

A new perspective on functional redundancy and phylogenetic niche conservatism in soil microbial communities



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ABSTRACT

Functional redundancy in soil microbial communities seems to contradict the notion that individual species have distinct metabolic niches in multi-species communities. All soil microbiota have the metabolic capacity for “basic” functions (*e.g.*, respiration and nitrogen and phosphorus cycling), but only a few soil microbiota participate in “rare” functions (*e.g.*, methanogenesis and mineralization of recalcitrant organic pollutants). The objective of this perspective paper is to use the phylogenetic niche conservatism theory as an explanation for the functional redundancy of soil microbiota. Phylogenetic niche conservatism is defined as the tendency for lineages to retain ancestral functional characteristics through evolutionary time-scales. The present-day soil microbiota is the result of a community assembly process that started when prokaryotes first appeared on Earth. For billions of years, microbiota have retained a highly conserved set of core genes that control the essential redox and biogeochemical reactions for life on Earth. These genes are passed from microbe to microbe, which contributes to functional redundancy in soil microbiota at the planetary scale. The assembly of microbial communities during soil formation is consistent with phylogenetic niche conservatism. Within a specific soil, the heterogeneous matrix provides an infinite number of sets of diverse environmental conditions, *i.e.*, niches that lead to the divergence of microbial species. The phylogenetic niche conservatism theory predicts that two or more microbial species diverging from the same clade will have an overlap in their niches, implying that they are functionally redundant in some of their metabolic processes. The endogenous genetic factors that constrain the adaptation of individuals and, thus, populations to changing environmental conditions constitute the core process of phylogenetic niche conservatism. Furthermore, the degree of functional redundancy in a particular soil is proportional to the complexity of the considered function. We conclude with a conceptual model that identifies six patterns of functional redundancy in soil microbial communities, consistent with the phylogenetic niche conservatism theory.

Key Words: basic function, conceptual model, core gene, environmental factor, genetic factor, niche overlap, rare function, soil biodiversity

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INTRODUCTION

Soil represents a vast reservoir of diverse microbial life, containing between 2 000 and 8.3 million bacterial species per gram soil (Gans *et al.*, 2005; Schloss and Handelsman, 2006). Soil microbiota are responsible for degradation, transformation, and biosynthesis reactions in biogeochemical cycles as well as the detoxification of natural and human-made pollutants. The loss of a few species does not generally affect the soil functions because the same functions can be performed by multiple species (Jurburg and Salles, 2015; Grządziel, 2017). This functional redundancy could explain why the number of microbial species (alpha-diversity) is not related to soil functions (Wittebolle *et al.*, 2008; Louca *et al.*, 2016; Sheng *et al.*, 2016).

The deliberate elimination or suppression of mi-

crobial groups has little effect on soil processes such as decomposition of organic matter (Griffiths *et al.*, 2001a, b), indicating that multiple soil microbiota carry out the same functions (Grządziel, 2017; Nannipieri *et al.*, 2017). Functional redundancy is common for some microbially-mediated processes. We can define functions as “basic” or “rare”, depending on how frequently they occur in the soil environment. All soil microbiota have the metabolic capacity to perform “basic” soil functions such as respiration, nitrogen and phosphorus cycling, and organic matter decomposition (Wittebolle *et al.*, 2008; Nelson *et al.*, 2016; Grządziel, 2017). However, “rare” functions like methanogenesis or the mineralization of recalcitrant organic pollutants are mediated by specific groups, and there is far less redundancy in “rare” than “basic” functions (Girvan *et al.*, 2005). Soil microbiota with the same functional

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characteristics should have shared ancestry and have experienced similar adaptations to environmental conditions. This is consistent with the observations of Darwin (1859), which indicate that closely-related species share functional characteristics.

Suenaga (2015) used a metagenomics approach to compare the essential genes that encode enzymes for dissimilatory sulfate reduction and denitrification as well as the extradiol dioxygenases, which cleave the aromatic ring of catechol compounds during the aerobic microbial degradation of natural and xenobiotic aromatic compounds. The screening of thousands of clones revealed a high degree of similarity in the gene clusters of diverse prokaryotes, with some novel genes in the flanking regions. Mutations in the genes encoding such key enzymes would provide an adaptive phenotype optimized for a specific niche (Chattopadhyay *et al.*, 2013). This is particularly evident in the extradiol dioxygenases, because the genes from a common ancestor that produced more thermostable extradiol dioxygenases have diverged through the nucleotide mutations, with modern lineages being less thermostable but possessing greater catabolic activity (Suenaga, 2015). Furthermore, Tringe *et al.* (2005) found that functional profiles of soil metagenomes were highly correlated with soil properties, suggesting that specific functions were selected by the environment (Louca *et al.*, 2018).

Global warming and other anthropogenic factors are causing rapid environmental changes in all ecosystems, including the soil ecosystem. As microbial-mediated processes are crucial to sustain soil functions, it is essential that we understand the root causes and consequences of functional redundancy of soil microbiota. Therefore, the objective of this perspective paper is to determine if the phylogenetic niche conservatism theory (Harvey and Pagel, 1991) could explain the functional redundancy of soil microbiota. The genetic and environmental factors leading to functional redundancy are presented, and the evidence for phylogenetic niche conservatism is shown in a conceptual model that describes the expected patterns of functional redundancy during the assembly of soil microbial communities.

PHYLOGENETIC NICHE CONSERVATISM AND FUNCTIONAL REDUNDANCY IN SOIL MICROBIAL COMMUNITIES

A fundamental concept in the phylogenetic niche conservatism theory is the definition of a niche, *i.e.*, the set of biotic and abiotic conditions in which a species

persists and maintains a stable population (Hutchinson, 1957). Two types of niches are distinguished: the fundamental niche and the realized niche (Hutchinson, 1957). The fundamental niche describes the abiotic conditions in which a species can persist, whereas the realized niche describes the conditions in which a species persists when other species (*e.g.*, competitors and predators) are present. As the fundamental niche can be conserved during evolutionary timespans, the phylogenetic niche conservatism theory predicts that modern lineages will have similar genetic, physiological, and ecological characteristics to their ancestors (Harvey and Pagel, 1991; Holt and Gaines, 1992; Wiens and Graham, 2005). Another aspect of the phylogenetic niche conservatism theory is that underlying biological processes constrain niche divergence between closely related species and, therefore, prevent populations from expanding into new niches (Losos, 2008).

The phylogenetic niche conservatism theory is consistent with the observed pattern of high niche similarity in related species, and it also explains the evolutionary mechanisms leading to that similarity (Losos, 2008; Wiens, 2008). As illustrated in Fig. 1, there are endogenous genetic, physiological, and ecological constraints that limit the ability of individuals and, thus, populations to rapidly adapt to changing environmental conditions (Pyron *et al.*, 2015). Selective forces resulting from environmental variations experienced by a population tend to force the population to maintain their niche through time (Pyron *et al.*, 2015). Three patterns are expected to emerge: niches are conserved (more similar than expected), constrained (divergent within a limited subset of available niches), or divergent (less similar than expected), on the basis of the degree of phylogenetic relatedness between species (Fig. 1).

Functional redundancy of soil microbiota is very likely a result of the first pattern, where niches are conserved and the species overlap due to a high degree of similarity at the genetic, physiological, and ecological levels (Fig. 1). Species that co-occur due to niche constraint (Fig. 1) are probably going to be functionally redundant as well. Although Fig. 1 illustrates niche overlap for two species, we expect multiple species to co-occur in soil niches as there are thousands to millions of species in soil microbial communities and an incalculable number of niches in the heterogeneous soil matrix. We also realize that niches are dynamic, not static, and the boundaries of a particular niche fluctuate with changing abiotic and biotic conditions, which allows population expansions and contractions in the niche (*i.e.*, population dynamics).

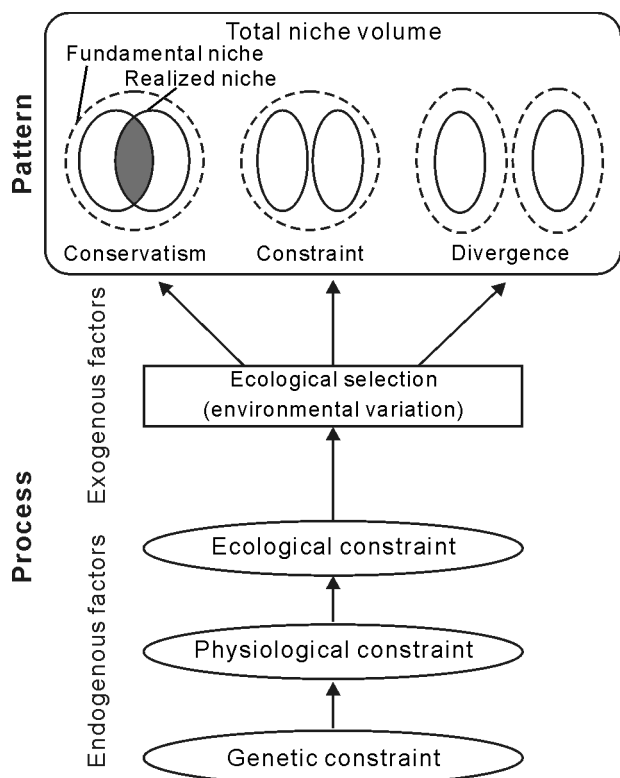


Fig. 1 Ecological and evolutionary consequences of phylogenetic niche conservatism for microbial communities. Endogenous factors constrain the phenotypes present, whereas exogenous factors represent selective pressures from ecological and environmental conditions that contribute to evolutionary processes. This leads to the three patterns of phylogenetic niche conservatism between species: niche conservatism, niche constraint, and niche divergence, where each species is represented as a circle and the niche is the dotted circle (adapted from Pyron *et al.* (2015)).

COMMON ANCESTORS WITH CORE METABOLIC PROCESSES

The present-day soil microbial community is the outcome of the genetic and environmental adaptations of prokaryotes that descended from common ancestors on Earth. Their “basic” functions are the core metabolic processes that allow soil microbiota to alter the chemical speciation of virtually all elements on Earth (Falkowski *et al.*, 2008). These metabolic processes involve the biogeochemical cycles of six major elements (hydrogen (H), carbon (C), nitrogen (N), oxygen (O), sulfur (S), and phosphorus (P)) that represent the major building blocks for all biological macromolecules (Schlesinger, 1997). These biogeochemical cycles have evolved on a planetary scale to form a set of nested, abiotically-driven acid-base reactions and biologically-driven redox reactions (Falkowski *et al.*, 2008), leading to a linked system of elemental cycles (Kluyver and Donker, 1926).

Core metabolic processes have survived intact and allowed prokaryotes to persist for billions of years, even though the Earth has undergone extraordinary environmental changes since its formation, such as the Great Oxygenation Event, ice ages, and massive volcanic outgassings (Knoll, 2003). Therefore, genes encoding for the core metabolic processes are highly conserved. These genes created and coevolved with biogeochemical cycles and were passed from microbe to microbe primarily by horizontal gene transfer (Falkowski *et al.*, 2008; Suenaga, 2015). This is consistent with molecular biology studies based on gene order, which indicate that early cellular evolution was probably communal, with promiscuous horizontal gene flow as the principal mode of evolution (Woese, 2002). Core metabolic processes are controlled by gene clusters and families that are similar in thousands of organisms (Suenaga, 2015). In prokaryotes, gene homology is assured by horizontal gene transfer, *i.e.*, the movement of genetic material among organisms by transformation, transduction, and conjugation. This process often involves bacteriophages and plasmids (Varga *et al.*, 2012, 2016) and differs from the vertical transmission of DNA from parent to offspring (Robinson *et al.*, 2013). In this manner, the genes responsible for the major extant catabolic and anabolic processes were distributed among organisms billions of years ago, before cellular differentiation and vertical gene transmission evolved as we know them today (Falkowski *et al.*, 2008). Therefore, soil microbiota inevitably possesses genes for core metabolic processes within their DNA, which account for the functional redundancy in soil biogeochemical processes in modern-day microbial communities. Horizontal gene transfer is a historical evolutionary process that explains why diverse soil microbiota can perform many of the same functions. For instance, diverse groups of bacteria and archaea are able to fix atmospheric diatomic nitrogen (N_2) because they possess nitrogenase enzymes (Kechris *et al.*, 2006). All ammonia-oxidizing bacteria and archaea produce ammonia monooxygenase, the key enzyme that oxidizes ammonia to hydroxylamine (Könneke *et al.*, 2005; Hallam *et al.*, 2006). Furthermore, the sulfate-reducing Deltaproteobacteria, gram-positive bacteria, and Archaea share the same dissimilatory sulfite reductases that are responsible for sulfate respiration (Klein *et al.*, 2001). As no single clade is responsible for these specific functions, prokaryotic phylogeny is weakly associated with N_2 fixation, ammonia oxidation, and sulfite reduction (Louca *et al.*, 2018). Considering that these and other metabolic processes are not monophyletic (Aguilar *et al.*, 2004; Martiny *et al.*, 2013, 2015), it is

to share the same functions when their niche overlaps (A_1B_1 pattern) until the environmental conditions change and their functions cease (Fig. 2). This is likely to occur when microbe A and microbe B are performing “basic“ functions that both can do equally well. If microbe A is more efficient at acquiring resources or performing the function, it may be dominant and outcompete microbe B, resulting in the A_1B_0 pattern (Fig. 2). For their long-term survival in the overlap niche, microbe B has to have a deep phylogenetic trait such as the ability to perform the function when environmental conditions are no longer suitable for microbe A (*e.g.*, at the limits of A’s tolerance for a particular stress, such as pH, salinity, oxygen, temperature, among others).

There are six possible patterns of functional redundancy for microbe A and microbe B (Fig. 2). These patterns reflect the ability of microbes to transform substrates, such as glucose (State X), to the reaction product, carbon dioxide (State Y). This is an abstract representation that should apply to any microbially-mediated reaction. Although a substrate can be transferred directly from State X to State Y, we acknowledge that other reactions may take place under certain environmental conditions, and produce an intermediate product such as pyruvic acid, State Z, that will eventually be converted to carbon dioxide, State Y (Fig. 2). Thus, there is more than one way to implement the same function. As soil microbiota are ubiquitous, but often are present in dormant or resting states, awaiting an opportunity to “bloom” (Jurburg and Salles, 2015), this model allows for co-occurrence of active and dormant species within the same niche. For instance, the A_1A_2 and A_1A_0 patterns suggest that microbe A is active and transforms State X to State Y directly (A_1) or through another pathway (A_2 transfers the substrate from State X to State Z, then State Y), whereas microbe B remains dormant. This is obviously a simplistic view of soil microbiota functions, but it explains how functional redundancy occurs within the context of the phylogenetic niche conservatism theory.

PERSPECTIVES AND FUTURE DIRECTIONS

Functional redundancy of soil microbiota has developed through evolution and reflects local adaptation to environmental conditions. It seems likely that soil microbial community assembly follows the principles of phylogenetic niche conservatism, but this remains to be proven experimentally. Soil metagenomics studies allow for rapid characterization of thousands of soil microbiomes and should prove helpful for establishing the

phylogenetic supertree representing the species assembled in a particular community. Evaluating the functional genes of the soil microbiota should provide more insights to understand functional redundancy as well as the occurrence of “rare” functions within soil microbial communities.

Functional redundancy in soil microbiota is widely accepted, but generally not explained. A deeper understanding of soil biodiversity requires a theoretical basis to resolve many ecological and evolutionary issues, such as the co-existence of species in the heterogeneous soil matrix, the relationship between community structure and function, among others. Many theories could be considered as potential explanations of this phenomenon, such as neutral theory, trade-off, gene drift, high dimensional niches, fluctuating selection, dormant cells, or patchy environmental conditions, but none of these are fully accepted by ecologists. We propose the phylogenetic niche conservatism theory simply because it provides a better explanation of our understanding of the issue of functional redundancy. It remains to be confirmed whether this is the best theory for explaining functional redundancy in soil microbial communities.

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