value value k_m of the same trait. The invasion fitness λ_m (see BOX 4) is defined as the specific growth rate (d^{-1}) of an initially rare mutant within local the environment (e.g. ambient temperature) where a resident population is well stablished. The resident population is assumed to be a demographic attractor in steady-state and therefore has $\lambda_r = 0$. Shaded areas represent the trait-space combinations (k_r, k_m) for which a rare mutant with phenotype or trait value k_m can invade a resident population consisting of individuals with phenotype or trait value k_r; that is, the regions for which $\lambda_m > 0$. Clear areas represent the regions for which $\lambda_m < 0$, therefore where the rare mutant cannot invade the resident phenotype. The evolutionary process can be seen as a sequence of successfully established invasions, where the mutant phenotype k_m then becomes the new resident k_r. The strategy or trait value for which evolution can come to a halt are called *evolutionarily singular strategies* (ESS). Near such points the fitness landscape as experienced by a rare mutant is locally flat. ESS can be i) a local fitness maximum representing a possible endpoint of evolutionary change; ii) a local fitness minimum at which evolutionary branching can occur; or iii) a degenerate case (these are without real-world significance). A given singular strategy can be evolutionarily stable (either convergent or non-convergent) or evolutionarily unstable (either convergent or non-convergent). [right-panel] The adaptive dynamics (AD) invasion function of a particular ecological system defines a PIP for resident and mutant phenotypes. When the invasion function is positive for a particular pair of phenotypes, the resident may be replaced by the invading mutant. Intersections of the invasion function's zero contour line with the 45 degree line indicate potential evolutionary end-points. Knowing the slope of the countour line at these singular points suffices to answer four separate questions: (1) Is a singular phenotype immune to invasions by neighboring phenotypes? (2) When starting from neighboring phenotypes, do successful invaders lie closer to the singular one? (3) Is the singular phenotype capable of invading into all its neighboring types? (4) When considering a pair of neighboring phenotypes to both sides of a singular one, can they invade into each other?. Picture credits: © Ulf Dieckmann (1997) (Dieckmann, 1997)

2016). The evolution of cancer cells may also impose limits to the predictability of precision cancer medicine (Lipinski et al., 2016). Several studies have addressed the effect of eco-evolutionary feedbacks under different microbial scenarios (Bonachela et al., 2017, Kotil and Vetsigian, 2018, Martin et al., 2016, Vetsigian, 2017, Tarnita, 2018). The introduction of such feedbacks in plankton models is, however, a more recent line of research than in other microbial systems (Norberg et al., 2012, Merico et al., 2014, Smith et al., 2016, Chen et al., 2018). However, in most current models of microbial ecosystems, species traits do not evolve nor adapt over time. For example, current model projections of plankton community structure under future climate change scenarios assume that species have fixed traits (environmental preferences) and will not adapt to the new conditions (Dutkiewicz et al., 2013). The need to include adaptive dynamics in the next generation of microbial models is widely recognized (Irwin et al., 2015) and several important contributions have been made in this direction (e.g. (Norberg et al., 2001, Williams and Lenton, 2008, Merico et al., 2014, Sauterey et al., 2015, Smith et al., 2016, Sauterey et al., 2017, Lomas et al., 2014, Edwards and Steward, 2018, Chen et al., 2018)).

The ability to adapt to changes in resource concentration may be linked to mutations in genes that regulate cell size or shape, as well as the number and efficiency of membrane transporters (see Section). Likewise, the ability to adapt to environmental changes in temperature or irrandiance may be linked to mutations in the genes that regulate biochemical reactions involved in catalytic efficiency or light harvesting capabilities. Eco-evolution also applies to social behaviour in microbes, such as cellular adhesion to form aggregates with collective functioning (Garcia et al., 2015) (see Section). This long-term evolutionary capacity of microbes to adapt to changing environments or social contexts on decadal scales may be more predictive than short-term physiological responses (or acclimation) in determining the winners and losers under future climate change scenarios (Dutkiewicz et al., 2013). The absence in most models

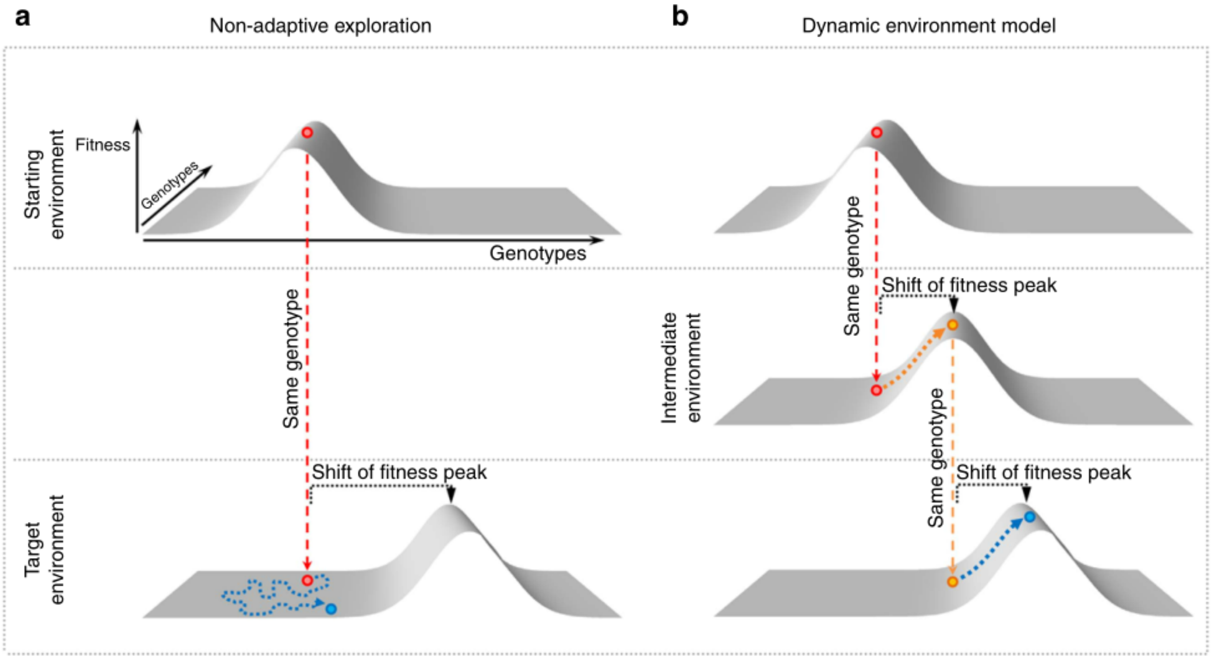

Fig. 11: Non-adaptive evolution (a) versus adaptive evolution (b) of a simulated ecotype on a fitness landscape for a two-dimensional genotype space. The red genotype is well-adapted because it is located on the fitness peak of this starting Dynamic Fitness Landscape (DFL). A change in the local environment shifts the fitness peak, so that the red genotype is no longer of high fitness (bottom). a) Abrupt (or fast) environmental changes requires the non-adaptive exploration (any direction) of the neutral part of the landscape. b) Gradual (or slow) environmental changes allow for Adaptive Evolution (AD) through small mutation steps (hill climbing) as defined by the pairwise invasibility plots (see Figure 10). Picture credits: 🅭 Szappanos et al. (2016) (Szappanos et al., 2016)

of mechanisms allowing the *adaptive radiation* of species-traits resulting from random mutations combined with natural selection implies that once a dominant species is established, it will remain unchanged and with no possibility to be unchallenged by newly created species (Dieckmann, 1999, Geritz et al., 1998) (i.e. resident phenotypes vs. mutant phenotype PIP -- see Figure 10). Finding ways to include ecological evolution in models (e.g. evolutionarily singular strategies and/or trait-diffusion frameworks) is an active field of research (Doebeli, 2002, Fritsch et al., 2017, Szappanos et al., 2016, Chen et al., 2018). Adding eco-evolutionary dynamics to microbial models may help understand fundamental hypotheses of species evolution such as the «Red Queen Dynamics»(Bonachela et al., 2017). Theoretical models can help improve our understanding of ecological evolution by testing hypothesis about the conditions for adaptive evolution, the waiting time to adaptation, the duration of adaptive processes and the different characteristics of the emerging species (Gavrilets, 2004). These features are expected to depend on different evolutionary factors and parameters, such as the rates of migration and mutation, the strength of selection for local adaptation, population size, or the spatial structure of the population.

Several « ecological evolution » (eco-evo) frameworks for modelling Adaptive Dnamics (AD) of traits based on evolutionarily singular strategies (ESS) and pairwise invasibility plots (PIP) (Smith, 1982, Diekmann and Law, 1996, Dieckmann, 1997, Geritz et al., 1998) or modelling Trait Diffusion (TD) based on solving the mean and variance of trait distributions (Norberg et al., 2001), were developed more than 20 years ago. These modelling frameworks for eco-evo are based on the notion of Dynamic Fitness Landscapes (DFL) that its rooted on the original concept of *adaptive landscapes* (Wright, 1932, Shpak, 2012) (see Figures 11 and 12). Although the definition of the "fitness" metric is context dependent (Metz and Geritz, 1992, Metz, 2018), for deterministic models the fitness of an ecotype under the local environmental conditions is usually measured as the biomass-specific growth rate (d^{-1}) of the population. DFL give the relationship between genotype and survival fitness for a given environmental condition (Loewe, 2016a). The horizontal axes (independent variables) represent the *genotype space* (the set of all possible genotypes) and the vertical axis (dependent variable) represents the *genotype's viability* (probability of survival or growth rate) (see Figure 12). Due to feedbacks between survival fitness and genotype frequency, the fitness landscape is not static but dynamic because of its density-dependency on gene frequencies, which vary through time (Mustonen and Lassig, 2009, Shpak, 2012, Richter, 2013, Richter and Engelbrecht, 2014, Doebeli et al., 2017). They also change in response to variations in the abiotic environmental conditions Thus the original view of evolution along static fitness landscapes is now recognized to be misleading since evolution happens along dynamic fitness landscapes (Mustonen and Lassig, 2009). The basic idea of evolutionary ecology is that ecotypes in a community differ in fitness because their different genotypes make them suitable

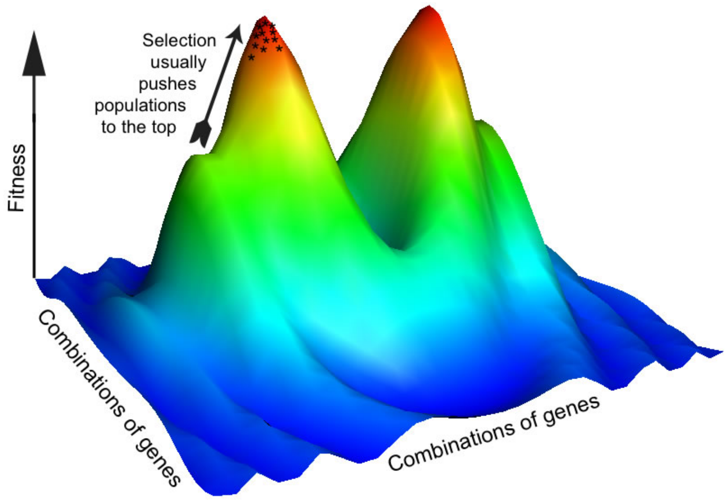

Fig. 12: Dynamic Fitness Landscape (DFL) in a 2D genotype space showing two peaks. Fitness peaks for a given genotype depend on the local environment, but environmental conditions (e.g. nutrient concentration) may also be affected by population dynamics (i.e. gene frequencies) over time so there is a feedback between fitness and organisms. Environmental changes can trigger perpetual changes in fitness, resulting in a constant need for adaptation. Picture credits: 🅭 Laurence Loewe (2016) (Loewe, 2016b)

for different environments (Doebeli et al., 2017). This allows the community to track environmental changes and avoid catastrophic collapse (see Figure 11). The relationship between genotype and fitness is mediated by the phenotype. Therefore, the conceptual framework of DFL can be applied to discrete genetic sequences (i.e. number of loci and number of alleles per locus) that define the genotype, as well as to continuous quantitative traits (e.g. organism size, optimum temperature, etc) that define the phenotype. Either way, the population evolves to a state where its average fitness is maximized (Nagylaki, 1992). That is, the divergence of populations along DFL under the joint action of different selection pressures results in the evolution of traits and, ultimately, speciation (Geritz et al., 1997, Ostman et al., 2014). The presence of competitive trade-offs for the uptake of resources has been shown to lead to adaptive evolution and the gradual establishment of microbial ecotypes (Gudelj et al., 2007, Ostman and Adami, 2013, Ostman et al., 2014).

More broadly, the flows of genetic material in microbial populations and communities can be classified as *horizontal*, i.e. moving from one organism to another that is not its offspring; and *vertical*, i.e. moving from one generation to the next (see Figure 13). Horizontal gene transfer is widespread among bacteria and archaea, because these prokaryotic microorganisms lack internal nuclear membranes to contain and protect their DNA. Thus, prokaryotes rapidly acquire genes from other prokaryotes and even from eukaryotes. Many researchers have therefore abandoned the term *species* and instead refer to different prokaryotic taxa as *ecotypes*. Cohan originally defined an ecotype as: «a set of strains using the same or very similar ecological niches, such that an adaptive mutant from within the ecotype outcompetes to extinction all other strains of the same ecotype; an adaptive mutant does not, however, drive to extinction strains from other ecotypes» (Cohan, 2001). The stable ecotype model (SEM) of bacterial speciation (Cohan, 2006) thus gives a prominent role to natural selection regarding the formation and maintenance of separate genetic clusters (see Figure 14) (Shapiro et al., 2012). In contrast, most gene transfer is vertical for eukaryotic microorganisms, such as green algae, fungi and protozoa, because they have nuclear membranes isolating their genetic material. Many ecological models represent different ecotypes and strains. However, it has also proven useful to develop models and analyse data in terms of the *probability distribution of traits* using continuous functions, without explicitly representing ecotypes or strains (Norberg, 2004, Follows and Dutkiewicz, 2011). Such models have been applied to population genetics and evolution (McGill and Brown, 2007), and recently for understanding biogeographical distributions and Biodiversity-Ecosystem Function (BEF) relationships of marine plankton (Smith et al., 2016, Chen et al., 2018) on ecological timescales (see Section).

Both horizontal and vertical gene flows generate genetic (and hence phenotypic) variations, and thus in effect they ”diffuse” trait values through populations and communities. This maintains microbial biodiversity and sustains the adaptive capacity of microbial ecosystems. These trait variations are then *filtered* by competition and environmental factors to shape the compositions of populations and communities, and ultimately by ecological evolution to determine the course of evolution. The Trait Diffusion (TD) framework (Merico et al., 2014) simulates the diffusion of trait values through successive generations, as a result of various processes such as vertical gene transfer and/or de-novo mutations. TD can thus be viewed as a mean of representing in microbial models the maintenance of species-trait diversity via endogenous mechanisms. These mechanisms of adaptive evolution can include mutation or rapid evolution

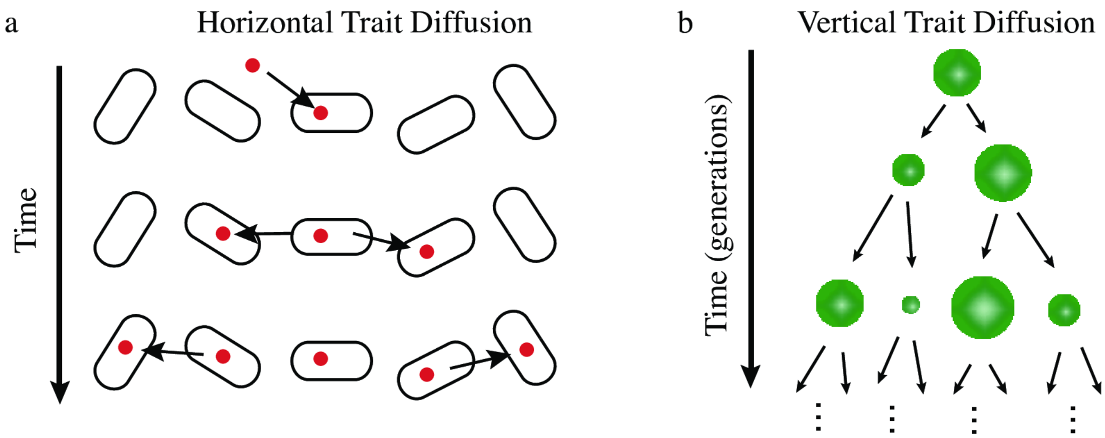

Fig. 13: Genes and associated traits can diffuse a) horizontally, independent of any genetic relationship among the organisms (red dots denote a gene of interest moving between bacterial cells), and b) vertically, i.e. through inheritance from generation to generation, as denoted here for phytoplankton reproducing to produce offspring of differing size.

(Yoshida et al., 2003), which alter the genotype; as well as trans-generational phenotypic plasticity, which is independent of changes in the offspring genotype. The different ecotypes would evolve driven by the three major factors controlling evolutionary dynamics of microbes: random mutation, genetic drift, and natural selection. Therefore, the TD approach gives a simple yet powerful mathematical framework to parametrize these eco-evo factors without the need to simulate them explicitly (Smith et al., 2016). TD assumes that the rate of trait diffusion is directly proportional to growth rate and its derivatives. This framework could readily be applied to model the effects of trait diffusion on the eco-evolutionary dynamics of other eukaryotes (e.g., fungi) and possibly also with some modification of prokaryotes. However, TD does not represent horizontal trait diffusion, which can dominate the flow of genes and traits among prokaryotes migrating within spatially heterogeneous environments (Niehus et al., 2015). Such migration is likely common given that micro-scale variability is commonly observed (Section). Rates of horizontal trait diffusion must depend on the presence of other organisms and phages (viruses) as well as growth rates.

Currently the TD framework is well developed for one trait (e.g. cell size linked to nutrient uptake strategy); that is, for one-dimensional (1D) dynamic fitness landscapes of ecological evolution. However, the dimensionality of DFL is probably very large for most organisms, with different traits being important along different environmental gradients. For procaryotic microbes, two major environmental gradients dominating the ecology and evolution of the ecotypes are the concentration of resources (i.e. uptake strategy) and the temperature of the environment (i.e. thermal tolerance). For eukaryotic phytoplankton, a third environmental gradient is the solar irradiance (i.e. light harvesting and photoprotection). Therefore, the simulated microbial ecotypes should be able to evolve by varying the value of their optimal traits (e.g. N_{opt}, T_{opt}, I_{opt}) under an hypervolume of environmental conditions (see Figure 9). Dynamic fitness landscapes are variable in space and time due to changes in the environmental conditions. Therefore, the rate of trait-diffusion (i.e. a mathematical parametrization of the genotype mutation rate) of the microbes should be sufficiently fast to track the environmental changes, in order to capture the adaptive capacity of the population or community of interest. Furthermore, even in relatively stable environments, fitness landscapes can change with the genetic state (i.e. ecotype frequencies) of the population as a result of density-dependent selection (Gavrilets, 2004). The evolutionary trajectories are expected to follow the changes in DFL resulting from i) variability of the environment and ii) inter-specific competition. Basically each population should try to ”climb” the fitness gradient (including both biotic and abiotic factors) in order to maximize their chances of survival (i.e. attain the fastest possible biomass-specific growth rate of the population) under any given environmental condition. The resulting trajectories may be the result of a ”tug of war” between two opposite directions: *convergent evolution* to maximize performance under the current environmental conditions and *divergent evolution* to avoid strong competition for a limited set of resources among phenotypically similar populations (Darwin, 1859).

Further work is needed to develop improved models and better understand the roles of trait diffusion in the eco-evolutionary dynamics of microorganisms. One particularly promising area is modelling horizontal trait diffusion and its effects among prokaryotes, which are important in epidemiology, the micro-biome of the human gut, and many commercial applications. Trait diffusion also needs to be considered in the context of the Complex Adaptive Systems (CAS), which define systems with the capacity of *self-organization* where 1) patterns emerge from the interaction among its components, and 2) these interactions are in turn affected by the patterns they produce (i.e. there is feedback between the system’s components and its emergent properties) (Holland, 1992, Levin, 1998).

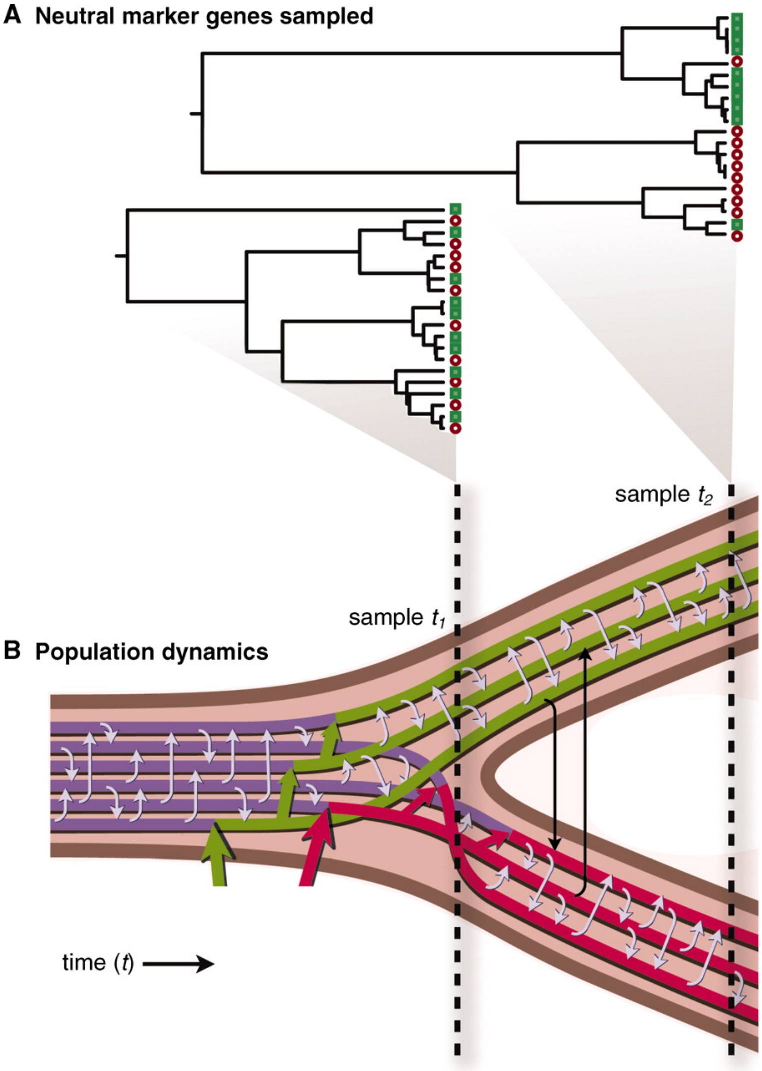

Fig. 14: Ecological differentiation in recombining microbial populations leading to evolutionary branching of two distinct ecotypes. (A) Example genealogy of neutral marker genes sampled from the community at different times. (B) Underlying model of ecological differentiation. Thin gray or black arrows represent recombination within or between ecologically associated populations. Thick colored arrows represent acquisition of adaptive alleles for red or green habitats. Picture credits: © Jesse Shapiro et al. 2012 (Shapiro et al., 2012)

Microbial ecosystems are good examples of CAS when organisms migrate within spatially heterogeneous environments (Norberg, 2004) (Section). Spatially explicit CAS models yield unexpected dynamics, and even without considering TD have already given new insights concerning the evolution of cooperation, restraint (Werfel and Bar-Yam, 2004), group selection and the meaning of fitness (Goodnight et al., 200999). Spatial heterogeneity is expected to be especially important in microbial communities in which mobility is limited, as for instance in soil-dwelling microbiomes where variability in the porosity of the soil constrains the diffusion of the different molecules that are present in the environment (see Section).

Biodiversity & Ecosystem Functioning

Unveiling the relationship between biodiversity and ecosystem functioning is one of the major goals of ecological theory (Hooper et al., 2005, Duffy et al., 2007, Thompson et al., 2012), and it is becoming increasingly important in microbial systems (Glockner et al., 2012, Smith et al., 2016, Vallina et al., 2017). The simplest measure of biological diversity is the number of species that are present in a given place, but diversity can be measured using many indices and scales (Whittaker et al., 2001, Tuomisto, 2010). Species richness and the Shannon index (Shannon, 1948) are among the most commonly used due to their simplicity. However, these metrics do not always have a direct translation to *functional diversity* -- from the point of view of ecosystem functioning, rather than the richness per-se it is the species identity and role that matters, both related to the species traits and trade-offs (Vallina et al., 2017). Scale is also an essential component of ecological theory because the response of dependent variables can change across spatial and temporal scales (Levin, 1992). There are three main terms for measuring biodiversity over spatial scales at a given time (snap shot): alpha, beta, and gamma diversity (Whittaker, 1972). *Alpha diversity* represents the mean diversity of species within a focal ecosystem or study region and is usually computed as the average value of the local species richness at each niche, habitat or site that the ecosystem contains. *Beta diversity* refers to the diversity of species that are unique to each habitat of the ecosystem and thus provides a measure of compositional heterogeneity. Finally, *gamma diversity* represents the total integrated diversity of the ecosystem from all habitats and thus provides a measure of its overall diversity.

Most microbial communities are important for ecosystem functioning, in particular soil microbial communities; plant-associated microbiomes (both microbes living within the roots or attached to them) (Loreau, 2010b); and planktonic communities, either bacteria (Fuhrman, 2009) or micro-algae (Litchman et al., 2015a). Since these habitats can have different sizes and the geographical limits among them are diffuse, there is no consensus on what spatial scales are the most appropriate to quantify alpha diversity. The suggestion is that it can be measured using habitats or sites of any scale that are delimited just for the purpose of analysis. Beta diversity can then be computed as the ratio between gamma over alpha diversity(Whittaker, 1972). These three definitions of biodiversity are also equally applicable over temporal scales at given location (focal point), or mixing space and time in the analysis. For example, the shape of the productivity-diversity relationship (PDR) for marine unicellular algae (i.e. phytoplankton) at the scale of the global ocean using alpha diversity of species richness has been observed to be unimodal, with diversity peaking at intermediate levels of productivity (Irigoien et al., 2004). Numerical simulations showing the same global pattern when looking at weekly-averaged data suggested that predator-mediated coexistence by selective feeding (i.e. killing-the-winner, see Section) explains the positive slope at low nutrient supply, while transient competitive exclusion explains the negative slope at high nutrient supply of this unimodal PDR curve (Vallina et al., 2014a).

Diverse communities are often more efficient in resource exploitation than single species communities and there is no a-priori limit to the total number of species (increasing the packing and elaboration of axes of the niche hyperspace) (Loreau, 2010a). This also applies to temporally-variable environments through local selection and dominance of the most efficient ecotypes. For example, higher diversity of thermal preferences has a positive effect on ecosystem functioning on a seasonal basis because it leads to *niche complementarity* of the species, which allows covering the whole temporal gradient in temperature. Likewise, a higher diversity of uptake strategies has a positive influence on ecosystem functioning through a *sampling probability* effect: the more uptake strategies are potentially available, the higher the chance of sampling a faster-growing strategy (Tilman et al., 1997, Hooper et al., 2005). The stability of aggregate ecosystem properties like total production or biomass has thus been suggested to increase with species diversity either through functional redundancy or functional complementarity (de Mazancourt et al., 2013). Species are redundant when they occupy the same environmental niche and fulfill the same functional role, and are complementary when they occupy different environmental niches within the same ecosystem and fulfill different functional roles (Loreau, 2010a). Functional redundancy helps sustain ecosystem functioning in the face of species extinctions through the replacement of species with similar ones, while functional complementarity decreases the variance of aggregated properties (i.e. increases the stability at the community level) through the species asynchrony with environmental variability (Vallina et al., 2017). Different species that have distinct ecological niches would respond differently to environmental changes, leading to an asynchrony of individual population dynamics (Loreau and de Mazancourt, 2013). Asynchronous responses of the populations will thus have a «buffering effect» on aggregate properties, leading to the *insurance hypothesis of biodiversity* for ecosystem functioning (Yachi and Loreau, 1999). This is a major prediction of niche theory regarding biodiversity and ecosystem functioning (BEF) that seems to be well supported with observational data for terrestrial plants (Loreau, 2010a) and freshwater phytoplankton (Ptacnik et al., 2008).

Neutral theory (see Section), on the other hand, states that coexisting species are ecologically equivalent and therefore the rate of competitive exclusion becomes infinitely slow (Hubbell, 2001). Thus, in the view of neutral theory, diversity has no functional consequences (Loreau, 2010a). Under this modelling framework, the dynamics of an isolated microbial community then becomes a slow random drift to extinction due to the stochastic probability of both birth and death processes, leading to transient non-equilibrium coexistence. However, for non-isolated communities this random drift can be counterbalanced by the immigration by dispersal into the local community of new species coming from an external pool of microbial communities or metacommunity, leading to permanent coexistence. The identity of species continuously change but the microbial community properties such as the species abundance distribution (SAD) remains invariant. The main drawback of neutral theory for microbial ecosystem modelling is that there is a large body of evidence that most species in natural ecosystem are not functionally equivalent -- many studies have shown that microbial ecotypes have deterministic niche differences and that ecological displacements by competitive exclusion are common (Litchman and Klausmeier, 2008, Follows and Dutkiewicz, 2011, Ghoul and Mitri, 2016b, Coyte et al., 2015). In addition, neutral theory in its current form is seen as incompatible with niche theory (Loreau, 2010a).

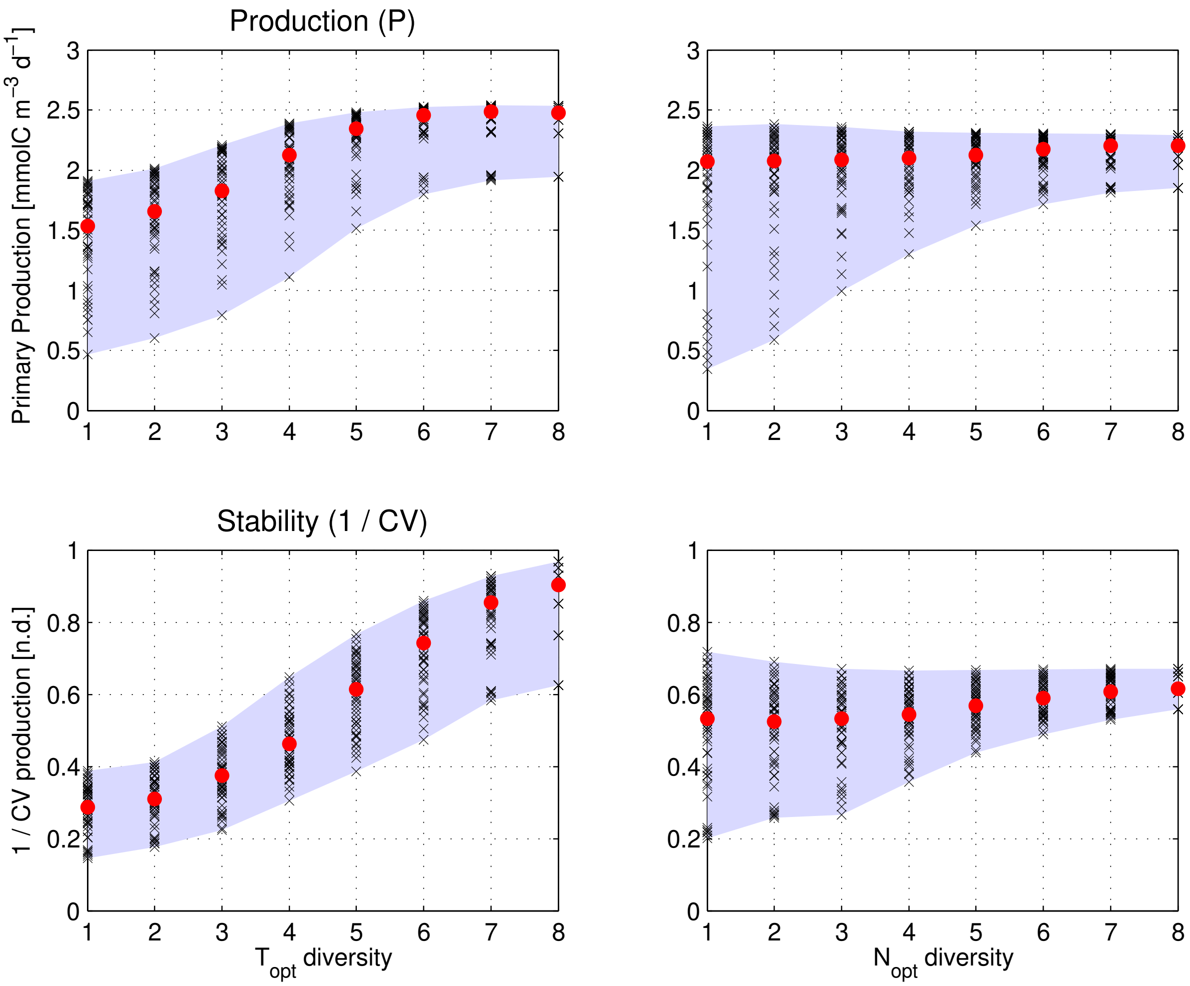

Fig. 15: Phytoplankton annual average community-level primary production (mmolC m^{-3} d^{-1}) and its temporal stability (inverse of the coefficient of variation normalized by its maximum value; n.d.) as a function of the diversity in thermal preferences (left panels) and the diversity in nutrient uptake strategies (right panels). The red dots correspond to the median value of the distribution. The gray shaded area spans from the minimum to the maximum value of the distribution. Increasing the diversity of thermal preferences of the phytoplankton community leads to a strong increase in the median, minimum and maximum value of the community-level production and its temporal stability over a seasonal cycle. Increasing the diversity of uptake strategies of the phytoplankton community leads to a strong increase of only the minimum value of the community-level production and its temporal stability over a seasonal cycle, to a weak increase of the median value, and has no effect on the maximum values of the distribution. Picture credits: 🅭 Vallina et al. (2017) (Vallina et al., 2017)

There is also the middle-ground possibility that both theories (niche and neutral) may be partially correct and be in fact complementary to explain microbial community assembly. Observational data show that rank-abundace distributions (RAD) of microbial communities are often highly skewed, with a few dominant ecotypes and a long tail of low abundant ecotypes that form the so-called *rare biosphere* (Pedros-Alio, 2006, 2012, Fuhrman, 2009, Ser-Giacomi et al., 2018). The tail of rare ecotypes is thought to be the result of bottom-up controls (being in sub-optimal environments for growth) and top-down killing-the-winner processes (being subject to relatively smaller mortality) (Pedros-Alio, 2006). Global ocean simulations resolving many ecotypes of phytoplankton based on niche theory, for example, also show the same pattern (Follows and Dutkiewicz, 2011). This suggests that: i) the few dominant ecotypes of the RAD are in their optimal environmental niches and thus are outperforming most of the ecotypes by ecological selection; ii) the many rare ecotypes of the RAD are far from their optimal niches and have been probably recruited through immigration by dispersal; and iii) within either category but particularly for the long tail of rare ecotypes, coexistence is probably happening because ecotypes have very similar fitness and thus can be viewed as close to *competitively neutral*. Eventually, environmental conditions may change and some rare ecotypes could then become dominant (and viceversa) (Pedros-Alio, 2006). Therefore, the rare biosphere of microbes can be seen as a ”seed-bank” of biodiversity and way to store *potential* ecosystem functioning (Zorach and Ulanowicz, 2003).

Under temporally varying and/or spatially heterogeneous habitats, keeping a rare biosphere of microbes waiting to become dominant when conditions change may thus lead to what is known as *overyielding*. Overyielding occurs when the production of a multi-species community is higher than the production of each of its species as a mono-culture. Niche differentiation and functional complementarity are thought to lead to overyielding production on microbial ecosystems. There are two major mechanisms by which biodiversity can lead to overyielding: *sampling probability* effect and *niche complementarity* effect (for details see Fig.2 in (Hooper et al., 2005)). These mechanisms explain the BEF response curve of simulated microbial communities such as phytoplankton when the species functional diversity is given by their range of uptake strategies and temperature tolerances (Vallina et al., 2017). An increase in the range of nutrient concentration niches (N_{opt}) leads to sampling probability, while an increase in the range of temperature niches (T_{opt}) leads to niche complementarity. Note that the BEF response curve for each of these mechanisms is different: sampling probability has no effect on the maximum values of the ecosystem functioning indicators (e.g. productivity and stability), while niche complementarity increases both the maximum and minimum values of these indicators (see Figure 15). These BEF responses for simulated microbes agree well with the general BEF curves predicted for terrestrial plants under theoretical scenarios of sampling probability and niche complementarity (Tilman et al., 1997).

Regarding *niche complementarity*, a microbial ecosystem with a spatial environmental gradient of temperature will be more productive if all its temperature niches are being occupied simultaneously by locally adapted ecotypes. This is because the *fundamental niches* for temperature (negative-skew gaussian bell curves) are *closed at both ends* and thus a single ecotype will generally not be able to cover (i.e. survive at) the whole range of ambient temperatures under a mono-culture (see Figure 9, upper-center). Regarding the *sampling effect*, a microbial ecosystem with a spatial environmental gradient of nutrient concentration will be more productive if *at least* one fast growing ecotype is present in the community. That is, there is no need to have a diversity of uptake strategies (i.e. affinity-adapted vs. rate-adapted) simultaneously as long as one rate-adapted (i.e. opportunist) species is present. This is because the fundamental niches for nutrients (Michaelis-Menten curves, see Figure 2) are *not closed on the upper side* since high nutrient concentrations are (usually) not harmful for growth, and thus a single ecotype will be able to cover (i.e. survive at) the whole range of resource concentrations under a mono-culture (see Figure 9, upper-left). In this case, the probability of sampling at least one rate-adapted ecotype increases with biodiversity. Therefore, having a high diversity of uptake strategies translates into having a higher chance of having a highly productive microbial community. The effect on ecosystem functioning of diverse uptake strategies is thus not the result of functional complementarity but the result of sampling probability (Tilman et al., 1997). The concept of *thermal niche* and *nutrient niche* are therefore quite different from the point of view of BEF in microbial communities because they lead to different mechanisms of overyielding (Hooper et al., 2005). The concept of *irradiance niche* for photo-autotrophic microbes falls somewhere in the middle of these two extreme categories if there is photo-inhibition at high solar radiation (see Figure 9, upper-right). The same reasoning applies to temporal environmental gradients (see Figure 15) (Vallina et al., 2017).

Micro-scale variability

Micro-scale variability plays a central role in determining the functioning of microbial communities and the various processes that they govern. It is especially important in contexts in which, due to limited mobility, cells explore a limited range of environments and interact mostly with individuals in their closest neighborhoods. Nano- and micro-scale variability are well appreciated features of soil ecosystems (Kuzyakov and Blagodatskaya, 2015, Fierer, 2017). In terrestrial ecosystems, bacterial distributions in the soil show a high degree of clustering, due to the combined effect of extrinsic (e.g. pore size, availability of organic matter) and intrinsic factors (e.g. reproductive pair correlations) (Raynaud and Nunan, 2014). Regardless of the environmental conditions in which they thrive, bacterial biofilms are a paradigmatic example in which short-scale variability is well-known to be of paramount importance. Biofilms are dense and highly diverse communities in which cells remain encased in a secreted polymer matrix that holds them together and hence reduces their mobility dramatically. They are central for global scale processes, such as biogeochemical cycling, play a central role in the interaction between bacteria and multicellular organisms, and provide a myriad of potential biotechnological applications (Fux et al., 2005, Paerl and Pinckney, 1996, Halan et al., 2012). However, the contribution of biofilms to each of these processes is usually controlled by the secretion of different metabolites, whose efficiency is strongly determined by the spatial arrangement of the different species within the matrix (Nadell et al., 2016). Due to the importance that spatial structure has for biofilm functioning, several models have attempted to understand the means by which individual cells interact among them and with the environment during biofilm proliferation as well as the ecological and evolutionary implications of the nascent patterns of spatial variability (Nadell et al., 2010, van Gestel et al., 2015). Most of these models rely on individual-based approaches, in which each cell is treated as a discrete entity (Kreft et al., 2001, Karina B. Xavier, 2005, Martínez-García et al., 2018), but frameworks based on reaction-diffusion descriptions of the growth dynamics have been proposed as well (Horn and Lackner, 2014).

Less obvious has been the existence of micro-scale patterns of spatial variability in environments where microbes are subject to external mixing forces, such as the aquatic environment. Over 30 years ago, however, such microscale patchiness in the distributions of organic matter, bacteria, and other microorganisms was observed and appreciated as an important feature of marine ecosystems and the biogeochemical cycles that they mediate (Azam et al., 1994). More recently, patchiness in the distribution of marine phytoplankton has been widely observed and confirmed to impact the productivity of simulated plankton ecosystems (Brentnall et al., 2003, Mandal et al., 2014). Spatial heterogeneity of microbial distributions in aquatic systems arises from the clustering of organisms (see Figure 16). Also, in the presence of potential mixing forces such as external flows and micro-scale eddy stirring, organisms can cluster in certain turbulent regimes (see Figure 17). More generally, environmental heterogeneity at larger scales has long been known to impact ecological dynamics and enhance biodiversity by providing distinct environmental niches physically separated (e.g. (d'Ovidio et al., 2010, Levy et al., 2014)). Micro-scale aggregates ($<$ 1 mm) of particulate organic matter, phytoplankton, and bacteria constitute microbial hotspots in the ocean (Azam et al., 1994), with distinct environmental niches that are important for aquatic ecology and biogeochemistry. Furthermore, because plankton undergoing limited migration (incomplete mixing) in aquatic environments constitute Complex Adaptive Systems (CAS), a CAS modelling approach for simulating the biodiversity and adaptive dynamics of such systems has recently been developed (Norberg, 2004). Although the emphasis was given on larger spatial scales, the same principle applies for migration between distinct micro-environments.

The ubiquity of micro-scale variability suggests that CAS dynamics are common in the eco-evolutionary dynamics of microorganisms. Also, recent modelling studies have revealed novel insights into the complex eco-evolutionary dynamics of microorganism in spatially heterogeneous environments. Evolution and maintenance of social cooperation, restraint, and altruism can be explained by considering eco-evolutionary dynamics with migration under environmental heterogeneity (Werfel and Bar-Yam, 2004) (see Section). A similar model predicted complex dynamics for group selection (Goodnight et al., 200999). Migration between distinct habitats enhances substantially the degree to which horizontal gene transfer impacts the genetic diversity and evolution of prokaryotes (bacteria and archaea) (Niehus et al., 2015). Phytoplankton distributions in coastal waters have also been shown to display great vertical heterogeneity or intermittency, with layers of increased fluorescence and concentration, probably resulting from a fine balance between layer formation and destruction through mixing (Prairie et al., 2011). These peaks or anomalies in concentration over the background value can have disproportionate effects on the biological dynamics. They are usually modelled using the same approach employed in turbulence theory (Mandal et al., 2016).

Fractal patchiness at the micro-scale can occur when motile phytoplankton are exposed to turbulent flow, leading to increases in local concentration of an order of magnitude. They are the result of a balance between cell motility and fluid shear (Durham et al., 2013). Motile bacterioplankton can exploit ephemeral micro-patches of resources through chemotaxis in turbulent environments (see Figure 17). This gives them an advantage over non-motile competitors, albeit subject to a trade-off against the energetic cost of locomotion. There exists therefore an optimal swimming speed of $\approx 60\ \mu\text{m s}^{-1}$ for standard marine conditions (Taylor and Stocker, 2012, Stocker and Seymour, 2012). Compared to typical plankton ecosystem models based on mean-field (background) concentrations, the newly developed models that account for the micro-scale variability (anomalies) in the distributions of plankton and nutrient concentration have yielded substantially different simulated spatio-temporal patterns of biomass and productivity at macroscopic scales (Mandal et al., 2016). These models have also predicted that micro-scale variability may enhance trophic transfer and potentially also biodiversity (Priyadarshi et al., 2017).

The distribution of micro-scale aggregates can be represented either explicitly as in agent- or individual-based models (Werfel and Bar-Yam, 2004, Goodnight et al., 200999), by direct numerical simulations (DNS) of turbulence at high spatial resolution (Taylor and Stocker, 2012), or statistically in ecosystem models at low spatial resolution by decomposing the concentration fields into mean and fluctuating parts. The last approach is analogous to the Reynolds decomposition employed widely in fluid dynamics (Mandal et al., 2014, 2016, Priyadarshi et al., 2017). Accounting for micro-scale variability compounds the already formidable challenge of modelling the combined effects of ecological dynamics and physical transport by advection and diffusion (Mandal et al., 2016), which are relevant to many microbial systems. Future studies that better account for micro-scale variability have much potential to yield new insights into the eco-evolutionary dynamics of microorganisms. Remaining challenges include developing models that are both sufficiently robust for application over wide environmental gradients (e.g. in 3-D models of ocean circulation and marine ecosystems) and computationally efficient enough to be practically useful for simulation studies. Promising approaches have begun to incorporate the effects of heterogeneous environments as ”interaction structure” within the compact Adaptive Dynamics equation that is already widely used to model eco-evolutionary trait dynamics (see Section) (Allen et al., 2013b)

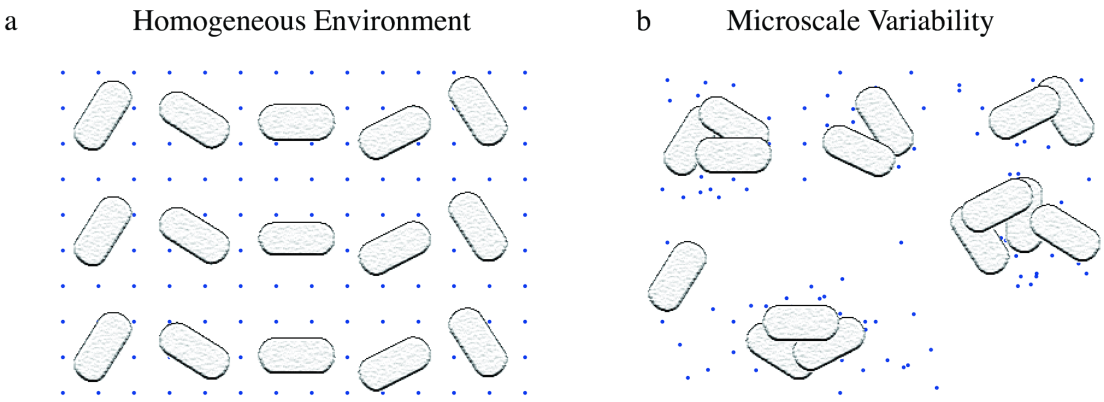

Fig. 16: Many theoretical models were first developed assuming A) homogeneous environmental conditions as denoted here for the distribution of bacterial cells and their growth substrate (blue dots). B) Now more and more models are accounting for spatial heterogeneity, as depicted here for a patchy distribution of bacteria and their substrate. Environmental heterogeneity is typical of many natural environments and in many cases yields substantially different predictions of both ecological and evolutionary dynamics.

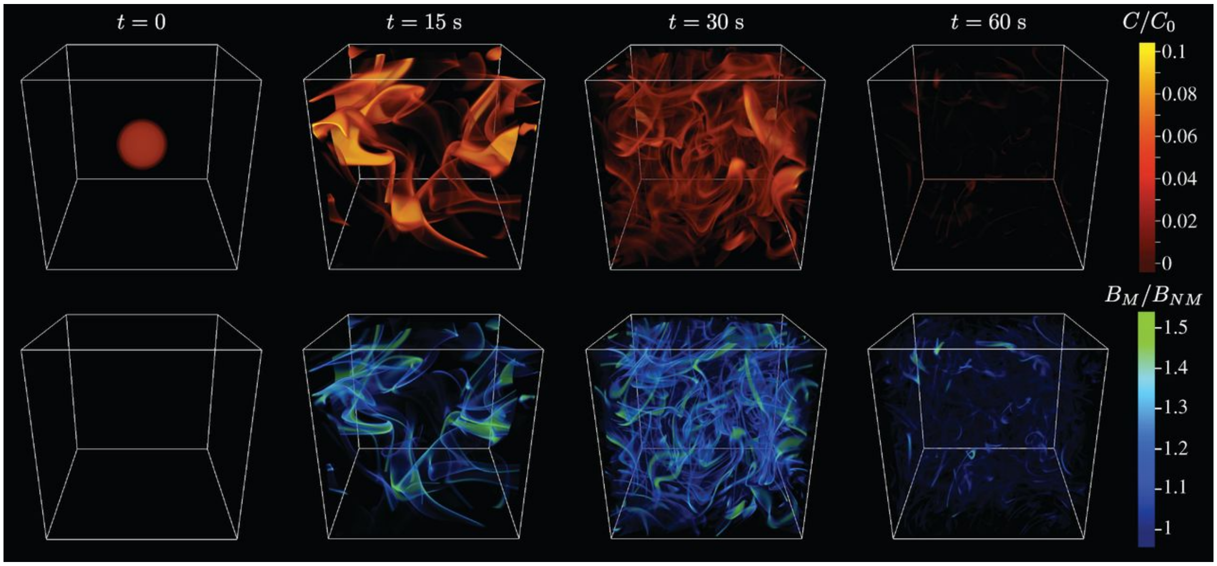

Fig. 17: Stirring of a nutrient patch and response of chemotactic bacteria within a domain of ≈ 0.5 meter length using direct numerical simulations (DNS). As a nutrient patch is stirred by a turbulent flow (top row, showing nutrient concentration C), chemotactic bacteria respond by accumulating within nutrient filaments (bottom row, showing concentration of motile bacteria BM), thereby enhancing their uptake. Picture credits: © John R. Taylor and Roman Stocker 2012 (Taylor and Stocker, 2012)

Social behavior in microbes

Microbes very often coordinate their behavior with each other in order to perform several tasks, such as foraging, dispersal, reproduction, or nutrient acquisition(Crespi, 2001). This vast variety of collective behaviors, together with their lab manageability, fast evolution, and the various possibilities of molecular and genetical manipulations, have turned microbes into a recurrent model to investigate social behaviors and inspired many theoretical models. Microbial collective behaviors are very often controlled by the secretion of substances to the extracellular medium, named exoproducts. Exoproducts may serve to coordinate behavioral synchronization via quorum-sensing communication (Miller and Bassler, 2001, Czárán and Hoekstra, 2009), but they can also establish different types of ecological interactions among cells. For instance, mutualistic interactions may arise in mixed cultures in which each species benefits from the exoproducts of its partner in the mix (cross-feeding); antagonistic interactions have been also observed, as represented by the different forms of chemical warfare that facilitate the elimination of competing individuals in some bacterial species (McNally et al., 2017, West et al., 2007) (see Figure 18a). Especially interesting from an evolutionary perspective are cooperative interactions, actions that incur in a cost for the executor and whose benefit is shared with other individuals in the population. A paradigmatic example in which such dilemma arises is the synthesis of public goods, exoproducts that are costly to produce and benefit both the producer and its neighbors (see Figure 18a). In a well-mixed population of public-good producers and non-producers, every individual interacts with each other, and therefore the payoffs for each species due to public-good production are:

$$f_{\text{NP}}(N_{\text{P}}) = r\,c\,(N_{\text{P}}/N) \tag{48}$$

$$f_{\text{P}}(N_{\text{P}}) = f_{\text{NP}} - c \tag{49}$$

where the subscripts NP and P stand for non-producers and producers respectively. N_{P} is the number of producers within the population of total size N, r gives the benefits provided by the public good, and c is the cost of the cooperative behavior (i.e. the investment in the public good). Therefore, the total revenue of the public good depends on the number N_{P} of producers, how much c they invest in the production, and the growth multiplication factor r of the public good. Additionally, each individual obtains and equal share from this total production, regardless of whether it contributed to the production or not, but producers have to cope with the additional production cost. In such simplified scenario, non-producers will always outcompete producers because they get their shared benefit of the cooperative behavior without bearing its cost, and any initial mix of species will converge to a extinction of cooperators. This result, hence, poses an interesting *evolutionary dilemma* that can be summarized in two questions. First, why would an individual decrease its own fitness to confer fitness benefits on other individuals? And second, what are the mechanisms that stop the invasion of non-cooperative mutants (represented here by non-producers) and avoid the extinction of cooperation?

Several models have proposed mechanisms that could turn cooperation evolutionarily stable (see Section) and solve this dilemma: 1) the increase in population size due to cooperation makes the system more robust against extinctions induced by demographic fluctuations (Constable et al., 2016); 2) individuals that transiently neither execute nor benefit from the cooperative behavior are resistant to mutants and provide a pool to recover cooperation (Hauert et al., 2002); 3) the partial privatization of the benefits of cooperation by cooperators (Gore et al., 2009, Jin et al., 2018); 4) the effect of external forces, such as environmental flows (Drescher et al., 2014, Uppal and Vural, 2018); and 5) any form of assortment that makes cooperators more likely to interact with other cooperators in game-theoretic frameworks (Nowak, 2006). Some of the mechanisms to achieve assortment are: the existence of a spatial structure in the environment that, combined with individual limited mobility or cell properties such as adhesion and/or directed movement, keeps related cells together (Nowak and May, 1992, Tarnita et al., 2009, Allen et al., 2013a); recognition of cooperators and non-cooperators in order to choose the partner in the interactions (Pacheco et al., 2006, Antal et al., 2009); reciprocity via individual reputation or/and memory in the interactions (Nowak and Sigmund, 2005, Axelrod and Hamilton, 1981); or multilevel selection, which considers that different selective pressures acting at the individual and the group level favor groups dominated by cooperators (Traulsen and Nowak, 2006, Keller, 1999). However, these models very often oversimplify the ecological context in which interactions occur, as well as the possible existence of eco-evolutionary feedbacks that emerge due to the rapid evolution of microbes and that can reshape their ecology (see Section) (Tarnita, 2017, Estrela and et al., 2018). The necessity of modelling the ecological context and eco-evolutionary feedbacks is supported by numerous experimental studies. For instance, the cooperative nature of Pyoverdin production (an iron-chelating molecule hypothesized to be a public good) in *Pseudomonas* strongly depends on the environmental conditions in which strains evolve (Zhang and Rainey, 2013). Hence, any sociobiological label assigned to these secretion behaviors is only meaningful when posed in the proper ecological context, which should be recognized in any modelling framework (Tarnita, 2017, Estrela and et al., 2018).

Beyond the production and release of public goods and other exoproducts, cooperation relates to division of labor, whereby individuals in a population specialize in different tasks. This leads to fitness differences across cells, as illustrated by cell differentiation in *Dictyostelium discoideum* fruiting bodies: upon starvation, single-living cells aggregate and develop a multicellular fruiting body, in which only a proportion of cells become spores and eventually reproduce, while the rest die to form a stalk (see Figure 18b). Other examples of cooperation are provided by persisters, cells that exist in a quiescent non-growing state, or programmed cell death. In both cases, the existence of non-growing phenotypes alleviates the competition for resources, which favors the growth of conspecifics (West et al., 2007). These fitness differences between phenotypes that are specialized in different tasks depend on the ecological context in which populations thrive, which emphasizes the necessity of developing more comprehensive models that include a description of the environmental dynamics. Persister cells, for instance, while growing slowly, show antibiotic resistance and could thus outcompete fast-growing susceptible phenotypes in antibiotic-rich environments. Considering that persistence is acquired through a reversible phenotypic switch (Balaban et al., 2004), a model that explicitly describes fluctuations in the concentration of antibiotics in the environment has shown that, rather than a cooperative behavior, persistence could constitute an adaptation that is tuned in stochastic environments by the statistical properties of changes in antibiotic concentration (Kussell et al., 2005).

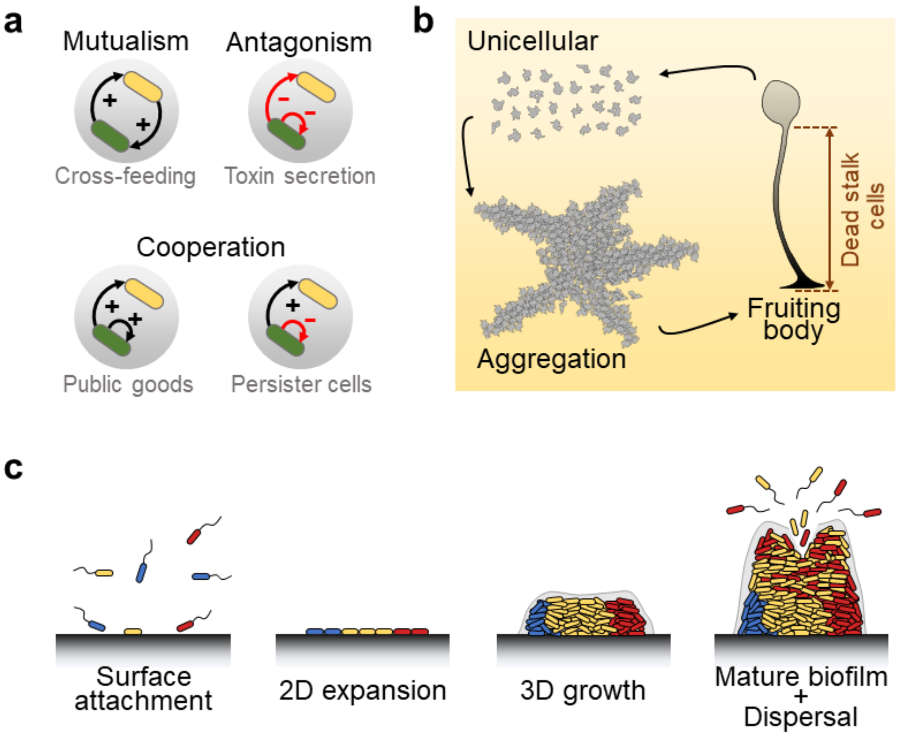

Fig. 18: a) Cell secretions may establish different types of ecological interactions. Mutualistic interactions, as represented by cross-feeding, appear when each of the species in the mix benefits from the secretions of the other species in the mixes. Antagonistic interactions are represented, for instance, by chemical warfares in bacteria, in which exoproducts kill competing cells. The costs associated to the actor (green cell) in these behaviors may be just a reduced growth rate due to allocation of resources into chemical production, but sometimes the release of the substances requires cell death. Cooperative behaviors may be classified in two major categories depending on whether the actor also receives a benefit or only pays a cost without receiving a direct fitness benefit. Public good production is an example of the former, while persistent cells constitute an example of the later (see main text for a detailed explanation of both behaviors). The existence of these non-growing phenotypes alleviates the competition for resources, which favors the growth of conspecifics. b) The life cycle of *Dictyostelium discoideum* is an example of division of labor in microbes. Starvation triggers the coordinated aggregation of free-living amoebae and the beginning of a developmental program that culminates with the formation of a fruiting body. Within the fruiting body, about 80% become dormant spores, whereas the other 20% facilitates spore dispersal by forming a stalk of dead cells. c) Biofilms present a huge diversity of social behaviors, ranging from the secretion of exoproducts that establish mutualistic, competitive or cooperative interactions, programmed cell death, to quorum-sensing, to division of labor.

Finally, all the behaviors discussed in this section frequently occur simultaneously and are hard to disentangle from each other. An example of such complex scenarios are biofilms, conglomerates of cells that often belong to hundreds of different species and grow attached to surfaces, subject to external flow stresses (Kempes et al., 2014, Drescher et al., 2014, Persat et al., 2015, Martínez-García et al., 2018) (Figure 18c). Division of labor has been reported in *Pseudomonas* biofilms, with some phenotypes specializing in biofilm growth and others in dispersal. Quorum-sensing plays an important role in initiating and structuring the biofilm, as well as in regulating the secretion of several exoproducts. Cell cooperation is crucial in the secretion of the extracellular matrix that holds cells together, and in the production of numerous public goods that regulate various aspects of biofilm progression and functioning. The secretion of other substances, such as antibiotics or bacteriocins, establishes competitive interactions between cells. And, finally, programmed cell death aids in structuring the biofilms (see (West et al., 2007, Nadell et al., 2016) for a review). Importantly, due to their reduced mobility, biofilm-dwelling bacteria mainly interact with cells in their local environment (see Section). This makes biofilms a very appropriate system to develop theoretical frameworks that couple ecological factors and the various forms of assortment that influence the outcome of social interactions (Nadell et al., 2016, Martínez-García et al., 2018).

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