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How Thermodynamics Illuminates Population Interactions in Microbial Communities

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In traditional population models of microbial ecology, there are two central players: producers and consumers (including decomposers that depend on organic carbon). Producers support surface ecosystems by generating adenosine triphosphate (ATP) from sunlight, part of which is used to build new biomass from carbon dioxide. In contrast, the productivity of subsurface ecosystems with a limited supply of sunlight must rely on bacteria and archaea that are able generate ATP solely from chemical or electric energy to fix inorganic carbon. These "light-independent producers" are frequently not included in traditional food webs, even though they are ubiquitous in nature and interact with one another through the utilization of the by-products of others. In this review, we introduce theoretical approaches based on population dynamics that incorporate thermodynamics to highlight characteristic interactions in the microbial community of subsurface ecosystems, which may link community structures and ecosystem expansion under conditions of a limited supply of sunlight. In comparison with light-dependent producers, which compete with one another for light, the use of Gibbs free energy (chemical energy) can lead cooperative interactions among light-independent producers through the effects of the relative quantities of products and reactants on the available chemical energy, which is termed abundant resource premium. The development of a population theory that incorporates thermodynamics offers fundamental ecological insights into subsurface microbial ecosystems, which may be applied to fields of study such as environmental science/engineering, astrobiology, or the microbial ecosystems of the early earth.

Keywords: microbial ecology, mutualism, mathematical models, abundant resource premiums, syntrophy, chemolithotrophy

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INTRODUCTION

By the look of terrestrial ecosystems, life on Earth first appears to consist of abundant plant and animal communities. However, upon closer observation, there exists rich and diverse communities of fungi, bacteria, and archaea, many of which are not readily visible. According to Bar-On et al. (2018), the total biomass of the earth's ecosystems is approximately 550 gigatons of carbon (Gt C) with an estimated 81.8% of plants, 12.7% of bacteria, 2.2% of fungi, and 1.3% of archaea, whereas animals only comprise 0.4%. They also reported that approximately 70 Gt C of biomass is present in the marine sub-seafloor sediments and the oceanic crust, as well as terrestrial substratums deeper

than 8 m, which is dominated by bacteria and archaea. Total bacterial and archaeal cell numbers are estimated to be upwards of 1×10^{30} cells with nearly 3/4 residing deep in the subsurface (Flemming and Wuertz, 2019). Explorations of ocean drilling research projects have revealed that bacterial and archaeal communities are present at depths of 2.5 km below the ocean floor (Parkes et al., 1994; Ciobanu et al., 2014; Inagaki et al., 2015; Glombitza et al., 2016; Trembath-Reichert et al., 2017; Tanikawa et al., 2018). These findings suggest that there are widespread microbial communities in the subsurface realm that are not normally perceived.

Life cannot function without a constant supply of energy. As producers, plants harness sunlight as their primary energy source. However, in subsurface ecosystems where the availability of light is limited, the primary energy source would be derived from geochemical origins rather than solar energy. For example, hydrothermal vent systems are the natural plumbing systems that supply chemical substances as energy sources (e.g., hydrogen gas, methane, and dissolved iron) from the interior of the Earth. Unlike animals that depend solely on aerobic respiration for ATP generation, bacteria and archaea have evolved diverse metabolic processes that enable them to harness a variety of chemical reactions that use energy sources from geochemical origins (**Table 1**). These organisms synthesize ATP without relying on sunlight or organic substrates to produce their own biomass from inorganic carbon. By extending the ecological concept of producers to these microbes, they can be called "light-independent producers," which would include denitrifiers, nitrifiers, iron oxidizers/reducers, sulfate reducers, methanotrophs, methanogens, etc. These functional (or trait-based) groups may include species that depends on organic substrate as energy source, but microbes harnessing the reactions listed in **Table 1** are independent of organic substrate. Some light-independent producers may use molecular oxygen, although this may also be a photosynthetic by-product.

The presence of light-independent producers is not limited to subsurface ecosystems and also occurs in general and extreme environments. Due to their access to chemical substances, they are often observed in the interfaces between oxic (oxygen plentiful) and anoxic (oxygen-free) environments, and can move energy-source reactions forward. These environments are temporarily or spatially created, even in surface ecosystems such as sediment-water interfaces, soil aggregates, and biofilms (e.g., see review by Lau et al., 2018). Some light-independent producers can tolerate extreme pH or temperature conditions and are widely observed in mine drainage, soda lakes, hot springs, polar regions, and hydrothermal vents (Sorokin and Kuenen, 2005; Sattley and Madigan, 2006; Martin et al., 2008; Kimura et al., 2011). Although the contribution of these microbial communities to ecosystem productivity in surface ecosystems may be less important than the primary productivity of plants, light-independent producers drive important biogeochemical cycles by catalyzing energy-source reactions (Falkowski et al., 2008; Burgin et al., 2011).

The potential for subsurface primary production that is independent of solar energy has been suggested by several reviews (Gold, 1992; Stevens, 1997; Colman et al., 2017), but there are relatively few studies available that deal with the population dynamics and interspecific interactions among light-independent producers. The interspecific interactions among these producers are often associated with the use of chemical substances involved in energy-source reactions. Understanding these interactions requires not only knowledge of the biological interactions, but also the chemical interactions and energy that depends on the presence of the chemical substances in the system. Therefore, in this review, we introduce theoretical approaches based on population dynamics, which incorporates thermodynamics to highlight characteristic interactions in microbial communities in subsurface ecosystems on an energetic basis.

ENERGY AND NUTRITIONAL GROUPS

To expand our understanding of energy in ecosystems and how organisms use this energy for growth, we first summarize the concepts of energy and nutritional groups. Organisms, especially microorganisms, can be classified into primary nutritional groups based on the direct source of energy and carbon (**Figure 1**). As the definition of nutritional groups is somewhat ambiguous, we clarify them in light of recent research regarding bacterial and archaeal communities.

In ecology, energy flow has often been treated as a process that occurs in parallel with carbon flow. This is true for organisms that use carbon substrates as energy sources, however, the energy sources of microorganisms are not necessarily sunlight or carbon substrates. Energy is converted to ATP and then used for biomass synthesis. Producers use a part of ATP in the process of converting inorganic carbon to organic carbon (biomass). In addition to energy and carbon sources, we introduce the processes of ATP synthesis and carbon assimilation, which may highlight the differences between the carbon and energy needs of living organisms.

Classifications Based on Energy Source

In traditional textbooks, the direct energy source for life is described as either being sunlight or chemical reactions. Organisms that use sunlight are called phototrophs and those that harness energy from chemical reactions are called chemotrophs. According to these definitions, animals and fungi are classified as chemotrophs. Some chemotrophs use organic carbon for energy-source reactions (e.g., aerobic respirators and fermentation bacteria), and others only use inorganic substances (e.g., the reactions listed in **Table 1**). The former are termed chemoorganotrophs and the latter as chemolithotrophs. In addition to light and chemical energy, some microbes have been found to gain energy directly from electrons in the form of electric energy (Lovley, 2006, 2008; Thrash and Coates, 2008; Torres et al., 2010). As these electrons are supplied from the progression of the oxidation-reduction reaction (the redox reaction, a type of chemical reaction that involves the transfer of electrons), the distinction between chemical and electric energy gain is somewhat vague. Electron flow is also generated during photosynthesis and aerobic respiration, and is essential for one of the two ATP synthesizing processes described below.

TABLE 1 | Possible examples of energy-source reactions for the light-independent producers.

	Process	Reaction	Electron donor	Electron acceptor	Negative of standard Gibbs energy change of reaction, $-\Delta rG°$ (kJ per mol of electron donor)
I	Aerobic methane oxidation	$CH_4 + 2O_2 \rightarrow HCO_3^- + H_2O + H^+$	CH_4	O_2	790
II	Denitrification using hydrogen sulfide ion with SO_4^{2-} production	$HS^- + 1.6NO_3^- \rightarrow SO_4^{2-} + 0.8N_2 + 0.2H_2O + 0.6OH^-$	HS^-	SO_4^{2-}	721
III	Methane oxidation using manganese oxide	$CH_4 + 4MnO_2 + 7H^+ \rightarrow HCO_3^- + 4Mn^{2+} + 5H_2O$	CH_4	MnO_2	635
IV	Methane oxidation using iron oxide	$CH_4 + 8Fe(OH)_3 + 15H^+ \rightarrow HCO_3^- + 8Fe^{2+} + 21H_2O$	CH_4	$Fe(OH)_3$	598
V	Anaerobic ammonia oxidation (ANAMMOX)	$NH_4^+ + NO_2^- \rightarrow N_2 + 2H_2O$	NH_4^+	NO_2^-	362
VI	Complete ammonia oxidation (COMAMMOX)	$NH_4^+ + 2O_2 \rightarrow NO_2^- + H_2O + 2H^+$	NH_4^+	O_2	269
VII	Denitrification using hydrogen sulfide ion with S^0	$HS^- + 0.4NO_3^- + 1.4H^+ \rightarrow S^0 + 0.2N_2 + 1.2H_2O$	HS^-	NO_3^-	252
VIII	Ammonia oxidation	$NH_4^+ + 1.5O_2 \rightarrow NO_2^- + H_2O + 2H^+$	NH_4^+	O_2	190
IX	Nitrite reduction using hydrogen	$3H_2 + NO_2^- + 2H^+ \rightarrow NH_4^+ + H_2O$	H_2	NO_2^-	174
X	Nitrite oxidation	$NO_2^- + 0.5O_2 \rightarrow NO_3^-$	NO_2^-	O_2	79
XI	Aerobic Fe oxidation	$Fe^{2+} + 0.25O_2 + H^+ \rightarrow Fe^{3+} + 0.5H_2O$	Fe^{2+}	O_2	44
XII	Methanogenesis	$4H_2 + CO_2 \rightarrow CH_4 + 2H_2O$	H_2	CO_2	30
XIII	Fe oxidation using nitrate	$Fe^{2+} + 0.2NO_3^- + 2.4H_2O \rightarrow Fe(OH)_3 + 0.1N_2 + 1.8H^+$	Fe^{2+}	NO_3^-	26
XIV	Sulfate reduction using hydrogen	$H_2 + 0.25SO_4^{2-} \rightarrow 0.25H_2S + 0.5OH^- + 0.5H_2O$	H_2	SO_4^{2-}	18
XV	Methane oxidation using sulfate	$CH_4 + SO_4^{2-} \rightarrow HCO_3^- + HS^- + H_2O$	CH_4	SO_4^{2-}	17

For the calculation of $-\Delta_rG°$, the values of $\Delta_fG°$ at 25°C and 1 bar are cited from CHNOSZ package for R (http://chnosz.net). $-\Delta_rG°$ for ferrihydrite was taken from Majzlan et al. (2004).

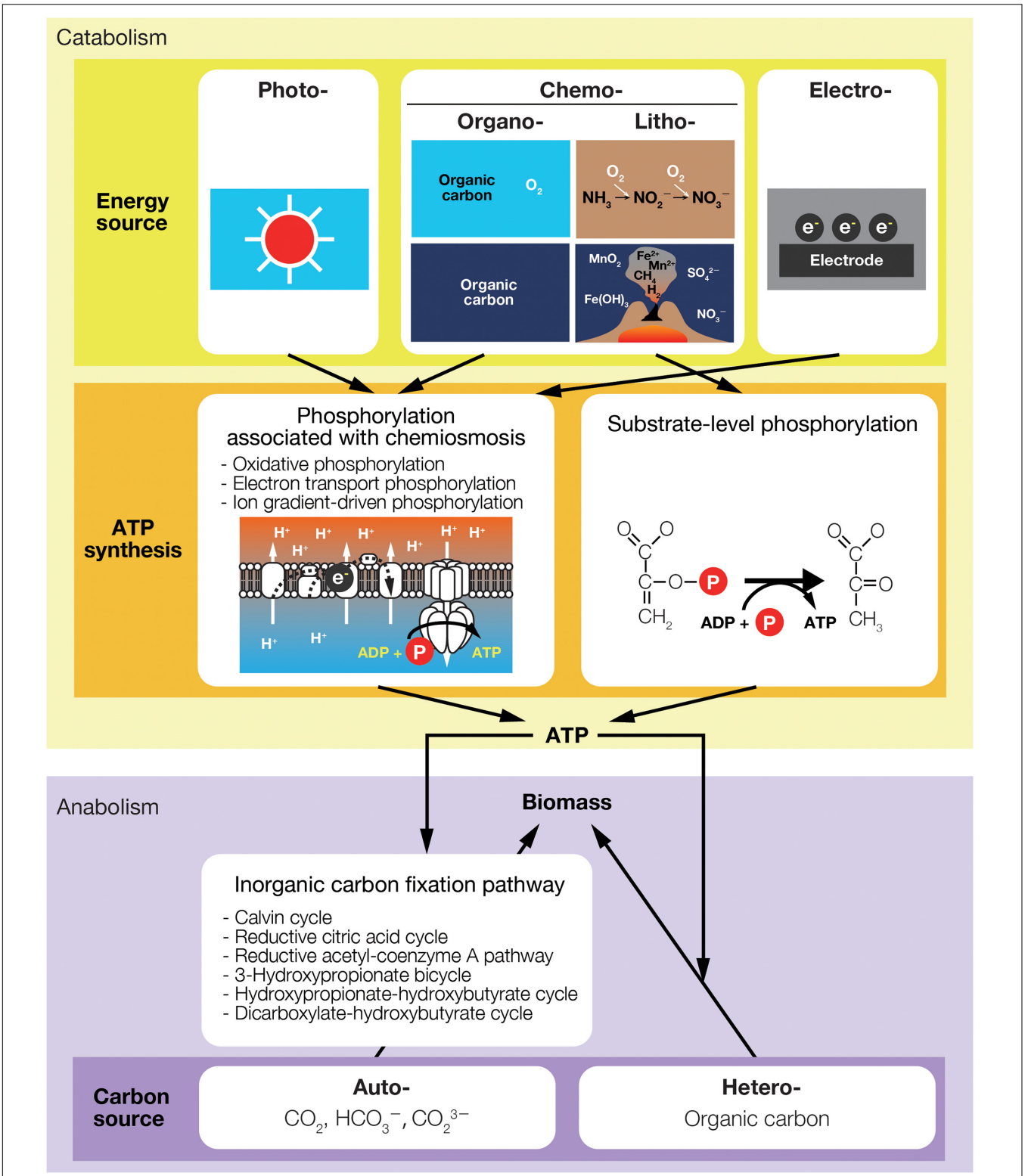

FIGURE 1 | Primary nutritional groups and types of energy sources, ATP synthesis, and carbon sources for life. The names of primary nutritional groups are built by combining the Greek terms meaning the direct source of energy [photo (light), chemo (chemical), or electro (electric)] and carbon [auto (using inorganic carbon) or hetero (using organic carbon)] and "troph(s)" meaning nourishment. Chemo-(auto or hetero)-trophs that use organic carbon for energy-source reactions (e.g., aerobic respirators and fermentation bacteria) are especially termed chemo-organo-(auto or hetero)-trophs and others that only use inorganic substances for energy-source reactions (e.g., the reactions listed in **Table 1**) are termed chemo-litho-(auto or hetero)-trophs.

ATP Synthesis

No matter which energy form is used, life eventually converts energy into ATP by adding one phosphate group to adenosine diphosphate (ADP), in a process called phosphorylation. Phosphorylation (i.e., ATP synthesis) in living organisms is achieved by two different biochemical pathways. Phosphorylation can occur via the direct transfer of a phosphate group from a phosphorylated intermediate metabolic compound to ADP. This is known as substrate-level phosphorylation and is exemplified by glycolysis (the first pathway of aerobic respiration) and fermentation (**Figure 1**). ADP-ribose-derived ATP synthesis in the cell nucleus might be considered as this type of phosphorylation (Wright et al., 2016). Alternatively, phosphorylation can be achieved by the electron flow generated from an energy-source reaction. The electron flow eventually creates ion gradients across membranes, or chemiosmosis, which enables ATP synthase to synthesize ATP (Mitchell, 1961; Dimroth, 1987; Russell, 2007; especially see Müller and Hess, 2017 for a discussion on the terms describing this type of phosphorylation). In this paper, we have termed the latter type as "phosphorylation associated with chemiosmosis." In terms of energy production, substrate-level phosphorylation is generally less efficient than phosphorylation associated with chemiosmosis. However, the faster substrate-consumption rate of substrate-level phosphorylation can surpass phosphorylation associated with chemiosmosis under some conditions (Vazquez et al., 2010; Zheng, 2012).

Photosynthesis and aerobic respiration partly share similar phosphorylation processes, which are associated with chemiosmosis of hydrogen ions when electrons move down the electron transport chain. For light reactions occurring in plants, electrons are released after the light absorption by photosynthetic pigments and drive chemiosmosis across the thylakoid membrane. Similarly, most energy-source reactions, including aerobic reactions and the reactions listed in **Table 1**, are involved in electron transfers and, therefore, categorized as redox reactions that can be spontaneously carried out in the absence of sunlight. For example, during aerobic respiration, 24 moles of electrons are translocated from 1 mole of glucose to oxygen:

$$C_6H_{12}O_6(\text{electron donor}) + 6H_2O \rightarrow 6CO_2 + 24H^+ + 24e^- \quad (1a)$$

$$6O_2(\text{electron acceptor}) + 24H^+ + 24e^- \rightarrow 12H_2O \quad (1b)$$

$$6O_2 + C_6H_{12}O_6 \rightarrow 6CO_2 + 6H_2O, \quad (1c)$$

where e^- indicates an electron. The overall reaction of Eq. (1c) is the well-known equation for aerobic respiration, which is the sum of the oxidation reaction (Eq. (1a)) that involves the loss of electrons from an electron donor ($C_6H_{12}O_6$) and the reduction reaction (Eq. (1b)) that is involved with the gain of electrons of an electron acceptor (O_2). Although the electron flow involved in Eq. 1 is eventually eliminated from Eq. 1c, this flow is used to generate ATP throughout chemiosmosis in mitocondria.

In general, chemical substances that act as electron acceptors are plentiful in oxic environments, while those that act as electron donors are abundant under anoxic conditions. Surface ecosystems have unique oxic environments where plants constantly supply the abundant organic substrate, which acts as an electron donor. In contrast, both electron acceptors and donors (except for organic substrates) come into play in oxic-anoxic interfaces and can supply energy for light-independent producers.

Classification Based on the Carbon Source

Some fraction of the energy stored as ATP is used to maintain the metabolism of an individual, while some is allocated to the growth of the population. Population growth is often quantified as the amount of carbon that is newly added to the overall population. For nutritional classifications, the source of carbon groups organisms into autotrophs that fix inorganic carbon to build biomass and heterotrophs that use organic carbon to synthesize biomass. Note that the classification of organisms according to carbon source is made based only on the form of carbon used as building blocks. It is independent of the direct energy source (light, chemical, or electric) to generate ATP, even though the carbon may be used in the energy-source reaction. The Calvin-Benson-Bassham (CBB) cycle is the only carbon-fixation pathway in eukaryotes (algae and plants). Some autotrophic bacteria also fix carbon dioxide in the CBB cycle, while others have evolved unique, inorganic carbon-fixation pathways (Berg et al., 2010; Berg, 2011; Hügler and Sievert, 2011).

According to these two classifications, plants and phytoplankton are photo-autotrophs, while animals and most fungi are chemo-heterotrophs. In subsurface ecosystems where there is no light, microbial communities are composed of chemo-autotrophs and chemo-heterotrophs. Here, we exclude discussions of photo-heterotrophic bacteria, but this nutritional group may be abundant and comprise approximately 10% of the microbial community in the euphotic zone in the upper ocean (Kolber et al., 2001). Some bacteria and archaea are known for their versatile metabolic strategies, which enable a cell to use both inorganic and organic carbon as building blocks, or the different types of energy source reactions (Eiler, 2006; Hügler and Sievert, 2011). These organisms that can switch metabolic strategies in response to environmental conditions are called mixotrophs.

For surface ecosystems, the primary and basic energy source is light. Plants and phytoplankton as producers harness light energy to synthesize ATP, part of which is used to fix carbon dioxide (inorganic carbon) into biomass. The direct energy source of consumers and decomposers is chemical as they generate ATP from aerobic respiration, a reaction using oxygen and organic substrates. Since both of these substrates are the by-products of photosynthesis, the original energy source for consumers and decomposers is light energy. Although consumers and decomposers also allocate organic carbon to the building blocks of biomass, carbon flows are a good indicator of energy flow

within feeding interactions because it is closely linked with the energy transfer among organisms that use organic substrates as their energy source.

In contrast, the ultimate energy source of subsurface ecosystems should be chemical energy (including electrical energy), which may not rely on the supply of organic substrates as the photosynthetic by-product from surface ecosystems. Direct or indirect carbon transfers from light-independent producers to chemoorganoheterotrophs that belong to the same nutritional group as animals can also be linked to energy transfers through the microbial community. However, the energy consumption of light-independent producers and the consequential interspecific interactions among them highlights the unique relationship between population growth and energy, which can be understood as the use of energy as opposed to organic carbon.

CHARACTERISTIC INTERSPECIFIC INTERACTIONS AMONG LIGHT-INDEPENDENT PRODUCERS

Of the interspecific interactions of light-dependent producers, resource competition is an important factor that determines growth, fitness, and productivity. Although the ultimate limiting resource for light-dependent producers can be the availability of essential nutrients (primarily nitrogen and phosphorus as the building blocks of biomass), water, and/or space, only those interactions associated with the availability of light energy as a limiting resource is discussed here. However, it should be noted that the availability of nutrients and water affect the ability of light-dependent producers to capture light energy. For example, a phosphorus deficiency in chloroplast stroma inhibits ATP synthase activity (Takizawa et al., 2008; Karlsson et al., 2015; Carstensen et al., 2018).

There is experimental, observational, and theoretical evidence indicating that plants and phytoplankton may specialize in separate light niches in response to different light environments (Litchman, 2000; Litchman and Klausmeier, 2001; Silvertown, 2004; Six et al., 2007; Sterck et al., 2011). Although some shade-tolerant plants may acquire new niches due to the presence of others, plants reside in the same canopy are often competitive and they never increase the light intensity, or light energy (**Figure 2A**).

The availability of light energy in a terrestrial ecosystem is mainly determined by the amount of sunlight received at the Earth's surface. An example of a model that describes the availability of light, L, under a canopy is,

$$L = L_0 f\left(\sum_i c_i B_i\right) \tag{2}$$

where L_0 is the light intensity at the top of the canopy (the light available prior to any consumption), c_i is the light adsorption coefficient of species i, and B_i is the biomass of species i. f describes the total light consumption by the existing species, which is a decreasing function with a maximum value of 1 that holds when no plants exist (Grovar, 1997). Any increase in B_i is associated with the consumption of light and, thus, decreases the availability of light and inhibits the light-dependent growth rate of other species.

Interspecific interactions via the use of chemical energy also significantly affect the growth of light-independent producers, although not always in a negative manner. The Gibbs energy, G, in thermodynamics is a measure of the availability of chemical energy in a system. The amount of Gibbs energy depends on all of the chemical substances present in a system and is described as:

$$G = \sum n_j \mu_j \tag{3}$$

where n_j is the number of moles of substance j, and $\mu_j = \left(\frac{\partial G}{\partial n_j}\right)_{T,P,n_{k\neq j}}$ denotes the partial molar Gibbs energy, or chemical potential, when temperature, pressure, and the amount of all other substances are held constant. μ_j depends not only on the substance j, but on other substances in the system, as the interaction of substances affects the availability of chemical potential μ_j. Unlike the change of L in Eq. (2), which is described by direct consumption by plant species, the change in G can only be indirectly described by changes in the molar concentrations of reactants and products associated with the progression of the energy-source reaction (**Figure 2B**).

The Gibbs energy change of a reaction, $\Delta_r G$, is an important and useful thermodynamic property that enables us to estimate the availability of chemical energy for microbes under a given environmental condition. $\Delta_r G$ denotes the amount of chemical energy dissipated from a reaction on a kJ per mole basis. Hence, a negative $\Delta_r G$ (i.e., $-\Delta_r G$) denotes the maximum available energy for species when it catalyzes one mole of reaction to dissipate energy. If species 1 generates energy from the following overall reaction, then:

$$A_1 + e^- \rightarrow A_2 \quad \text{(A reduction)}, \tag{4a}$$

$$B_2 \rightarrow B_1 + e^- \quad \text{(B oxidation)}, \tag{4b}$$

$$A_1 + B_2 \rightarrow A_2 + B_1 \quad \text{(reaction 1 : the overall reaction of Eqs. (4a) and (4b))}, \tag{4c}$$

where X_1 and X_2 are two different compounds (or two different redox states) composed of the same element. X_2 has more

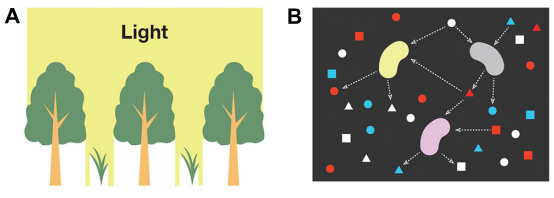

FIGURE 2 | Interspecific interactions associated with the utilization of **(A)** light and **(B)** chemical energy.

electrons than X_1. In Eq. (4c), B_2 serves as an electron donor and A_1 serves as an electron acceptor. The negative Gibbs energy change of this reaction is

$$-\Delta_r G = -\Delta_r G^\circ + RT \ln \frac{\{A_1\}\{B_2\}}{\{A_2\}\{B_1\}} \quad (4d)$$

where $-\Delta_r G^\circ$ is the standard Gibbs energy change of reaction 1 (kJ mol^{-1}), R is the gas constant (8.31 $\times$ 10^{-3} kJ K^{-1} mol^{-1}), T is the absolute temperature (K), and $\{X_j\}$ is the activity of X_j. Activity can be approximated as the molar concentration when the interaction forces of the substances can be ignored: $\{X_j\} \approx n_j/v$, where v is the volume. $^\circ$ indicates the standard-state condition where all reactants and products (chemical substances utilized for and released from the energy-source reaction) have activity = 1. $-\Delta_r G^\circ$ is given by,

$$-\Delta_r G^\circ = \Delta_f G_{A_1}{}^\circ + \Delta_f G_{B_2}{}^\circ - \left(\Delta_f G_{A_2}{}^\circ + \Delta_f G_{B_1}{}^\circ\right), \quad (4e)$$

where $\Delta_f G_x{}^\circ$ denotes the Gibbs energy change accompanied by the x formation (here, $x = A_1, A_2, B_1$, or B_2). $\Delta_f G_x{}^\circ$ is the relative level of Gibbs energy of x from all of the reference states of the elements composing x [e.g., the relative level of Gibbs energy of CH_4 in comparison with C(solid) as graphite and H_2 (gas)]. $\Delta_f G_x{}^\circ$ is a constant that is intrinsic to substance x under standard conditions. As $\Delta_r G^\circ$ is the difference between the sum of $\Delta_f G^\circ$ for the by-products and the sum of $\Delta_f G^\circ$ for the reactants, it is a reaction-specific quantity that is determined by the combination of reactants and by-products. $\Delta_f G_x{}^\circ$ values are available from the CHNOSZ package for R[1]. The second term of $-\Delta_r G$ in the right-hand side of Eq. (4d) indicates the effect of the relative quantities of products and reactants on the available chemical energy. This is termed "abundant resource premium" (ARP) (Seto and Iwasa, 2019a) and is especially important for the growth of light-independent producers, which results in characteristic mutualistic interactions, or obligately mutualistic metabolism.

The growth of light-independent producers always decreases the total amount of Gibbs energy of a system; similarly, the growth of light-dependent producers reduces the availability of light. However, unlike light consumption by plant species, which often results in competition, the progression of reaction 1 does not always decrease the availability of chemical energy for other light-independent producers. When species 2 harnesses a reaction that utilizes A_2 we get,

$$A_2 + C_2 \rightarrow A_3 + C_1 \text{ (reaction 2)}, \quad (5a)$$

where the negative Gibbs energy change of reaction 2 is

$$-\Delta_r G = -\Delta_r G^\circ + RT \ln \frac{\{A_2\}\{C_2\}}{\{A_3\}\{C_1\}}. \quad (5b)$$

To distinguish $\Delta_r G$ in Eqs. (4d) and (5b), from here we will use the symbol $\Delta_r G_i$, where subscript i denotes the reaction number. Because the supply of A_2 increases $-\Delta_r G_2$ due to the presence of the ARP term, species 2 may generate more energy when species 1 exists (**Figure 2B**). The consumption of A_2 also increases $-\Delta_r G_1$, which consequentially increases the energy gain of species 1. Hence, the consumption of the by-product of the energy-harvesting reaction can lead to mutualism between species 1 and 2 owing to the presence of ARP. An example of a mutualistic interaction which is similar to this type occurs between ammonia-oxidizers and nitrite-oxidizers in **Table 1** [the combination of reactions (VIII) and (X)], which are microbes interacting via the supply and consumption of nitrite ion ($NO_2{}^-$). Although these microbes compete for oxygen, one can predict that the presence of a nitrite-oxidizer may increase the energy acquisition per reaction of an ammonia-oxidizer under oxic conditions where the availability of oxygen may not limit the growth of nitrite-oxidizer and ammonia-oxidizer. These microbes have been confirmed to occur in clusters and be in frequent contact with each other within sludge flocs (Mobarry et al., 1996).

A more intuitive example of the mutualism between light-independent producers that completes material recycling within their energy-source reaction is a combination of Eq. (4c) and

$$A_2 + C_1 \rightarrow A_1 + C_2 \text{ (reaction 3)}, \quad (6a)$$

where the negative Gibbs energy change of reaction 3 is

$$-\Delta_r G_3 = -\Delta_r G_3{}^\circ + RT \ln \frac{\{A_2\}\{C_1\}}{\{A_1\}\{C_2\}}. \quad (6b)$$

An example can be found in the iron cycle between Fe^{2+} and Fe oxides (e.g., the combination of reaction (IV) and (XI) or (XIII) in **Table 1**) such as Fe $(OH)_3$ that is readily formed in the presence of Fe^{3+} at a circumneutral pH. Experimental studies have reported the possibility of micro-scale bacterial iron cycling at oxic-anoxic interfaces (Emerson and Revsbech, 1994; Sobolev and Roden, 2002; Roden et al., 2004). Another example is the sulfate cycle, which is closely associated with the methane and nitrogen cycles [e.g., the combination of reactions (II) and (XV) in **Table 1**] (Lau et al., 2016).

POPULATION DYNAMICS UNDER AVAILABLE CHEMICAL-ENERGY LIMITATIONS

The availability of chemical energy changes in response to changes in the amount of chemical substances in the surrounding environment, however, this effect has been neglected in population dynamics models in traditional microbial ecology. The population growth of light-dependent producers (plants and phytoplankton) is often limited by the availability of energy. Similarly, the population dynamics of light-independent producers are often limited by the acquisition rate of chemical energy. Interestingly, modeling this provides a framework for understanding mutualistic interactions among light-independent

[1]http://chnosz.net

producers, which has not been previously recognized in the ecological sciences. In a previous paper, we introduced a microbial population dynamics model in relation to energy production per reaction that included the ARP term (Seto and Iwasa, 2019a). For a microbial population that harvests energy from reaction i,

$$\frac{dx_i}{dt} = q_i \{c_i F_i (-\Delta_r G_i) - m_i\} x_i \tag{7a}$$

where F_i denotes the biomass-specific catalytic rate of the energy-source reaction, q_i is the biomass yield of species i for a given energy gain from ATP that is generated from an energy-source reaction, c_i is the fraction of energy that can be used for ATP synthesis ($0 < c_i < 1$) and excludes energy expenditure such as loss by heat transfer, and m_i is the rate of energy loss that occurs to maintain cellular activity. For simplicity, we call x_i the population density of the ith species, but it is more appropriate to call it the ith functional group, as multiple species typically share the same energy-source reaction. The term in curly brackets in Eq. (7a) describes the biomass-specific rate of the net energy gain. A reaction requiring two substrates (an electron acceptor and an electron donor) may be simultaneously limited by the low availability of both substrates. There are several proposed models that encompass dual-limitations from the abundance of electron donors and acceptors (Bae and Rittmann, 1996; Jin and Bethke, 2003, 2007; LaRowe et al., 2012). Here we have adopted the simplest model—the double-Monod model. For Eq. (4c) (reaction 1) it is described as,

$$F_1 = r_1 \frac{A_1}{K_{A_1} + A_1} \frac{B_2}{K_{B_2} + B_2} \tag{7b}$$

where r_1 is the maximum microbial catalytic rate of reaction 1, and K_X is the half-saturation constant for X.

The growth of chemoheterotrophs (e.g., aerobic bacteria and fermentation bacteria) is often described by the Monod equation, where the growth rate of microbial population x appears to be limited solely by the availability of the concentration of the organic substrate R:

$$\frac{dx}{dt} = Fx \quad \text{where} \quad F = \frac{rR}{K + R}. \tag{8}$$

Equation (7a) can be approximated as Eq. (8) if the following three conditions are satisfied: (i) the decreasing rate – mx is added to Eq. (8), (ii) the concentration of one of the two substrates is significantly higher than its half-saturation constant such that the corresponding factor is replaced by 1, and (iii) the effect of ARP on $-\Delta_r G$ can be ignored because of the high value of $-\Delta_r G°$. Assumptions (ii) and (iii) are plausible for aerobic bacteria and fermentation bacteria. The incubation of aerobic bacteria is usually conducted under aerobic conditions (i.e., high oxygen concentration), whereas fermentation bacteria only require a single organic substrate, which is used to generate energy from substrate-level phosphorylation. Additionally, the energy-source reaction that uses the organic substrate generally has a high $-\Delta_r G°$. The relative abundance of reactants and by-products can affect $-\Delta_r G$ only when the contribution of ARP on $-\Delta_r G$ is so large that $-\Delta_r G$ cannot be approximated as $-\Delta_r G°$. When the availability of reactants is significantly higher than products, for example $(\{A1\}\{B2\})/(\{A2\}\{B1\}) = 10^6$, ARP is approximately 33.5 kJ mol^{-1} at 1 bar and 298.15 K. The ARP increases with increasing temperature if all other variables and parameters are fixed. However, the activities of chemical substances and $-\Delta_r G°$ often depend on temperature sensitivity, which may occasionally decrease $-\Delta_r G$ with increasing temperature. As shown in Eq. 4e, the value of $-\Delta_r G°$ is determined by the combination of reactants and products under constant temperature and pressure conditions. The $-\Delta_r G°$ of light-independent producers is typically lower than 1000 kJ mol^{-1}, whereas $-\Delta_r G°$ can exceed 2000 kJ mol^{-1} for aerobic respiration when glucose is used as an electron donor. This suggests that the ARP term does not affect the growth dynamics of microbes that harness aerobic respiration, but in the case of light-independent producers, it may have a significant effect on microbial growth and steady-state behavior.

Due to the ARP effect, the model's behaviors are qualitatively different from those observed in traditional microbial population growth models that follow the Monod-type equation (Seto and Iwasa, 2019a). The steady-state population density of the Monod-type equation increases with increasing r_i and decreasing K_X, as these changes increase the resource-utilizing ability or the resource consumption rate of the species. Meanwhile, the steady population density of the population dynamics that follow Eq. (7) is maximized at an intermediate r_i and K_X. This is because the increase in the resource-utilizing ability positively affects population growth when the abundance of the reactants is relatively larger than that of the by-products, but it negatively affects the energy acquisition per reaction as by-products accumulate in the surroundings, or $-\Delta_r G$ becomes low.

The unique steady-state response of light-independent producers to r_i and K_X may provide them with a distinctive resource-utilizing strategy. If several species compete for the same resource, the steady-state analysis of the Monod-type population dynamics model predicts that the species that can deplete the abundance of resources to the lowest level will exclude others at the steady-state (R^*-rule; Tilman, 1982), which may act as a major selective force for many microbial species. Following the R^*-rule, when all of the species have the same parameter values except for r, only the species with the highest r will eventually dominate the system and maintain the highest population-density level. In contrast, in our model, if several species harness the same energy-source reaction with the same parameter values except for r coexist within a system, the species with the highest r will also exhibit the fastest growth rate and dominate the system, but will maintain a relatively lower population density. Modeling studies have predicted that a small population is more strongly threatened by stochastic processes than a large population if the population is isolated, which would subsequently cause local extinction (Matthies et al., 2004). This implies that subsurface ecosystems may shape a

unique evolution of specialization in the resource utilization of light-independent producers.

ARP-DRIVEN MUTUALISTIC INTERACTIONS

Understanding two-species population dynamics is the first step toward identifying the complex interspecific interactions among light-independent producers. We previously undertook mathematical analyses of two models, the structures of which are illustrated in **Figure 3**. These models deal with mutualistic interspecific interactions that occur through the use of different chemical forms of an element labeled as A_1, A_2, and A_3 (Seto and Iwasa, 2019b, 2020), where a larger subscript number denotes having more electrons. Although light-independent producers can compete for the same resource(s) used in energy-source reactions, we focused on two cases of mutualism where, (i) species 2 uses the by-product of species 1 (the combination of Eqs. (4c) and (5a), i.e., reactions 1 and 2), and (ii) each species receives its own resources from the other species and provides them with the by-products as a resource (the combination of Eqs. (4c) and (6a), i.e., reactions 1 and 3). We call the former type of interspecific interaction a one-way interaction, and the latter a recycling interaction.

For both models, the presence of species 2 increases the steady-state biomass of species 1 and expands the realized niche of species 1 from its fundamental niche. For the one-way interaction model, the interspecific interaction can only be commensalism in the absence of ARP (i.e., the second term on the right-hand side of $-\Delta_r G$ is eliminated) because the presence of species 1, which supplies the resources for species 2, can expand the conditions for the survival of species 2 and its realized niche. This is a standard effect known as "niche construction" or "niche changing" (Erwin, 2008; Laland et al., 2016). The ARP term allows species 1 to increase the fitness of species 1 in the presence of species 2 because species 2 reduces the abundance of the by-product of species 1, resulting in the expansion of the realized niches of species 1. Hence, both species are able to live in conditions in which neither of them could survive alone. Meanwhile, for the recycling interaction model, the same tendency is true for a model with and without the ARP term. As confirmed by the analysis of the one-species model, an increase in the resource-utilizing ability of species in the two models eventually leads to a decline in steady-state population density. However, the presence of a mutualistic partner allows a species to keep its steady-state population density at a higher level than when it would if alone. This implies that a species with a higher resource-utilizing ability may be able to robustly survive in a system if a species that works in a mutually beneficial manner is present and in close proximity.

The mutualistic relationship observed between species 1 and 2 occurs when the population growth of both species depends on the amount of chemical energy including the ARP term. If the growth rate is limited by not the energy acquisition process (catabolism) but the biosynthetic process (anabolism), these two species may compete for essential nutrients to build biomass. This suggests that interspecific interactions among light-independent producers may change depending on which process ultimately limits the microbial growth rate.

The presence of a mutually beneficial partner increases the rate of the energy-source reaction, which may drive the geochemical process that proceeds very slowly in the absence of light-independent producers. Species 1 in **Figure 3B** is able to survive only in the presence of species 2 that sufficiently accelerates the reaction from A_1 to A_2 when it is unlikely to carry forward abiotically. A reaction spontaneously proceeds with releasing energy when $\Delta_r G < 0$ (i.e., $-\Delta_r G > 0$). However, the rate of reaction is not determined by the value of $\Delta_r G$, but, rather, it depends on activation energy and environmental factors (e.g., temperature, coexisting chemical substances, water availability, and pH), which affect the intensity of the competition between abiotic and microbial reactions (Kirby et al., 1999; Melton et al., 2014; Liu et al., 2017). Microbes, like enzymes in biochemical systems, can often accelerate the reaction rate by lowering the energetic barrier required for the reaction to commence. For instance, in the presence of the iron-oxidizing bacteria *Thiobacillus ferrooxidans*, the iron oxidation rate increases up to several orders of magnitude in comparison with the rate under abiotic controls (Lacey and Lawson, 1970; Nordstrom, 1985).

In contrast, rapid abiotic reactions may inhibit the growth of microbes that compete for the same resources. Under neutral pH conditions, it is hypothesized that the growth of iron-oxidizing bacteria is constrained under low oxygen conditions, where microbial iron oxidation can outcompete rapid abiotic iron oxidation (Druschel et al., 2008). Micro-scale iron recycling between iron-oxidizing and -reducing bacteria may enable iron-oxidizing bacteria to overcome abiotic iron oxidation.

DISCUSSION

The Productivity of Subsurface Microbial Ecosystems

The presence of abundant microbial biomass in subsurface ecosystems implies there is considerable productivity of light-independent producers. However, research on the productivity of subsurface microbial ecosystems has been advanced only recently due to limited access to the subsurface biosphere.

Estimations of the productivity of hydrothermal vent ecosystems based on calculations of $\Delta_r G$ have suggested that the productivity of light-independent producers contributes only a small fraction of the total photosynthetic biomass produced in the oceans (McCollom and Shock, 1997; McCollom, 2007). The vast biomass stock, despite low productivity in the subsurface biosphere, may have three explanations. First, the energy sources of subsurface ecosystems may be heavily dependent on organic substrates supplied by surface ecosystems. The dominance of heterotrophic microbes that use organic carbon to build biomass has been confirmed for some sedimentary subsurface ecosystems (Biddle et al., 2006; Morono et al., 2011). Second, microorganisms might adapt or acclimate to energetic stress by lowering the maintenance energy (m in our model). To thrive under limited access to energy sources, microbes in the

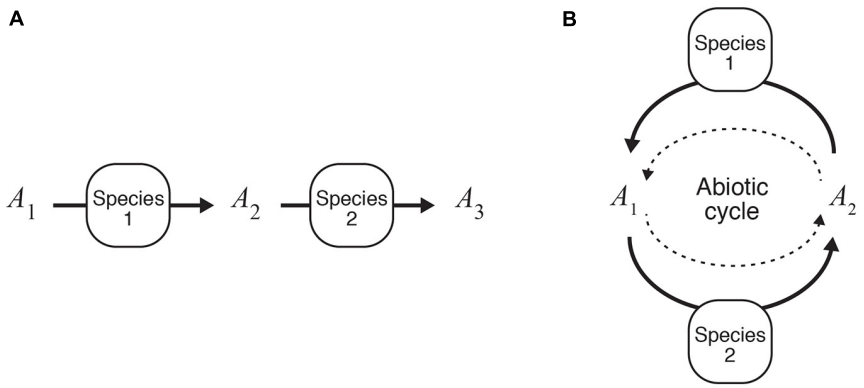

FIGURE 3 | Mutualistic catabolic interactions. **(A)** One-way interactions (Seto and Iwasa, 2019b). **(B)** Recycling interactions (Seto and Iwasa, 2020).

subsurface have often been observed to reduce maintenance energy by switching their metabolic modes; and, as a result, the mean cell-doubling time may then range from a few years to thousands of years (Jørgensen and Boetius, 2007; Valentine, 2007; Hoehler and Jørgensen, 2013). Finally, microbes under low oxygen environments require less energy to synthesize biomass than those under oxygen-rich conditions, which may result in relatively high biomass conversion efficiency (q in our model) in the subsurface biosphere. Nitrogen and sulfur sources in oxygen-rich conditions often exist as NO_3^- and SO_4^{2-}. To generate amino acids as building blocks of biomass, NO_3^- and SO_4^{2-} should be converted into ammonia and hydrogen sulfide ions, and, in the presence of oxygen, more energy is required to carry out these reactions (McCollom and Amend, 2005).

An interesting question is whether the biodiversity-ecosystem functioning (BEF) relationship in subsurface microbial ecosystems is similar across surface and subsurface ecosystems. Controlled experiments in terrestrial ecosystems have shown increased plant biomass and primary productivity with increasing plant diversity (Hector et al., 1999; Tilman et al., 2001), whereas a mechanistic model that incorporates a food-web structure has demonstrated that plant biomass does not always increase with plant diversity (Thébault and Loreau, 2003). Studies examining BEF relationships for soil microorganisms reported somewhat contradictory results; some studies emphasized the link between the physiological or functional diversity and ecosystem functions, especially process rates or activities (e.g., nitrification rate and denitrification activity), in soil microorganisms (Balser and Firestone, 2005; Bell et al., 2005; Webster et al., 2005; Philippot et al., 2013), and the other demonstrated the irrelevance of microbial diversity to ecosystem functions (especially carbon mineralization) (Balser and Firestone, 2005; Wertz et al., 2006). Ecosystem functions of microbes are often evaluated by the process rates of carbon and nitrogen, but as we introduced so far, the energy-source reactions of light-independent producers drive the flows of not only carbon and nitrogen but also other elements such as iron and sulfur. This may result in the underestimation of the effect of microbial diversity on their ecosystem functioning. The extension of our model would help to provide a theoretical framework for understanding the BEF relationship for light-independent producers and overall subsurface microbial ecosystems, including heterotrophic microbes. It would be interesting to address whether or how much the supply of organic substrates from surface ecosystems controls the productivity and biodiversity of these ecosystems, as suggested previously (Hubalek et al., 2016; Magnabosco et al., 2018).

Ecology of Light-Independent Producers as an Interdisciplinary Field

The application of a population dynamics model to the community of light-independent producers will develop our understanding of not only subsurface ecology, but environmental science/engineering, astrobiology, and the evolution of early life and ecosystems.

Microbial fuel cells are a technology that converts chemical energy to electricity by using electron transfer metabolisms (Du et al., 2007). While research has concentrated on the conversion of organic substrates to electricity, the application of light-independent producers is also expected to produce carbon compounds from CO_2 in a renewable manner. However, because of low product yields and productivity, the practical application of light-independent producers requires improved efficiency under industrial conditions (Claassens et al., 2016). For some microbial fuel cells that use organic substrates, higher power generation in co-cultures, as opposed to individual strains, has been reported (Logan et al., 2019). While more realistic modeling is needed, our approach will be useful in understanding productivity in co-cultures by linking population dynamics with the availability of chemical energy. This application will also be useful in understanding the different efficiencies of wastewater treatment by light-independent producers in pure and co-cultures (e.g., Parshina et al., 2005).

Theoretical, experimental, and field investigations have established the physical and chemical limits of microbial life under extreme conditions. In the field of astrobiology, the potential survival and existence of life on other planets has been debated based on these limitations. The activity of microbes, including light-independent producers, helps in the search for

life on extraterrestrial planets and in planetary protection against microbial contamination from and to Earth in the course of space missions. Although microbial life can be limited by multiple factors (e.g., the availability of water, gravity, temperature, pressure, and the intensity of UV/ionizing radiation) (Rummel et al., 2014; Moissl-Eichinger et al., 2016), the presence of the potential energy-source reaction is one important factor that restricts microbial activity. The limits on microbial growth are often measured based on single-culture experiments, but, as our results suggest, the presence of a mutualistic counterpart may expand limits on microbial growth. This suggests that the limits on microbial growth require an understanding of the effects of biological interactions, in addition to abiotic factors.

Although the energy source for the earliest life is still under debate, both phylogenetic and biochemical evidence suggest that the earliest life forms were chemoautotrophs (Pace, 1997; Lane et al., 2010; Judson, 2017), which may have used hydrogen and carbon dioxide as geochemical sources (Weiss et al., 2016). The early Earth was deficient in oxygen and organic matter previous to the evolution of oxygenic photosynthetic organisms, which limited the energy-source reactions for the light-independent producers listed in **Table 1**. One interesting question deals with how microbial metabolic diversity evolved and was constructed in the earliest ecosystem under extreme energy limitations. If the earliest life forms depended on chemical energy, the most likely place of origin would be the hydrothermal vent system, which creates an interface between thermal fluids with electron-abundant substances and the relatively electron-deficient substances in the bottom water. Another interesting question is how life could have abandoned this attractive energy source to expand the ecosystems. Our results suggest that the evolution of a mutualistic metabolic counterpart may have enabled life under extreme energy limitations to be freed from energetic constraints and invade other systems (Seto and Iwasa, 2019b, 2020). Especially for microbes harnessing reactions with low $-\Delta_r G^\circ$ and those that do not use either organic substrates or oxygen, the ARP may play an important role in potential growth, survival and community structure.

AUTHOR CONTRIBUTIONS

Both authors contributed to the writing of the manuscript.

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