			isotope probing (qSIP).

Title: Growth rate as a link between microbial diversity and soil biogeochemistry

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Abstract

The growth rate of a microorganism is a simple yet profound way to quantify its impact on the world. The absolute growth rate of a microbial population reflects rates of resource assimilation, biomass production, and element transformation, some of the many ways that organisms affect Earth's ecosystems and climate. Microbial fitness in the environment depends on the ability to reproduce quickly when conditions are favorable and adopt a survival physiology when conditions worsen, which cells coordinate by adjusting their relative growth rate. At the population level, relative growth rate is a sensitive metric of fitness, linking survival and reproduction to the ecology and evolution of populations. Techniques combining 'omics and stable isotope probing enable sensitive measurements of growth rates of microbial assemblages and individual taxa in soil. Microbial ecologists can explore how the growth rates of taxa with known traits and evolutionary histories respond to changes in resource availability, environmental conditions, and interactions with other organisms. We anticipate that quantitative and scalable data on the growth rates of soil microorganisms, coupled with measurements of biogeochemical fluxes, will allow scientists to test and refine ecological theory and advance process-based models of carbon flux, nutrient uptake, and ecosystem productivity. Measurements of *in situ* microbial growth rates provide insights into the ecology of populations and can be used to quantitatively link microbial diversity to soil biogeochemistry.

Introduction

Achieving growth in the face of a changing environment is a fundamental challenge for microorganisms living in soil. Microbial growth requires the coordination of a cell's system-level physiology, including the extraction of energy and substrates from the environment, synthesis of hundreds of molecules at appropriate concentrations, and the events of cell division. All of this coordination has to be done in such a way that allows the cell to modify its activities depending on changes in its surrounding environment – often on a very short time scale. Over billions of years of evolution, soil microorganisms developed strategies for growing in extreme cold and heat, in highly acidic and alkaline habitats, on the inside and outside of plant roots, and on mineral surfaces. Soil microorganisms have wide-ranging metabolic capabilities and can capitalize on diverse redox pairs and reactions that occur not only within, but also among, cells representing multiple domains of life[1].

As soil microorganisms grow, they assimilate, transform, and redistribute key elements in their environment[2], with far-reaching consequences for Earth's ecosystems and climate. Microorganisms aid in the process of extracting phosphorus and sulfur from their geological reservoirs, where they typically reside for thousands to millions of years, moving them into biological systems with much shorter residence times, typically ranging from weeks to months[3,4]. Assimilation and retention of nutrients like nitrogen and phosphorus in microbial biomass can constrain plant growth and limit the capacity of ecosystems to capture carbon (C) from the atmosphere[5]. Microbial redox transformations determine whether organic C molecules in soil reach the atmosphere as CO_2 or as CH_4, potentially amplifying the impact of the gas on Earth's climate.

Soil microorganisms exist in a range of physiological states, from dormancy to exponential growth, with profoundly different consequences for soil C and nutrient cycling. Relative growth rate, the rate of increase in mass or abundance per unit time relative to starting size, captures such variation and is a powerful index of how microorganisms adjust their physiology in response to the environment. Since traits that confer stress tolerance can hinder the ability of cells to grow quickly[6], many microbial species have developed distinct phenotypes for survival in stressful versus growth-conducive environments. These phenotypes vary profoundly, not only in their rates of growth, but also in their central C metabolic networks[7], cell sizes, and macromolecular compositions[8]. At the population level, growth concepts are intimately linked with fitness and capture the nuances that arise as microorganisms interact with each other and their surroundings (we use the term growth to refer to gross growth, rather than net growth which is a function of both growth and mortality rates). Along with per capita mortality rate, per capita growth rate, a measure of the average individual growth rate in a population, reflects how well microorganisms compete for resources and respond to challenges associated with stress and predation. Measures of relative growth, like per capita growth rate, are especially useful for understanding how growing microorganisms respond to the environment and can also be used to quantify the intensity of interactions, such as competition, predation, and mutualism[14].

Absolute growth rate, or the rate of change in mass or abundance per unit time, is useful for quantifying microbial contributions to element fluxes. Measurements of absolute growth rates relative to soil quantity (i.e., the rate of change in mass or abundance of microorganisms per unit time *per unit mass or volume of soil*) reflect rates of microbial element assimilation and use. Along with absolute mortality rate, absolute growth rate sets the standing stock of microbial biomass and ultimately drives changes in the taxonomic makeup of entire communities. Soil

72 microorganisms can exhibit rapid rates of turnover (the rate at which microorganisms in
73 populations or communities are replaced via growth and mortality), often with minimal changes
74 in population size or biomass. For this reason, microbial biomass and abundance alone are poor
75 predictors of element flux[15,16]. Measurements of absolute growth, along with other quantitative
76 metrics of physiologically active microorganisms, would provide a powerful means for testing
77 the impacts of microbial biodiversity on C and nutrient cycling at the ecosystem scale[17].
78 There is a rich history of measuring growth rates in soil microbial ecology, including decades
79 of measurements in culture[18,19] and *in situ*[20–24]. Many recent developments in soil ecology invoke
80 microbial growth rates to conceptually link microbial physiology to ecosystem services such as
81 climate mitigation[25], pollution reduction[26], and food supply[27]. *In situ* measurements of growth
82 rate, including those of specific taxonomic groups[16,28,29] and individual cells[30], enable rigorous
83 tests of the controls over the ecology of these organisms where they live and grow and how that
84 connects to larger scale ecological processes[31–33].
85
86 **Measurements of microbial growth rates in soil**
87 Methods measuring soil microbial growth rates *in situ* capture different processes, from
88 the synthesis of biomolecules that make up individual cells, to the expansion of populations, to
89 the gross production of biomass carbon at the assemblage level (Figure 1 and Supplementary
90 Table 2). Such methodological diversity is reflected in published estimates of relative growth
91 rates of soil microbial assemblages, which span at least four orders of magnitude from 0.0009
92 day^{-1} to 1.98 day^{-1}. Syntheses of *in situ* growth rate measurements can be used to identify sources
93 of variation within and between methods. Linear model analysis of published estimates of
94 assemblage-level growth rates indicates that method, ecosystem type, and soil depth can be

significant predictors of *in situ* growth (Figure 2a; whole model $R^2 = 0.24$; ecosystem: $F_{3, 276} = 7.10$, $p<0.001$; method: $F_{5, 276} = 71.90$, $p < 0.001$; depth: $F_{2, 276} = 9.75$, $p < 0.001$; see Supplementary Methods). Environmental factors like carbon availability[24], soil moisture[34], temperature, pH, and seasonality[35] are important determinants of soil microbial growth too. Systematic reviews and metanalyses are needed to comprehensively synthesize growth rate measurements and quantify the relative importance of environmental and methodological factors across ecosystems and under future climate scenarios.

Methodological variation may arise from multiple sources. For example, incubations may be biased if temperatures are held below or above those typical of the organisms' natural habitat and shorter incubations are less sensitive at detecting, and may thus exclude, taxa with slower growth rates compared to longer incubations (but see Caro et al. 2023). Methodological variation may also be a product of methods targeting different biomolecules, such as DNA, proteins, or lipids, which may have variable rates of synthesis and degradation that are contingent on the cell's physiological state. During exponential growth, cells synthesize macromolecules at near-constant differential rates and divide at a particular cell mass or size. Under these conditions of balanced growth, relative growth rate sets key cellular phenotypes like cell size and the mass fractions of nucleic acids, proteins, and lipids. In nature, relationships between replicative growth and rates of macromolecular synthesis may not always be so tightly coupled. Applying multiple methods could help identify the physiological adjustments that allow microorganisms to strike a balance between survival and proliferation in soil. For example, in response to C limitation, microorganisms may undergo reductive division[36], simultaneously catabolizing lipids for energy[37] while synthesizing DNA and protein in order to divide into smaller and more stress resistant cells, which could be explored using stable isotope probing (SIP) approaches to target

118 lipid[16], DNA[28,29,38], and protein[39] synthesis concurrently. A wide range of methods are needed to
119 capture the many strategies microorganisms may use to grow in soil.
120 Most measurements quantify relative growth rate, useful for understanding how
121 microorganisms respond to the environment. Measurements of absolute growth rate are needed
122 to understand how microorganisms move elements through ecosystems. Converting metrics of
123 relative growth rate, for example based on rates of tracer uptake per unit time, to absolute growth
124 rates, in units of mass or number or microorganisms per unit time, can be challenging because
125 direct measurements of biomass and abundance are difficult to obtain and validate[40]. Estimates
126 of absolute growth rate may also require known extraction efficiencies of biomolecules from
127 soils. For example, SIP-based methods measure growth based on rates of isotope incorporation
128 into target biomolecules, which require biomolecule extractions from soils. Extractions of DNA,
129 lipids, or proteins from soil seldom yield complete recovery. Extraction efficiencies may be low,
130 variable, or – in the case of DNA – may not typically be evaluated. Including recovery
131 standards[41] and developing better constraints on the recovery of necromass-derived biomolecules
132 would improve the accuracy of absolute growth rate measurements in soil.
133 Many approaches quantify growth rate at the scale of whole microbial assemblages,
134 which result in a single estimate of growth for a soil sample, an aggregate of thousands of
135 microbial populations. Methods that quantify the growth rates of microbial taxa[16,28,29,42] and
136 single cells[30] are promising avenues for developing quantitative links between specific
137 microorganisms and soil processes. Estimates of growth from over 46,000 measurements of rates
138 of DNA synthesis show tremendous variation in relative growth rates among bacterial groups in
139 soil (Figure 2b) and indicate that relative growth rates of soil bacteria are comparable to those of
140 marine bacteria[43], both of which are slow compared to growth rates in culture[44]. Future

141 comparative studies applying multiple approaches are needed to critically compare growth rates
142 of phylogenetically related microorganisms in nature.

143 Measurements of growth rate in soil indicate that bacterial groups also vary in their rates
144 of resource use and their responses to changes in nutrient availability[45–47], temperature[48–51],
145 disturbance[52–54], mineral composition[55], and climate[56,57]. Microbial contributions to respiration
146 and C and N assimilation appear to be highly taxon-specific, and variation in microbial
147 contributions to element fluxes can be meaningful when scaled to the ecosystem level[17,58]. Such
148 measurements offer a new set of data for testing and developing microbe-explicit representations
149 of C and N cycling. Measurements of relative growth rate have shown how interactions among
150 soil microorganisms – including competition[59], mutualism[15], and predation[60,61] – can influence
151 element flux, just as interactions between plants and animals can influence ecosystem processes.

152 Growth rate measurements have a clear place in testing the role of ecological theory in
153 soil microbial ecology. Like macroscopic organisms, microbial phenotypes in soil are
154 constrained by their evolutionary histories[62,63]. Phenomena such as negative density dependence
155 and r/K selection theory are key for understanding population growth of larger organisms, but
156 these concepts have failed to be strong predictors of growth patterns of microbes *in situ*[64,65]. As
157 such there is a great need for evidence-based ecological frameworks that are built on direct
158 observations of soil microbiomes[66]. Below, we describe how quantitative data on soil microbial
159 growth rates can be integrated into tests of microbial ecological theory and used to refine
160 process-based models of element flux and ecosystem productivity.

161

162 **Relevance to soil ecology**

The diversity, physiology, and ecology of microorganisms influence biogeochemical cycling[67], soil organic carbon (SOC) formation and loss[68], and plant productivity[69], with implications for pollution[26], food supply[27], and climate[25]. Quantitative *in situ* measurements of microbial growth could offer powerful insight into how microbes contribute to ecosystem processes and could help discover new tools for managing the soil microbiome to promote ecosystem services.

Microbial physiology and soil organic C cycling

The physiological properties of microorganisms play a key role in governing the formation and loss of SOC stocks[70] that are vital for mitigating greenhouse gas emissions and enhancing the sustainability of agricultural systems[71]. Measurements of *in situ* soil microbial growth could be used to inform and test emerging hypotheses on SOC cycling. For example, microbial necromass may constitute as much as 50% of the mineral-associated organic matter pool – the largest and slowest-cycling reservoir of SOC[72–74]. Thus, fast and efficient microbial growth and turnover should increase the production of microbial residues and the accrual of microbial-derived, mineral-associated organic matter[68,75]. *In situ* growth rate measurements that capture absolute growth at the assemblage scale (e.g. isotope ratio mass spectrometry enabled $H_2{}^{18}O$-DNA-SIP[38] and ^2H_2O-lipid-SIP[16]) could be used to identify relationships between growth rate, growth efficiency, and SOC formation at the ecosystem scale. Relationships between growth rate and growth efficiency, defined as the portion of consumed substrate that is converted into biomass, are critical for such conceptualizations of SOC formation but poorly defined for soil microbes. The mechanisms theorized to underpin relationships between growth efficiency and relative growth rate, such as maintenance requirements, overflow metabolism, and protein

synthesis costs, are physiological and may therefore be most apparent at the level of individual microbial cell, species, or population. Whether population scale physiology drives emergent relationships between microbial growth and SOC formation at the ecosystem scale could then be tested, for example, with using individual based modeling to couple observations of relative growth rate and growth efficiency at the population level (e.g. via soil isolates[76] or genome-informed trait-based modeling[77]) to assemblage level measurements of growth rate and rates of SOC formation.

Microbial processes affecting soil C accrual and persistence are represented in some numerical models of SOC cycling[78–81]. Measurements of microbial growth can be used to parameterize microbe-explicit biogeochemical models and test how microbial physiology modulates SOC responses to environmental changes. For example, growth rate measurements could be used to parameterize formulations of microbial dormancy[79] and density dependent growth[82] in ecosystem scale models. At the global scale, modeling growth efficiency is key to predicting the dynamics of soil C stocks[83] and growth rate may be an important factor to consider in these large-scale geochemical models too. Additional measurements of soil microbial growth rates will provide the data needed to test conceptual and quantitative models of how microbes influence the soil C cycle. There is a clear need for direct measurements of *in situ* growth rates using existing approaches to better understand the roles of the microbial community – and of individual microbial genes, metabolic pathways, and taxa – as conduits of energy and element cycling through soils.

Microbial diversity and ecological strategies

208 Amidst a wealth of archived genomic, transcriptomic, and proteomic data, frameworks
209 categorizing the ecological strategies of soil microorganisms have emerged to integrate these
210 data with biogeochemical concepts and mechanistic models[84–86]. Such frameworks are valuable
211 given that they can effectively reduce complex microbial assemblages into a manageable number
212 of functional groups and provide a basis for generating effective, hypothesis-driven insights into
213 soil microbial ecology[87]. Collectively, these frameworks represent diverse hypotheses about
214 interactions between microbial community structure and soil processes. Soil microbiologists are
215 well-positioned to begin experimentally testing these frameworks by coupling *in situ*
216 measurements of growth with 'omics data.
217 Many microbial frameworks have been derived from classic ecological theory (i.e.,
218 theory primarily developed from conceptual models of plant life history strategies) and these
219 microbial frameworks often lack experimental validation. For example, ecological strategies are
220 commonly assigned based on taxonomy[85] but tests of whether microorganisms use their assigned
221 strategies in nature are rare[65]. Alternatively, broad ecological strategies can be identified based
222 on genomic features[84] and gene expression[88], but our ability to translate microbial genes to
223 function and rate of function is nascent.
224 As an essential property of an organism's life history and metric of competitive ability, *in*
225 *situ* relative growth rate has a direct role in testing frameworks that build on classical ecological
226 theory. Relative growth rate could be assayed in multiple environments to determine whether
227 evolutionary adaptation to a selective environment has been accompanied by a loss of
228 reproductive potential in nonselective environments – in other words, whether a tradeoff has
229 occurred. For example, the relative growth rate of an organism with a "stress tolerator" strategy[84]
230 would be expected to be above average under stressful conditions and below average in the

absence of environmental stressors. Quantifying the growth of microorganisms where they live and grow in nature also provides access to a broader suite of trait dimensions than can be extrapolated from pure culture studies. Direct, *in situ* relative growth rate measurements could thus provide powerful, empirical means to develop alternative ways of organizing soil microbial diversity into ecologically meaningful units. Coupling these with measures of nutrient and energy fluxes will help test links between community composition and ecosystem dynamics.

Ecological interactions and soil food webs

Microorganisms influence energy flow and alter rates of nutrient cycling through their interactions with other microorganisms[89]. Predation in the rhizosphere changes the taxonomic structure of prokaryotic communities and alters rates of N mineralization, influencing vegetation productivity[90]. Mutualistic interactions between microbial taxa stimulate depolymerization of complex C compounds[91] and antagonistic interactions influence growth rates through negative density dependence[52], altering rates of C flux from microbial biomass to soil[82]. Taxon-specific estimates of relative growth rate would be valuable for assessing microbial interactions in which one soil microorganism influences another by altering its growth, reproduction, or any trait impacting fitness.

In soil microbial ecology, network analyses of co-occurrence patterns in molecular abundance datasets are used to infer *in situ* interactions between microorganisms. These analyses are based on the premise that microorganisms must co-occur to interact, and that interactions affecting demography will drive patterns in co-occurrence data. Environmental variability in time and space, dynamic species distributions, and other ecological complexities weaken and may obscure relationships between co-occurrence and interactions[92]. Assessing how the growth

254 rate of one organism impacts the growth of another could constrain inferences about interactions.
255 Multilayer network analyses could combine independent data streams like growth rate and co-
256 occurrence which would allow inferences to be cross validated, potentially improving the
257 accuracy of interaction studies.

258 Growth rates of microbial taxa, along with growth efficiency, could be used to construct
259 accurate food webs to quantify how energy and elements are transferred between microbial
260 taxa[93]. Compound-specific growth estimates (via stable isotope probing of ^{13}C and ^{15}N nutrient
261 sources) trace the flow of soil nutrients through microorganisms and quantify their rates of
262 transformation[94–96]. These approaches identify syntrophic interactions in soil by tracing
263 biogeochemical fluxes between organisms and nutrient pools[97,98] and identifying rates of
264 biomass production resulting from specific metabolic strategies[99,100]. There are several key
265 limitations to such approaches, such as the ability to resolve cross feeding. Experimental designs
266 that explicitly account for these limitations are especially useful. For example, Hungate et al.
267 (2021) correct for differences in potential sources of ^{18}O between predatory and non-predatory
268 soil bacteria (predators derive ^{18}O from labelled prey biomass and soil water while non-predators
269 derive 18O from soil water alone) in computations of growth rate, finding that obligate predators
270 respond to increases in prey resource availability by disproportionately increasing their relative
271 growth rates (compared to non-predator taxa) when C substrates, a common source of energy for
272 their heterotrophic prey, are added to soil[60]. Taxon-specific growth rates also provide a means for
273 assessing the importance of interactions in structuring individual populations. For
274 example, density dependent population growth (typically measured as net growth) reflects direct
275 interactions among individuals within a population, such as competition for resources which can
276 be assessed by quantifying relationships between population density and relative growth rate *in*

situ[52]. Growth rate is a clear and promising metric for defining ecological interactions, offering a way to quantitatively link interactions between individual taxa to the trajectory of entire populations and the flow of elements within the soil microbiome.

Conclusion

There is an urgent need to improve our quantitative understanding of how microorganisms contribute to soil processes, given their central role in ecosystem C storage, nutrient cycling, and productivity. Growth rate integrates the many ways that microbes affect soil processes and is a sensitive metric for studying cell and population-level responses to challenges in nature, including challenges from biotic interactions and changes in environmental conditions. Moving forward, diverse approaches are needed to accurately estimate the full range of microbial growth rates in soil and comprehensive reviews, metanalyses, and comparative studies will be critical for quantifying biological and methodological sources of variation. Understanding how microbial growth rates vary in soil will enable greater cohesion between emerging ecological concepts, microbial identity, and biogeochemistry. As soil ecological concepts and models are developed, it is critical that quantitative and sensitive measurements of *in situ* microbial growth be used alongside measurements of biogeochemical fluxes to understand how individual microbial taxa and whole assemblages influence soil processes.

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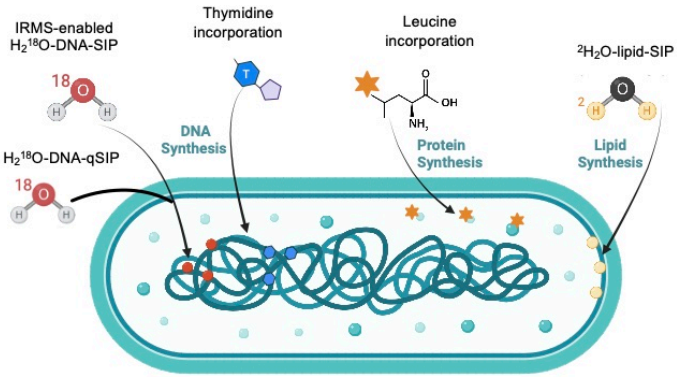
Figure captions:

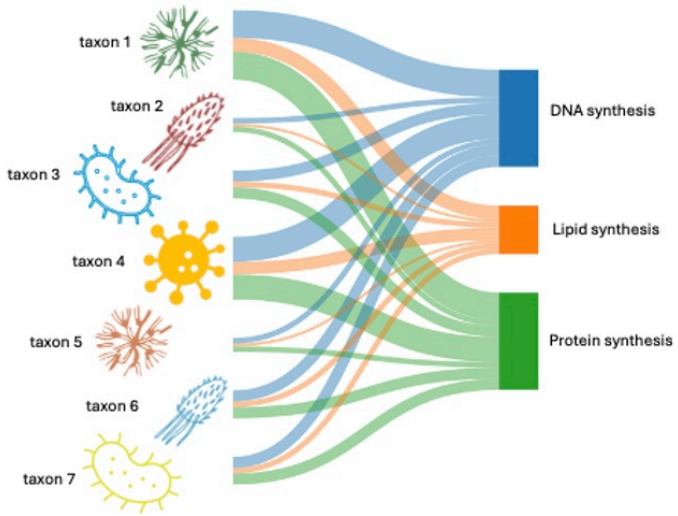
Figure 1: There are a range of methods to measure soil microbial growth rates *in situ*. a) Isotope tracing approaches capture the synthesis of various biomolecules, such as DNA, lipids, and proteins, providing an approximation of gross microbial growth. b) Biomolecules have variable rates of synthesis depending on a cell's physiological state and biochemical composition, which may contribute to variation among growth rate estimates in soil. Many methods capture the growth rate of entire assemblages of microorganisms in a sample. These measurements are useful for understanding how microorganisms, in aggregate, affect element fluxes but cannot capture the growth dynamics of individual populations. SIP stands for stable isotope probing and qSIP stands for quantitative stable isotope probing. c) Some methods leverage 'omics technologies to pair growth rate measurements with taxonomic information. These methods quantify the growth rates of individual taxa, allowing researchers to test hypotheses in microbial ecology. The figure shows a hypothetical heat map of taxon-specific growth rates in two distinct environments, an approach that can be used to explore whether microbial adaptations to a selective environment is accompanied by a loss of reproductive potential in nonselective environments (i.e. whether a tradeoff has occurred).

Figure 2: Relative growth rates of soil microbial assemblages and individual taxa in multiple ecosystems. a) Published estimates of relative growth rates of soil microbial assemblages in agricultural, forest, grassland, and tundra ecosystems. Measurements were made using isotope ratio mass spectrometry (IRMS) enabled $H_2{}^{18}O$-DNA stable isotope probing (SIP), $H_2{}^{18}O$-DNA quantitative stable isotope probing (qSIP), thymidine (Tdr) incorporation, leucine (Leu) incorporation, ^2H_2O-lipid-SIP, or soil C mass balance modeling. The middle line corresponds to the median, lower and upper edges correspond to the first and third quartiles, and whiskers extend to the highest and lowest point within 150% of the interquartile range. The y-axis is log transformed. Study information is in Supplementary Dataset 1.b) Distribution of relative growth rates of amplicon sequence variants measured by $H_2{}^{18}O$-DNA-qSIP in five ecosystems: tropical forest, temperate grassland, temperate conifer forest, boreal forest, and moist acidic tundra. The x-axis is log transformed. c) Distribution of relative growth rates of bacterial and archaeal phyla. The middle line corresponds to the median, lower and upper edges correspond to the first and third quartiles, and whiskers extend to the highest and lowest point within 150% of the interquartile range. The x-axis is log transformed. Study information is in Supplementary Dataset 2.

a)



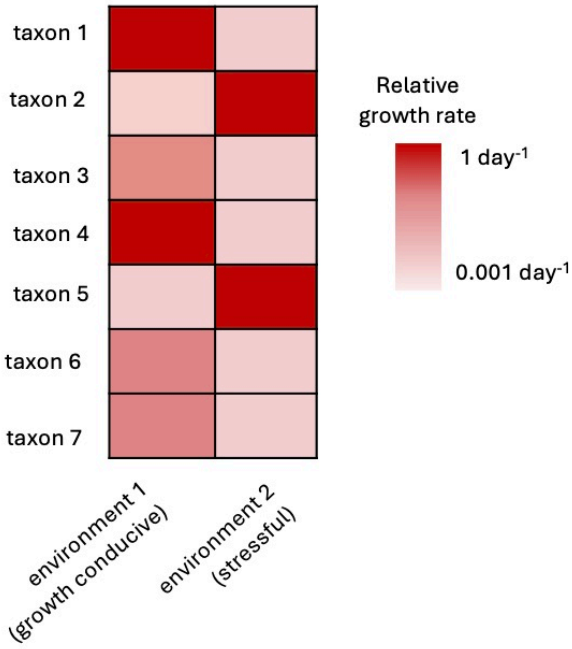
b)

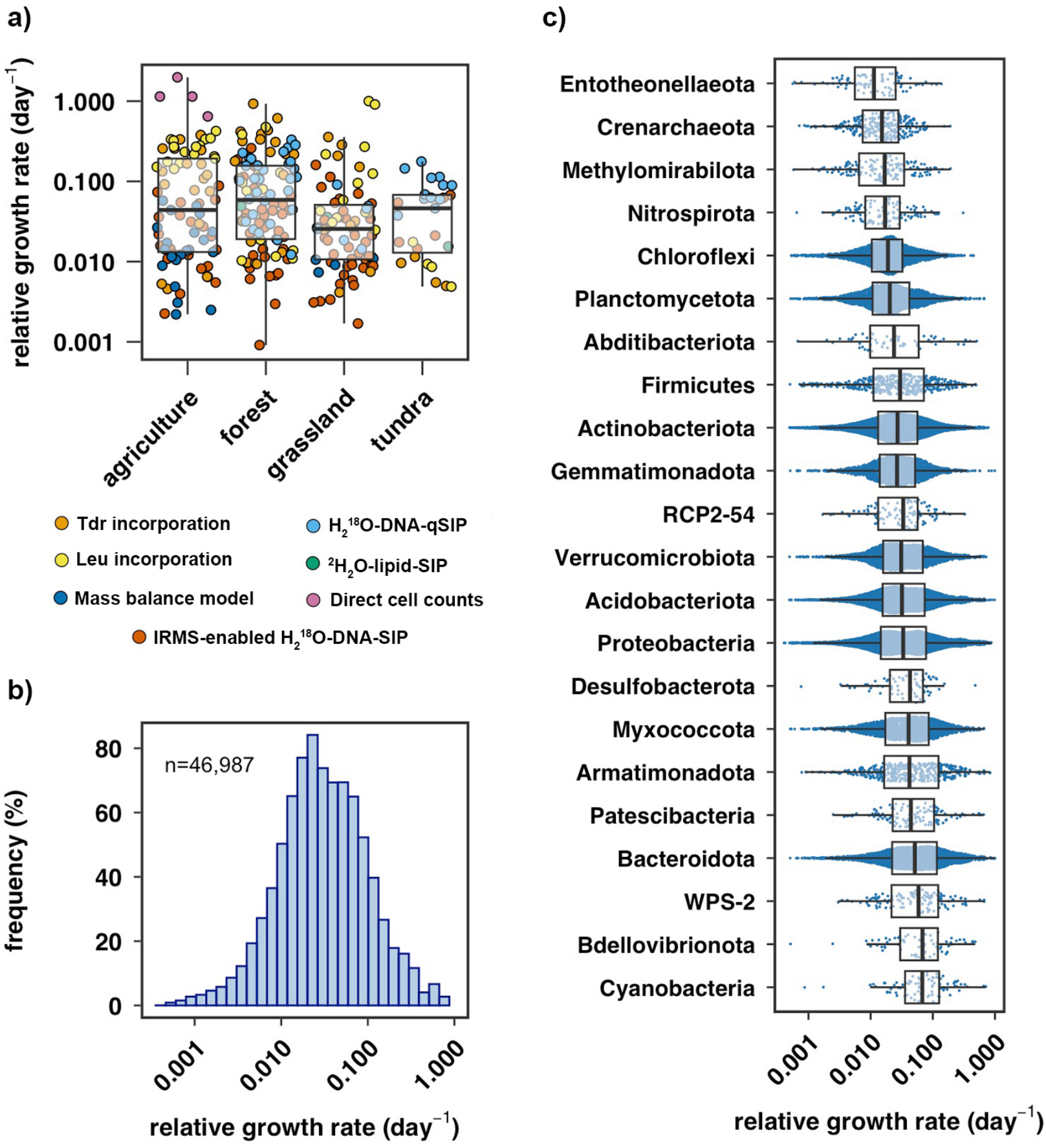


Taxon specific
- $H_2{}^{18}O$-DNA-qSIP
- ^2H_2O-lipid-SIP
- Peak to trough ratio
- Bromodeoxyuridine uptake

Assemblage level
- IRMS-enabled $H_2{}^{18}O$-DNA-SIP
- Leucine incorporation
- Thymidine incorporation
- Acetate incorporation

c)




a)
relative growth rate (day^{-1})
1.000
0.100
0.010
0.001
agriculture
forest
grassland
tundra
Tdr incorporation
Leu incorporation
Mass balance model
$H_2{}^{18}O$-DNA-qSIP
^2H_2O-lipid-SIP
Direct cell counts
IRMS-enabled $H_2{}^{18}O$-DNA-SIP
b)
frequency (%)
n=46,987
80
60
40
20
0
0.001
0.010
0.100
1.000
relative growth rate (day^{-1})
c)
Entotheonellaeota
Crenarchaeota
Methylomirabilota
Nitrospirota
Chloroflexi
Planctomycetota
Abditibacteriota
Firmicutes
Actinobacteriota
Gemmatimonadota
RCP2-54
Verrucomicrobiota
Acidobacteriota
Proteobacteria
Desulfobacterota
Myxococcota
Armatimonadota
Patescibacteria
Bacteroidota
WPS-2
Bdellovibrionota
Cyanobacteria
0.001
0.010
0.100
1.000
relative growth rate (day^{-1})