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Minireview

MINIREVIEW

Revisiting life strategy concepts in environmental microbial ecology

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One sentence summary: Qualitative and quantitative measures are important when designating microbial life strategies at finer phylogenetic resolution over time.

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ABSTRACT

Microorganisms are physiologically diverse, possessing disparate genomic features and mechanisms for adaptation (functional traits), which reflect on their associated life strategies and determine at least to some extent their prevalence and distribution in the environment. Unlike animals and plants, there is an unprecedented diversity and intractable metabolic versatility among bacteria, making classification or grouping these microorganisms based on their functional traits as has been done in animal and plant ecology challenging. Nevertheless, based on representative pure cultures, microbial traits distinguishing different life strategies had been proposed, and had been the focus of previous reviews. In the environment, however, the vast majority of naturally occurring microorganisms have yet to be isolated, restricting the association of life strategies to broad phylogenetic groups and/or physiological characteristics. Here, we reviewed the literature to determine how microbial life strategy concepts (i.e. copio- and oligotrophic strategists, and competitor–stress tolerator–ruderals framework) are applied in complex microbial communities. Because of the scarcity of direct empirical evidence elucidating the associated life strategies in complex communities, we rely heavily on observational studies determining the response of microorganisms to (a)biotic cues (e.g. resource availability) to infer microbial life strategies. Although our focus is on the life strategies of bacteria, parallels were drawn from the fungal community. Our literature search showed inconsistency in the community response of proposed copiotrophic- and oligotrophic-associated microorganisms (phyla level) to changing environmental conditions. This suggests that tracking microorganisms at finer phylogenetic and taxonomic resolution (e.g. family level or lower) may be more effective to capture changes in community response and/or that edaphic factors exert a stronger effect in community response. We discuss the limitations and provide recommendations for future research applying microbial life strategies in environmental studies.

Keywords: oligotrophy; copiotrophy; C-S-R framework; microbial traits

INTRODUCTION

Functional traits attributable to the physiology of microorganisms have been conceptualized as life strategies to explain their behavior and response to their environment. The life strategy concepts reviewed here (i.e. analogous to the r- and k-strategist, copiotrophy–oligotrophy continuum, and the competitive– stress tolerator-ruderals (C-S-R) framework; Andrews and Harris 1986; Grime and Pierce 2012) are

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intentionally used as ecological life strategies for animals and plants, but have since been applied to microbial ecology to explain the prevalence and distribution of microbial communities, and their response to changing environmental conditions. While copiotrophy–oligotrophy is a two-way continuum primarily based on the physiological traits of microorganisms to capture resources, the C-S-R framework is a three-way trade-off which also considers traits for survival or persistence. Unlike animal and plant ecology, there is an unprecedented diversity of microorganisms with highly diverse physiological characteristics even among members of the same taxonomic affiliation (e.g. genus/species level; Höppener-Ogawa *et al*. 2009; Hoefman *et al*. 2014; Larkin *et al*. 2016). Hence, extrapolating the life strategy of one microorganism to other closely related microorganisms can be erroneous. However, recent work has provided strong evidence that the rate of a metabolic process can be closely linked to phylogeny, while glucose-derived carbon was assimilated by many microorganisms, the rate of assimilation varied, but were rather conserved across different bacterial families (Morrisey *et al*. 2016). Presently, whether the response in microbial activity is deeply rooted in phylogeny remains an open question. Nevertheless, based on similarities in the functionally dominant physiological features (i.e. microbial traits), generalizations have been made in an attempt to have a unifying conceptual model where an attributable life strategy is an aggregation of physiological traits selected for by abiotic and biotic environmental selection pressures (Blagodatskaya, Ermolaev and Myakshina 2004; Fierer, Bradford and Jackson 2007).

Oligotrophy and copiotrophy are physiological traits. Oligotrophic and copiotrophic microorganisms are distinguishable by their growth kinetics and substrate affinity for metabolism (e.g. copiotrophs can be characterized by higher Michaelis-Menten constant, K_s and maximal specific growth rate, μ values; Chen *et al*. 2016b), and hence, the stability of population density as well as in the efficiency in resource utilization, among other characteristics and genomic features (e.g. genome size, number of rRNA gene operon; see Klappenbach, Dunbar and Schmidt 2000; Fierer, Bradford and Jackson 2007; Lauro *et al*. 2009). Although a consensus of what strictly defines an oligotroph and copiotroph has not been reached, microorganisms associated to these life strategies are thought to possess distinct physiological traits that determine their response to environmental changes (e.g. resource availability) to be described in a predictable manner (Fierer, Bradford and Jackson 2007). Many of these characteristics, including the genome size, rRNA operon numbers, signal transduction and transcription mechanisms, among others (see Klappenbach, Dunbar and Schmidt 2000; Lauro *et al*. 2009), are inherent to microorganisms, and reflect their ability to efficiently acquire and utilize resources.

Oligotrophs are characterized by their ability to grow under low substrate concentrations (e.g. carbon in the nano and pico molar range), and generally possess a higher substrate utilization efficiency. That is, compared to copiotrophs, oligotrophs have a higher biomass yield for each unit of substrate consumed. Therefore, oligotrophs exhibit relatively slow growth, and are less reactive to abrupt resource availability. Instead, oligotrophs exploit nutrient poor environments with low energy flows. In contrast, copiotrophs are more responsive to carbon sources upon availability. In addition to carbon, other resources such as nitrogen availability also appear to determine the predominant life strategies of soil microbial communities (Fierer *et al*. 2012; Ramirez, Craine and Fierer 2012; Männisto *et al*. 2016); under nitrogen poor conditions, oligotrophs are thought to prevail being more effective at scavenging for the nutrient from recalcitrant soil organic matter (Moorhead and Sinsabaugh 2006), provided other nutrients are not co-limiting. As with resource acquirement, oligotrophs and copiotrophs are hypothesized to possess distinct growth efficiency (Lipson 2015; Roller and Schmidt 2015). The parallel between conditions favoring oligotrophs and efficient organisms prompted Roller and Schmidt (2015) to propose that oligotrophs possess a higher maximal growth efficiency. The proposed model relating growth efficiency to the limiting resource concentration indicates that growth efficiency is directly related to the limiting resource concentration for both oligotroph and copiotroph until a threshold (i.e. maximal growth efficiency) is reached thereafter, growth efficiency remains relatively constant. However, the maximal growth efficiency of oligotrophs is reached at a lower limiting resource concentration owning to their ability to scavenge and grow when resource availability becomes scarce (Moorhead and Sinsabaugh 2006; Roller and Schmidt 2015). Moreover, the authors proposed that oligotrophs tended to minimize maintenance energy (Roller and Schmidt 2015), but this hypothesis needs further substantiation.

Hence, copiotrophs are anticipated to be succeeded by oligotrophs upon depletion of readily metabolizable resources. However, it is noteworthy that the preference for more labile or recalcitrant substrates is not mutually exclusive (examples given below). Several postulations have been made as to the reasons copiotrophs are unable to grow under low carbon substrate concentrations, or conversely, the inability of oligotrophs to develop under high substrate levels (Semenov 1991; Koch 2001). The inability of copiotrophs to grow under low substrate concentration includes possessing a relatively lower affinity for the substrate, combined with a lack of adequate regulatory mechanism for starvation (Koch 2001). The inability of oligotrophs to develop under high substrate levels is less obvious; postulated reasons include growth imbalance caused by energy depletion with the sudden availability of transportable non-metabolic substrates, and osmotic shock caused by the import of abruptly available substances into the cell (for further explanation, see Koch 2001 and references therein).

Although growth kinetics and substrate utilization parameters can be determined using relatively standard methodologies, the lack of isolates hinders characterizing the life strategies of the vast majority of yet uncultivable microorganisms in the environment. Consequently, in environmental studies, microbial life strategies are typically inferred from their relative response to resource (i.e. carbon and nitrogen) availability in a predictable manner (Table 1; Fierer, Bradford and Jackson 2007; Placella, Brodie and Firestone 2012; Männisto *et al*. 2016; Morrisey *et al*. 2016; Chen *et al*. 2016b). Copiotrophic microorganisms are anticipated to grow and increase in abundance under high substrate regimes, whereas microbial populations found to increase in abundance at late successional stages following depletion of easily available substrate are likely oligotrophic (Koch 2001; Senechkin *et al*. 2010). For instance, oligotrophs were isolated in higher numbers in an organically managed farmland where varying amounts of composted farm yard manure containing relatively low nutrients were used as soil additives (Senechkin *et al*. 2010). Hence, the soil physico-chemical status (e.g. carbon and nitrogen bioavailability) may indicate the predominant microbial life strategy in an environment.

Table 1. Copiotrophic- and oligotrophic-associated phyla (finer taxonomic affiliation given when available) in response to nutrient amendments and environmental surveys.

Habitat	Geographic origin	Treatment (incubation period)	Methodology used for microbial community analysis[a]	Copiotrophic-associated (sub)phyla[b]	Oligotrophic-associated (sub)phyla[b]	Reference
Forest soil (*Quercus alba*; white oak stand)	Duke Forest, North Carolina (USA)	Sucrose amendment at 0–800 g C m^{-2} yr^{-1} (twice weekly over 1 yr)	Phyla-specific qPCR	*Betaproteobacteria*, *Bacteroidetes*	*Acidobacteria*	Fierer *et al.* (2007)
Grasslands turned agricultural fields since 1982 and 2001	Cedar Creek Ecosystem Science Reserve and Kellogg Biological Station (USA)	N-Amended gradient up to 291 kg N $ha^{-1}yr^{-1}$. Control fields without N amendments (ongoing)	Shortgun metagenomic analysis, rRNA gene sequencing, and catabolic profiling	*Alphaproteobacteria, Gammaproteobacteria, Bacteroidetes, Actinobacteria*	*Acidobacteria*	Fierer *et al.* (2012)
Various soils	Widespread (across USA)	~125 g N m^{-2} in the form of NH_4NO_3 – study of N effect alone (1 yr)	Pyrosequencing of the 16S rRNA gene (F515/R805 primer pair)	*Actinobacteria*, *Firmicutes*	*Acidobacteria*, *Verrucomicrobia*	Ramirez, Craine and Fierer (2012)
Various soils	Widespread (across USA, South America, Europe and Antarctica)	Sample collection for sequencing without amendments	Pyrosequencing of the 16S rRNA gene (F515/R806 primer pair)		*Verrucomicrobia*[c] (class: *Spartobacteria*)	Bergmann *et al.* (2011)
Arid-degraded soil	Murcia (Spain)	Compost and sludge amendments at 12 kg m^{-2} (10 yr)	Meta-proteomic analysis	*(Alpha)proteobacteria* (order: *Rhizobiales*)	*Acidobacteria*, *Firmicutes*, *Actinobacteria*, *Plantomycetes*	Bastida *et al.* (2015)
Agricultural soil	Ithaca, NY (USA)	Glucose amendment (24 h)	^{13}C-Glucose labeling, and cloning and sequence analysis of the 'heavy' fraction	*Gammaproteobacteria, Betaproteobacteria, Bacteroidetes*		Padmanabhan *et al.* (2003)
Natural forest and managed Chinese Fir stands	Wanmulin Nature Reserve (China)	Sample collection at topsoil (0–10 cm) and subsoil (40–60 cm)	Growth parameters (e.g. V_{max}, K_s, μ) and PLFA profiling for microbial community	Tended to be Gram-negative bacteria		Chen *et al.* (2016a)
Agricultural soil	Jiangsu Province (China)	Inorganic fertilizer and pig manure compost amendments at 300 kg N ha^{-1} and 4500 kg ha^{-1}, respectively (twice per year over 8 yr)	High-throughput sequencing (Illumina MiSeq) of the 16S rRNA gene (F338/R806 primer pair)	*Gemmatimonadetes*.	*Acidobacteria*, Candidate division WS3	Chen *et al.* (2016b)

Table 1. (*Continued*).

Habitat	Geographic origin	Treatment (incubation period)	Methodology used for microbial community analysis[a]	Copiotrophic-associated (sub)phyla[b]	Oligotrophic-associated (sub)phyla[b]	Reference
Tropical rainforest soil	Osa Peninsula (Costa Rica)	Dissolved organic matter (DOM; from leaf litter) amendment at ~ 225 μg DOM-C g soil^{-1} (24 h)	Cloning and sequence analysis	*Gammaproteobacteria* (order: *Enterobacteriales*), *Firmicutes* (genus: *Bacillus*)	*Acidobacteria*, *Alphaproteobacteria*	Cleveland *et al.* (2007)
Pine forest meadow	Northern Arizona (USA)	Sample collection at top soil (0–15 cm), and amended with glucose at 500 μg C g^{-1} (7 days)	^{13}C-Glucose labeling, and quantitative SIP approach	*Betaproteobacteria*, *Gammaproteobacteria*, *Firmicutes*, *Actinobacteria* (family: *Micrococcaceae*)	*Acidobacteria*, *Actinobacteria* (family: *Rubrobacteraceae*)	Morrisey *et al.* (2016) Hungate *et al.* (2015)
Tundra heath	Raisduoddar (Norway)	Sample collection of lightly and heavily reindeer-grazed top soil (0–5 cm), and amended with NH_4NO_3 at 8.75 mg N g^{-1}(6 weeks)	High-throughput sequencing (Ion PGM Sequencing) of the 16S rRNA gene (27F/518R primer pair)	*Actinobacteria* (orders: *Actinomycetales*, *Acidimicrobiales*, *Solirubrobacterales*), *Gammaproteobacteria* (genus: *Rhodanobacter* spp.)	*Alphaproteobacteria* (order: *Rhizobiales*), *Gammaproteobacteria* (family: *Sinobacteraceae*), *Acidobacteria*, *Verrucomicrobia*, *Planctomycetes*, *Bacteroidetes*	Männisto *et al.* (2016)
Temperate grasslands	Widespread (Africa, Europe, Australia, North America)	Field plots amended with $(NH_2)_2CO$ and $Ca(H_2PO_4)_2$ at a rate of 10 g N m^{-2} yr^{-1} and 10 g P m^{-2} yr^{-1}, respectively (2–4 yr)	High-throughput sequencing (Illumina HiSeq) of the 16S rRNA gene (515f/806r primer pair)	*Actinobacteria*, *Alphaproteobacteria*, *Gammaproteobacteria*	*Acidobacteria*, *Planctomycetes*, *Deltaproteobacteria*	Leff *et al.* (2015)
Grassland, Hardwood and coniferous forests	Minnesota (USA)	Topsoil (0–5 cm) amended with glucose, glycine, and citric acid at a rate of 240 μg C g soil^{-1} (24 h)	Pyrosequencing of the 16S rRNA gene (27F/338R primer pair)	Differential response with soil types and C-sources tested. Only consistency is the response of *Betaproteobacteria* (order: *Burkholderiales*)		Eilers *et al.* (2010)

Table 1. (*Continued*).

Habitat	Geographic origin	Treatment (incubation period)	Methodology used for microbial community analysis[a]	Copiotrophic-associated (sub)phyla[b]	Oligotrophic-associated (sub)phyla[b]	Reference
Agricultural field	(New York, USA)	Topsoil (0–10 cm) amended with xylose and cellulose at a rate of 0.88 mg C g dw soil^{-1} and 0.42 mg C g dw soil^{-1}, respectively (five sampling points over 30 days)	^{13}C-Xylose and ^{13}C-cellulose labeling, coupled to SSU rRNA gene sequencing (515f/806r primer pair)	*Firmicutes*, (incorporate labeled compound after 1 day), *Bacteroidetes* (incorporate labeled compound after 3 days), *Actinobacteria* (incorporate labeled compound after 7 days)	*Verrucomicrobia*, *Planctomycetes*, *Chloroflexi*	Pepe-Ranney *et al.* (2016)
Agricultural soils with diverse management practices	Droevendaal (the Netherlands)	Isolation effort	Isolation of oligotrophs by repeated transfers in low organic carbon medium		*Alphaproteobacteria* (family: *Rhizobiaceae*)[d]. Uncultured Bacteroidetes (uncultured *Sphingoterrabacterium* sp.)[d]	Senechkin *et al.* (2010)
Oceans	Marine environments worldwide	Not applicable	Prediction of trophic strategies based on genomic data	*Gammaproteobacteria* (genus: *Photobacterium*), *Alphaproteobacteria* (genus: *Silicibacter*), *Bacteroidetes* (genus: *Flavobacterium*)	*Alphaproteobacteria* (genus: *Sphingopxis*, *Pelagibacter*, *Roseobacter*, *Dinoroseobacter*), *Cyanobacteria* (genus: *Anabaena*), *Plantomycetes* (genus: *Rhodopirellula*, *Planctomyces*)	Lauro *et al.* (2009)

[a]Methodology used for the identification of soil microbial community.
[b]Relatively more copiotrophic/oligotrophic phyla.
[c]Based on conjectural evidence.
[d]Exclusive growth on low organic carbon medium.

BACTERIAL OLIGOTROPHIC- AND COPIOTROPHIC-ASSOCIATED PHYLA

There is little consistency in the oligotrophic- and copiotrophic-associated phyla based on our literature survey of studies using naturally occurring microbial communities (Table 1). Therefore, rather than correlative studies or incidental interpretation of microbial life strategies, we focused on more compelling evidence and explicit studies aiming to elucidate microbial life strategies. These studies were mainly derived from pure culture work and DNA-based stable isotope labeling approaches, or community analyses rigorously supported by physiological characteristics to find consistency in the associated life strategies of microorganisms. As numerous studies affiliated microorganisms at the order or lower taxonomic (i.e. phyla/subphyla) levels to their life strategies, we were confined to rather low taxonomic resolution, which likely encompass a multitude of microorganisms collectively possessing wide physiological capabilities. Moreover, many microorganisms can oscillate between high and low substrate use efficiency, given sufficient time to adapt to oligotrophic and copiotrophic lifestyles. *Cycloclasticus oligotrophus* RB1, a formerly presumed oligotroph, was initially unable to grow in nutrient-rich medium, but showed growth after continuous subculturing at relatively high concentrations of aromatic hydrocarbons (Wang, Lau and Button 1996). Therefore, it is noteworthy that many microorganisms are not absolutely copiotrophs or oligotrophs. Rather, many microorganisms possess a broad range of physiological characteristics, and 'true' or 'strict' obligate copiotroph/oligotroph can be viewed as possessing a more restrictive physiological capacity (e.g. narrow substrate utilization range; Semenov 1991), in which case, microbial life strategies could be viewed as a continuum (Semenov 1991; Grime and Pierce 2012). Therefore, a shift in the relative abundance of a microbial taxon, assuming no confounding factors (e.g. nutrient co-limitation; see below), may not necessarily be indicative of microbial life strategies (i.e. strictly oligotrophic or copiotrophic), but rather where the taxon lies in the continuum compared to the whole community.

Among the phyla consistently associated with oligotrophic environments are the *Acidobacteria* and *Verrucomicrobia* (Table 1). Admittedly, our literature review may not be exhaustive and that oligotrophs are taxonomically heterogeneous, but studies consistently indicate that microorganisms belonging to *Acidobacteria* and *Verrucomicrobia* were more competitive under oligotrophic conditions (Table 1). In particular, through empirical evidence including soils from widespread environments ($n = 71$), and further supported by a meta-analysis, Fierer, Bradford and Jackson (2007) showed that *Acidobacteria* predictably meets the presumption of an oligotroph, in that *Acidobacteria* predominates in carbon-poor soils, as well as in the bulk soil where resources, if bioavailable, are present at relatively lower concentrations than in the rhizosphere (Eilers *et al.* 2010). However, this observation is not without dispute; acidobacterial relative abundance was also found to be positively correlated to organic carbon availability, albeit the correlation was underscored by soil pH which was shown to be the better predictor for *Acidobacteria* abundance and community composition (Jones *et al.* 2009). The apparent discrepancies in research findings are not entirely surprising given the metabolic tractability and wide physiological traits among members of this phylum (e.g. carbon and nitrogen utilization, pH tolerance; see review Kielak *et al.* 2016). Like *Acidobacteria*, *Verrucomicrobia* are cosmopolitan and abundant soil microorganisms, representing on average 23.5% of total bacterial abundance based on a survey covering widespread environments (North and South America, Europe, and Antarctica) (Bergmann *et al.* 2011). Yet, members of this phylum are poorly understood, partly due to a lack of cultured representatives (133 isolates, source: Ribosomal Database Project; http://rdp.cme.msu.edu/, accessed 2015). In the environment, the higher relative abundance of *Verrucomicrobia* detected in the subsurface soil, reaching a maximum abundance at 10–50 cm below the soil surface, indicated an oligotrophic life strategy as carbon availability decreases with the depth of the soil profile (Fierer *et al.* 2003; Bergmann *et al.* 2011). By contrast, in a recent study monitoring *Verrucomicrobia* abundance and community composition in a forest, pasture and abandoned pasture soils, verrucomicrobial numerical abundance was positively correlated with total carbon content, with a recorded highest abundance in the pasture soil that contained the highest total carbon content (Ranjan *et al.* 2015). Probing deeper into the response of *Verrucomicrobia* at the class level, the authors observed a significant decrease in the relative abundance of *Spartobacteria*, in contrast to the appreciable increase of subphylum 3 with forest-to-pasture conversion, demonstrating the need to focus at finer levels of resolution as not all members of a phyla respond similarly to changing environmental conditions (see below).

Overall, there is no consistent trend among copiotrophic-associated phyla in the studies surveyed, and community response at the phyla-level to resource availability is site or study specific, suggesting the presence of local overriding factors driving community response. While some studies have in common *Actinobacteria* and *Betaproteobacteria* as (sub)phyla associated with copiotrophy, others suggest that these phyla are better suited to oligotrophic conditions (Table 1). This apparent contradiction is addressed below. We provide other reasons beside microbial life strategy to explain community response.

OLIGOTROPHIC- AND COPIOTROPHIC-ASSOCIATED FUNGI

When compared to bacteria, fungi have generally more oligotrophic features (Blagodatskaya *et al.* 2007, 2014; Garcia-Pausas and Paterson 2011; de Vries and Shade 2013; Dungait *et al.* 2013; Koranda *et al.* 2014; Shahzad *et al.* 2014; Whitaker *et al.* 2014). Comparison of bacterial and fungal activities is mostly based on studies in which labeled substrates (e.g. ^{13}C-glucose) are added to soils, and ^{13}C-enrichment of biomarkers (e.g. phospholipid fatty acids, DNA, ergosterol) is used to distinguish the response of the bacterial and fungal communities in soils. Bacterial and fungal (including both saprotrophs and ectomycorrhizae) community dynamics in response to resource amendments were used to infer the life strategies of these broad microbial groups. Next to (Gram-negative) bacteria, fungi were regarded as oligotrophs, exhibiting slower growth and more efficient use of (recalcitrant) carbon resources. However, also within members of the fungal community, a distinction can be made to group them into copiotrophs and oligotrophs (Andrews 1992). Copiotrophic fungi, often referred to as molds or sugar fungi, are thought to grow rapidly under optimal conditions, and their spores germinate and grow in response to available energy sources. They typically exhibit a short exploitative phase with high competitive ability. Such fungi are termed 'resource unit restricted' because they are confined to a resource until the resource has been consumed, after which they produce asexual dispersal spores or sexual resting spores to colonize new resource-rich locations after dispersal or remain in the same location until the resource becomes available again. The

latter approach to resource acquirement has been aptly coined as the 'sit and wait strategy', whereby the mycelial network waits to re-colonize when resources become available (Boddy 1999). Hence, fungi with predominantly copiotrophic characteristics tend to act as pioneer decomposers of organic matter, and usually degrade the same range of labile compounds as bacteria (van der Wal *et al.* 2013). When grown as laboratory cultures, they were often shown to be intolerant of antibiotics or growth metabolites of other fungi (Deacon 2005). Fungi with copiotrophic characteristics include members of the genera *Acremonium*, *Alternaria*, *Aureobasidium*, *Cladosporium*, *Cephalotrichum*, *Mucor*, *Rhizopus* and *Thysanophora* (Chigineva, Aleksandrova and Tiunov 2009; Di Lonardo *et al.* 2013; Lunghini *et al.* 2013). However, as with bacteria, fungi characterized as copiotrophs can also exhibit oligotrophic features. For example, some *Mucor* species proliferate under low resource concentrations, showing the ability to develop in nutrient-poor environments (Fioretto *et al.* 2007; Potthast, Hamer and Makeschin 2010; Wang *et al.* 2015). It has been suggested that fungal oligotrophy represents a common environmental growth response (Wainwright 1993, 2005).

Oligotrophic fungi typically establish and develop relatively slower (e.g. producing perennial fruiting bodies on trees) than copiotrophic ones. A prominent attribute of oligotrophic fungi is related to their capability to degrade recalcitrant polymers to gain access to more labile substrates, which are chemically or physically complexed with other more resistant polymers (van der Wal *et al.* 2013). Many species of the fungal phylum *Basidiomycota* predominantly show oligotrophic features, like members of the genera *Fomes*, *Irpex*, *Phanerochaete*, *Pycnoporus*, *Schizophyllum* and *Trametes* (Baldrian 2006; Baldrian and Valásková 2008; Vě trovský *et al.* 2011). The same may hold for arbuscular mycorrhizal fungi (*Glomeromycota*) which decrease in abundance following nitrogen additions (Egerton-Warburton and Allen 2000; Chen *et al.* 2014, 2016a). Considering a different phylogenetic group, within the *Ascomycota* phylum, members of the genera *Beauveria*, *Cylindrocarpon*, *Fusarium*, *Geomyces*, *Paecilomyces* and *Penicillium* possess the capacity to decompose recalcitrant organic compounds (Garrett 1951; Nilsson 1973; Osono 2005; Seifert 2008). Wood and litter have low levels of nitrogen, and oligotrophic decay fungi have developed strategies to deal with this suboptimal nitrogen concentration. One of the mechanisms is to transfer nitrogen via fungal hyphae from soil to wood or litter (Frey *et al.* 2000; van der Wal *et al.* 2007). Other mechanisms of oligotrophic fungi to cope with nutrient-poor conditions are to scavenge nutrients from the air and rainwater, enabling them to grow on rock surfaces (Wainwright 1993).

DOES MICROBIAL LIFE STRATEGY EXPLAIN COMMUNITY RESPONSE?

While response in microbial community composition is associated with a shift in microbial life strategies (Fierer, Bradford and Jackson 2007, 2012; Placella, Brodie and Firestone 2012; Leff *et al.* 2015; Chen *et al.* 2016b), is it prudent to attribute changes in community response to microbial life strategies alone? Besides carbon and nitrogen, relative shifts in community composition and abundance are also influenced by the concurrent availability of other macro- and/or micronutrients (i.e. nutrient co-limitation: Veraart *et al.* 2015), making existing soil nutrient status and other edaphic factors relevant in determining community response. In Eilers *et al.* (2010), the authors showed that although there is some consistency in the response of specific phyla to readily degradable carbon sources across different soil types, community response varied depending on the carbon source (i.e. glucose, glycine and citric acid) and soil types tested, indicating that soil edaphic factors do, in part, play a (in)direct role in community response. In phosphate-limited environments, microorganisms capable of solubilizing adsorbed phosphate fraction (e.g. some microorganisms belonging to the genera *Enterobacter*, *Klebsiella* and *Pantoea*, within the phylum *Gammaproteobacteria*; Chung *et al.* 2005) will benefit from carbon and nitrogen availability. These microorganisms may not necessarily be rapid responders to an abrupt increase in carbon availability per se, but are in a competitively advantageous position in phosphate-poor environments allowing growth and cell proliferation, in which case, they may be misinterpreted as possessing a copiotrophic life strategy (Cleveland *et al.* 2007).

Although *Actinobacteria* had generally been considered to be more copiotrophic among soil microbial phyla (Ramirez, Craine and Fierer 2012; Leff *et al.* 2015), some members of the phylum (e.g. *Actinomycetales*) are able to depolymerize complex carbon substrates (e.g. lignin, cellulose; Barder and Crawford 1981). To explain the increase in *Actinobacteria* following nitrogen amendment, Männisto *et al.* (2016) suggest that upregulation of lignocellulolytic activity upon increased nitrogen availability (Barder and Crawford 1981) likely promoted the decomposition of more recalcitrant carbon compounds. Hence, the relative increase in *Actinobacteria* can be caused by increased decomposition of recalcitrant carbon substrate, instead of labile ones. Moreover, nutrient input (e.g. nitrogen) may pose an indirect effect on the soil microbial community, mediated through the shift in vegetation coverage (Leff *et al.* 2015). A shift in the plant composition does not necessarily translate to a significant shift in the belowground microbial community structure (Männisto *et al.* 2016), but it alters the quality of the litter and root exudates, with the latter known to select and shape the microbial composition of the rhizosphere, while driving microbial activity (Eilers *et al.* 2010; Ridl *et al.* 2016). Particularly evident in field studies, higher primary plant production as a result of nutrient input will also increase the availability of labile carbon for soil microorganisms (Leff *et al.* 2015), obscuring any direct effect of the nutrient input.

Therefore, microbial community response is likely triggered by multiple mechanisms acting simultaneously. Disentangling the direct and indirect effects of community response will be a challenge for future research, but may be realized using stable isotope labeling approaches to track the different fractions (e.g. locally borne or added resources, labile or recalcitrant resources) of substrate/nutrient metabolized by active microorganisms (e.g. Cleveland *et al.* 2007; Morrisey *et al.* 2016; Pepe-Ranney *et al.* 2016). However, the SIP approach comes with a caveat; the labeled substrate can be tracked provided it is incorporated into the microbial biomass, which may not occur under nutrient co-limiting conditions. Accordingly, labeled substrate used as an energy source will escape detection. Nevertheless, given that the majority of soil microorganisms are present in the form of a 'seed bank' (Lennon and Jones 2011; Ho *et al.* 2016b), the stable isotope probing approach has the added advantage of capturing only the relevant microbial communities actively metabolizing a resource.

The temporal dynamics of a microbial community in response to substrate amendments is relevant to infer microbial life strategies. Studies documenting a snapshot of the community following nutrient input may provide clues to the fast responding members of the community, but community response based on a rather arbitrary sampling time point will not provide a holistic depiction of the succession of community members. While some studies determined shifts in community

composition within 24 h, others performed the community analysis after a decade following a single pulse of nutrient (Table 1). Accordingly, soil microorganisms responded to a one-off (in)organic N amendment by decreasing respiration rate over ≥1 year (Ramirez, Craine and Fierer 2012). However, at relatively shorter time scales (<10 days), an immediate increase in soil respiration was observed after amendments with carbon-rich residues or readily metabolized compounds (Eilers *et al.* 2010; Ho *et al.* 2015). It is likely that the addition of labile carbon compounds alleviated carbon-limiting conditions, although a priming effect caused by the availability of the labile compounds cannot be excluded (Fontaine, Mariotti and Abbadie 2003). Depending on the duration of the experiment, labile carbon input may leave an imprint on the microbial community by shifting the composition, where oligotrophic microorganisms are succeeded by their copiotrophic counterparts. Prolonging the duration of the experiment, however, may see the re-emergence of oligotrophs. The succession of microbial groups within and between phyla or within members of a specific microbial guild containing different phyla showed that the soil is a highly dynamic environment (Noll *et al.* 2005; Ho, Lüke and Frenzel 2011; Placella, Brodie and Firestone 2012; Pepe-Ranney *et al.* 2016). Hence, the experimental time frame is essential to determine the dynamics of community response, which may be differentiated based on short- and long-term variation, or even permanent alteration to the soil microbial community with (consecutive) pulses of substrate/nutrient availability. Overall, considering a snapshot of the response of community members to resource amendments may not be sufficiently adequate to infer microbial life strategies.

An argument against determining microbial community response at phyla or high taxonomic levels as is commonly described (Table 1) is the high taxonomic variation within a single phylum. Like *Acidobacteria* and *Verrucomicrobia* that are likely comprised of copiotrophic and oligotrophic members (Fierer, Bradford and Jackson 2007; Jones *et al.* 2009; Ranjan *et al.* 2015), recent findings showed that the phylum *Actinobacteria* also consisted of both copiotrophic and oligotrophic members (Morrisey *et al.* 2016). While the authors showed that glucose, an easily degradable carbon source, was rapidly assimilated by many members of a microbial community (presumably copiotrophs), the rate of carbon assimilation was different within members of the same phyla, but comparable rates of carbon assimilation were detected by members of the same family. Furthermore, both copiotrophic and oligotrophic life strategies exhibited by members of *Actinobacteria* are consistent with their capacity to degrade both labile and complex carbon substrates (see above). Similarly, Männisto *et al.* (2016) showed that different families within the phylum *Gammaproteobacteria* responded contrastingly to increased nitrogen input, that is, families *Xanthomonadaceae* and *Sinobacteraceae* respectively responded positively and negatively to nitrogen amendments. These findings question the validity of associating life strategies to broad microbial phyla, and further suggest that it is imperative to consider the appropriate and finer phylogenetic resolution when documenting microbial community responses to infer microbial life strategies.

FROM TWO-WAY TO THREE-WAY CONTINUUM: C-S-R FRAMEWORK

Recognizing the inconsistency emerging from conceptualizing microbial community response and ecological characteristics as life strategies at broad taxonomic affiliations, Ho *et al.* (2013a) placed members of a specific microbial guild—aerobic methane oxidizers (methanotrophs)—in the C-S-R life strategy framework. Aerobic methanotrophs represent a unique group of microorganisms capable of oxidizing methane to carbon dioxide using the enzyme methane monooxygenase, and are confined to <30 genera belonging to three (sub)phyla (*Alphaproteobacteria*, *Gammaproteobacteria* and *Verrucomicrobia*) to date. Because aerobic methanotrophs are represented by a limited number of described genera and species, belonging to only three (sub)phyla, the authors were able to assign these microorganisms to their anticipated life strategies at the genus level based on published work (Ho *et al.* 2013a). Interpreting the functional traits of methanotrophs as life strategies within the C-S-R framework allows a three-way trade-off between the community members with the capacity to (i) rapidly capitalize on resource availability in productive environments (competitors), (ii) re-colonize and establish in environments facing frequent perturbations (ruderals), and (iii) withstand and persist under non-favorable conditions and stress (stress tolerators) (Grime and Pierce 2012; Ho *et al.* 2013a). Hence, besides using the physiological traits involved in capturing resources (e.g. substrate affinity, substrate utilization efficiency) to assign copiotrophic/oligotrophic life strategies, the C-S-R continuum allows the classification of microorganisms on the basis of a whole set of traits enabling the tolerance and survival of harsh conditions. Indeed, many microorganisms, including the methanotrophs, revert to a reversible metabolically inactive state (dormancy) in response to unfavorable conditions; the seed bank community is numerically dominant in the soil environment (Whittenbury, Davies and Davey 1970; Lennon and Jones 2011).

Grime and Pierce (2012) further proposed that 'filters' can be applied to reconstruct or predict the assembly of the microbial community in an environment within the C-S-R framework (Grime 2013). The authors introduced the 'twin-filter model' with the primary competition-stress-disturbance (CSD) filter preceding the proximal filter. Briefly, the primary CSD filter discriminates against primary adaptive traits essential for fundamental survival (e.g. energy acquisition and usage metabolism), whereas the proximal filter selects traits affecting survival, but not essential to the CSR framework, and typically relates to traits to overcome a sporadic or specific stress at a local scale (Fig. 1B; Grime and Pierce 2012). Therefore, the proximal filter acts as a 'secondary selection' of traits which are not competing with primary traits represented in the primary CSD filter. The application of the 'twin-filter model' thus implies the convergence of the community members in an environment, but also allows potential secondary trait divergence at the proximal filter level.

As a deductive exercise, supported by recent empirical evidence, we applied the 'twin-filter model' to methanotroph genera with known or assigned life strategies (Fig. 1A; Ho *et al.* 2013a). We used the indigenous methanotrophs in a rice paddy soil originating from Vercelli (Italy) as a model system for which we have sufficient knowledge; the methanotrophic community composition and ecological traits as well as community response to physical and chemical perturbations as *per* rice agricultural practice had been well documented (i.e. diurnal temperature fluctuations, recurring desiccation-rewetting events, prolonged desiccation and nitrogen fertilization; Noll, Frenzel and Conrad 2008; Ho and Frenzel 2012; Collet *et al.* 2015; Ho *et al.* 2016b,c). Some model perturbations are hypothetical, but they represent realistic projections of future scenarios as justified for these studies. Among the primary adaptive strategies of methanotrophs inhabiting rice paddy soils, we identify (i) low affinity for methane, the rice paddy being an environment with a

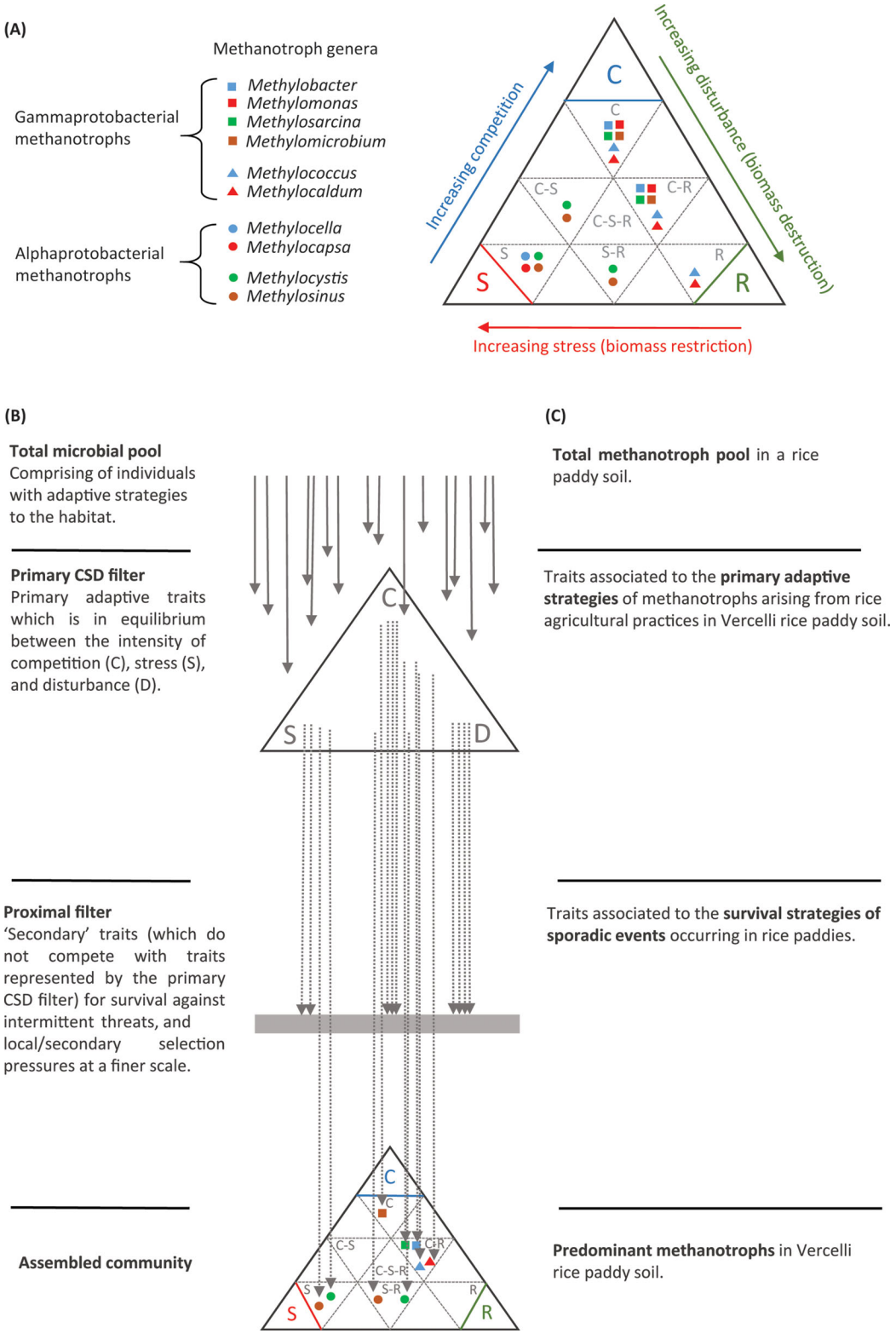

Figure 1. (**A**) Predominant methanotrophic community composition in a rice paddy soil. Assignment of methanotroph genera within the C-S-R framework based on a literature review of environmental studies given in Ho *et al.* (2013a). (**B**) Simplified scheme showing the selection of the assembled community from the total community pool using the 'twin-filter model' after applying the primary CSD filter, then the proximal filter, as modified from Grime and Pierce (2012). Application of the primary CSD and proximal filters using methanotroph genera with known or assigned life strategies (A), on the basis of adaptive traits arising from the physical and chemical conditions anticipated (i.e. diurnal temperature fluctuations, recurring desiccation-rewetting events, prolonged desiccation and nitrogen fertilization) in a rice paddy soil environment, for which there is accumulated knowledge (**C**). The methanotroph genera possessing filtered/selected traits are based on the findings of published work using the Vercelli (Italy) rice paddy soil as a model system. Collectively, these studies determined the response and resilience of methanotrophs to a heat shock at 37°C and 45°C (Ho and Frenzel, 2012), long-term drought (Collet *et al.* 2015), desiccation combined with a short heat stress (≤7 days) at 25°C and 75°C (Ho *et al.* 2016a), recurring desiccation-rewetting intensity (Ho *et al.* 2016b) and urea fertilization (Noll, Frenzel and Conrad 2008).

high energy flow (methane-producing environment); (ii) the ability to withstand fluctuating osmolarity and desiccation resulting from recurring desiccation-reflooding events as per rice cultivation practice; and (iii) the ability to detoxify products of ammonium oxidation with nitrogen fertilizer application. The proximal strategies may include the ability to form desiccation and heat-resistant resting cells with prolonged desiccation events. Moreover, some methanotrophs will benefit from their ability to form an extracellular capsule or slime layer to confer protection against osmotic stress and desiccation with increased frequency of desiccation-rewetting events (Wise, McArthur and Shimkets 2001). The assembled methanotrophic community composition in Vercelli rice paddy soil (Fig. 1C) should then approximate the predominant methanotrophs found in other rice paddies given that the 'twin-filter model' approach implies the convergence of the assembled community and assuming all factors considered are equal across the rice paddies. Yet, a survey showed that the community composition in tropical (Indonesia and Vietnam) rice paddy soils was dissimilar to the community composition in the Italian rice paddy soil; the tropical rice paddy soils were depleted in alphaproteobacterial methanotrophs (Lüke *et al.* 2014). This indicates that the range of predominant or specific traits respectively associated with the primary and secondary adaptive strategies differ, possibly as a result of selective factors (e.g. temperature/climatic conditions, rice plant–microbe and other biotic interactions; Hardoim *et al.* 2011; Sessitsch *et al.* 2012; Ho *et al.* 2016a) other than those considered here (i.e. rice agricultural practice) having an overriding effect in modulating community selection.

Nonetheless, the predicted life strategies of the methanotrophs within the C-S-R framework (Fig. 1A) was found to be consistent in other methane-emitting environments, as was documented for the methanotrophic community inhabiting a peatland (Putkinen *et al.* 2014), landfill cover soil (Henneberger *et al.* 2015) and methane seeps in a floodplain (Oshkin *et al.* 2014). In these studies, the genera *Methylobacter* and *Methylosarcina* were indicative for an environment with a high methane source strength, and showed predominance over alphaproteobacterial methanotrophs, being more competitive in a productive environment besides showing a rapid response to micronutrient availability (i.e. copper, a precursor for methane oxidation; Ho *et al.* 2013b). In a peatland succession study, Putkinen *et al.* (2014) showed alphaproteobacterial methanotrophs to become active during the later stages of succession corresponding with the highest stress level (lowering of water table level, nutrient status and pH) which conforms to their attributes as a 'stress tolerator' within the C-S-R framework. Besides elucidating the life strategies of methanotrophs, the C-S-R framework has also been considered for fungal life strategies (see recent reviews; Changnon *et al.* 2013; Crowther *et al.* 2014).

COMING FULL CIRCLE: CELL CULTURING AND ISOLATION, AIDED BY MOLECULAR TOOLS TO PREDICT THE LIFE STRATEGIES OF MICROORGANISMS

Because of high bacterial heterogeneity, and that a predicted life strategy can differ in microorganisms belonging to the same microbial taxa, a reliable method to determine microbial life strategy is through culture-dependent approaches (e.g. repeated culturing in low organic carbon medium; Senechkin *et al.* 2010). Indeed, 'strict' oligotrophs are distinguishable by culturing techniques (Senechkin *et al.* 2010; da Rocha *et al.* 2010). While being potentially insightful, correlative studies hinge on measured variables, typically macronutrients (i.e. carbon and nitrogen) and other environmental parameters (e.g. pH, soil characteristics) to derive ecological relevance from community responses. This excludes unmeasured variables (e.g. micronutrients, key trace elements, rare earth metals; Pol *et al.* 2014) which may become relevant for activity and community response. Arguably, it is not feasible to determine all variables, but it is necessary to go beyond correlative studies to confirm associated life strategies of microorganisms. Culture-dependent approaches (e.g. bacteria isolation) are time consuming, and come with inherent biases. For instance, only a minor fraction of soil microorganisms are retrieved from the environment through cell culturing and isolation. Nevertheless, culture-dependent approaches may still be a promising tool to capture the missing bacterial diversity (Shade *et al.* 2012). By using novel cultivation techniques, previously 'unculturable' bacteria can be isolated in the laboratory, provided essential aspects of their environment rendered by (a)biotic factors or interaction of these factors are replicated in the laboratory (Stewart 2012). For instance, isolation of novel bacteria belonging to the candidate division TM7 was achieved using the soil substrate membrane system where soil extract was used as the cultivation media to mimic the substrate available *in situ* (Ferrari, Binnerup and Gillings 2005). Given that a microbe rarely lives in seclusion, isolation techniques capitalizing on microbial interaction to provide key nutrients and other growth promoting factors as well as to relieve stress is another promising avenue when developing novel isolation techniques (Stewart 2012; Tyc *et al.* 2014; Ho *et al.* 2016a).

In an attempt to relate microorganisms to their associated life strategies, while circumventing the need for culturing all microorganisms, Lauro *et al.* (2009) predicted the life strategies of marine microorganisms based on the genomes of *Sphingopyxis alaskensis* RB2256 and *Photobacterium angustum* S14, respectively, representing an extreme oligotroph and copiotroph. Through comparative genomics of *S. alaskensis* RB2256 and *P. angustum* S14, discriminative genomic features (e.g. potential to sense and respond to extracellular stimuli, possessing a wide array of transporters, and to detoxify a broad range of substances; Lauro *et al.* 2009) defining the trophic extremes of a marine copiotroph and oligotroph were identified, and were subsequently used as yardsticks to predict the life strategies of other marine bacterial species. More importantly, the prediction also identified microorganisms exhibiting both copiotrophic and oligotrophic genomic features (e.g. *Planctomycetes*; moderate oligotroph), showing a continuum of life strategies bridging the extremes (Lauro *et al.* 2009). In line with metagenomic approaches, the functional profile of microbial communities can be predicted with quantifiable uncertainty, and assuming significant phylogeny–function relationship, based on the 16s rRNA gene (e.g. PICRUSt, phylogenetic investigation of communities by reconstruction of unobserved states; Langille *et al.* 2013). Many highly enriched, yet uncultured ecologically relevant microorganisms have been well characterized with regard to their genomic potential (e.g. putative microorganisms catalyzing anaerobic ammonium oxidation, ANNAMOX and the anaerobic methane oxidizer *Candidatus* Methylomirabilis oxyfera; Strous *et al.* 2006; Ettwig *et al.* 2010). This approach is thus a reconciliation of culture-dependent techniques (e.g. cell culturing, enrichment and isolation) and cutting-edge molecular tools to derive microbial life strategies (Goodwin, McPherson and McCombie 2016), and can also be applied in the C-S-R framework if a representative of a 'strict' competitor, ruderal and stress tolerator is known. Consequently,

this approach can be used to predict the life strategy of any bacterium—(un)cultured—provided the (partial) genome or sufficient genomic information is available, supported by physiological/phenotypic characteristics of the microorganism.

REINVENTING THE WHEEL FOR LIFE STRATEGY CONCEPTS IN ENVIRONMENTAL MICROBIAL ECOLOGY

Is there a need to develop novel life strategy concepts specifically for microbial community ecology, or is it sufficient to adopt and adapt borrowed concepts from animal and plant ecology, made relevant to microbial ecology? Although having a unifying conceptual model for microbial life strategies is tantalizing, generalizations and assumptions were made to fill the gap of knowledge when assigning life strategies. Based on our literature review, discrepancies in the apparent life strategies of microorganisms become evident at finer phylogenetic resolutions (e.g. family, genus and species level). Hence, it is not unreasonable to assume that considering microbial community response at finer resolutions may be more adequate when assigning life strategies to microorganisms. Nevertheless, significant relatedness between microorganisms does not necessarily reflect shared physiology. Hence, trait-based approaches have gained recognition in recent work demonstrating microbial life strategies and modeling of ecosystem processes (Crowther *et al.* 2014; Krause *et al.* 2014).

Based on microbial traits and considering the appropriate resolution of representative microorganisms catalyzing defined processes, animal and plant ecological concepts seem applicable to microbial ecology, showing some consistency across different environments such as in the case of the methanotrophs (Ho *et al.* 2013a). However, further systematic studies are needed to generate quantitative data under defined conditions to verify the life strategies of the methanotrophs (as well as other microorganisms) within the C-S-R framework (Grime and Pierce 2012). Extrapolating from plant life strategies (Bornhofen, Barot and Lattaud 2011; Grime 2013), the C-S-R framework exhibits potential as a predictive and interpretive tool for microorganisms responding to changing land-use and climate scenarios, as was also proposed by Grime (2013). Taken together, we advocate both qualitative and quantitative measures when designating microbial life strategies at finer phylogenetic resolution over time, cautiously heeding the words (rephrased) of George E.P. Box (Mathematician, University of Wisconsin, USA), 'all models are wrong, some are useful'.

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