MINI REVIEW
Where less may be more: how the rare biosphere pulls ecosystems strings

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Rare species are increasingly recognized as crucial, yet vulnerable components of Earth’s ecosystems. This is also true for microbial communities, which are typically composed of a high number of relatively rare species. Recent studies have demonstrated that rare species can have an over-proportional role in biogeochemical cycles and may be a hidden driver of microbiome function. In this review, we provide an ecological overview of the rare microbial biosphere, including causes of rarity and the impacts of rare species on ecosystem functioning. We discuss how rare species can have a preponderant role for local biodiversity and species turnover with rarity potentially bound to phylogenetically conserved features. Rare microbes may therefore be overlooked keystone species regulating the functioning of host-associated, terrestrial and aquatic environments. We conclude this review with recommendations to guide scientists interested in investigating this rapidly emerging research area.

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Introduction

Microbial communities typically show a skewed species abundance distribution, with relatively few dominant species co-existing alongside a high number of rare species (Nemergut et al., 2011). Although the importance of rare species is increasingly being recognized for macroorganisms (Lyons et al., 2005; Mouillot et al., 2013; Soliveres et al., 2016), many rare microbial taxa (for example, singletons) are routinely removed from data sets, thereby systemically overlooking a substantial part of the biosphere. Most of our knowledge is still based on dominant species, despite the increasing attention for the rare microbial biosphere (Pedrós-Alió, 2007; Reid and Buckley, 2011; Lynch and Neufeld, 2015). In this review, we place rare microbes in...
an interdisciplinary spotlight and discuss their relevance across a range of current hot topics in microbial ecology, including microbiome assembly and function, and biogeochemical cycling. We present patterns and consequences of rarity and link these to existing and emerging theoretical frameworks.

Microscopic organisms, both eukaryotic and prokaryotic, display a huge biodiversity (Locey and Lennon, 2016). Microbial communities drive Earth’s biogeochemical cycles (Falkowski et al., 2008) and are essential for animal and plant survival (Russell et al., 2014). An estimated 1.5–28% of all microbes are ‘conditionally rare taxa’, which are rare in most conditions but become dominant occasionally (Shade et al., 2014). These often-overlooked taxa may be key to understanding community assembly and function (Allan et al., 2011).

The increasing resolution provided by high-throughput sequencing technologies has shed new light on microbial diversity and revealed a diverse collection of microbes occurring at low densities: the ‘rare biosphere’ (Sogin et al., 2006). As such, the rare biosphere is currently one of the new frontiers of microbial ecology. Recent studies have shown that low-abundance species should be considered full members of microbial communities and not treated as analytical annoyances (Nipperess and Matsen, 2013; McMurdie and Holmes, 2014; Lynch and Neufeld, 2015).

We provide an overview of theories on why species are rare (including community assembly, evolutionary processes and biogeographic patterns), and how low-abundance species can drive ecosystem processes. We also provide evidence for the importance of rare microbes across different habitats, and present approaches to examine the most pressing questions surrounding them.

### Drivers of rarity

Rarity can be defined in several ways, including for instance local abundance, habitat specificity and geographical spread (Rabinowitz, 1981). These concepts are routinely applied to plants and animals, and can be easily transferred to microbial communities. Local abundance is the easiest and the most common index used to quantify species’ rarity in microbial ecology. However, microbial rarity may also be expressed as a restriction to a low number of habitats, thereby reflecting habitat specificity (Barberán et al., 2014) and geographic range (Tedersoo et al., 2014).

Rarity can result from stochastic processes, inherent trade-offs in life-history strategies, and biotic and abiotic interactions (Figure 1). Species rarity can for instance emerge simply by stochastic population fluctuation (Ai et al., 2013), without implying any specific physiological characteristics. Rarity is also an element of community assembly processes as a recently immigrated species is necessarily rare when it first enters a new community. External abiotic and biotic factors can have pivotal roles in species rarity. For instance, a highly specialized species showing a very narrow environmental niche may be abundant in a few habitats but remain rare in most others (Figure 1a). Local rarity may also be the result of fitness trade-offs, for instance, when stress resistance comes at the cost of a lower growth rate. Slow-growing species might not reach a high density, but may persist well under stressful conditions (Gudelj et al., 2010). An extreme case is dormancy, in which microbes

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**Figure 1** Potential mechanisms that can drive local rarity. Rarity can be linked to two types of mechanisms: (1) mechanisms related to species characteristics (a, b), and (2) mechanisms related to local biotic and abiotic conditions (c, d). Drivers of rarity include (a) narrow niche breadth, (b) high intraspecific competition, (c) low competitive abilities and (d) frequency-dependent predation. In all panels, rare species are indicated in red, while abundant species are indicated in blue.
completely stop growth but gain greatly in stress resistance (Gobet et al., 2012). Many microbes can remain generally inactive and at low density most of the time, only becoming dominant when more favorable conditions arise (Aanderud et al., 2015). Biotic interactions also have also an important role in explaining rarity. An uncompetitive species may often remain rare rather than going extinct. Rare persistence has been demonstrated for microbes that are sensitive to antibiotics produced by competitors (Narisawa et al., 2008), unable to build protective structures such as biofilms (Schluter et al., 2015) or incapable of using crucial resources (García-Fernández et al., 2004). The dependance of one species on another may lead to negative frequency dependency, where the fitness of the dependent phenotype decreases when it becomes more abundant. A well described example involves social cheaters depending on public goods produced by other species (Kummerli and Brown, 2010; Jousset et al., 2013). Cheats may be highly successful while rare, but their competitive advantage rapidly dwindles as they spread (Figure 1b). The strength of frequency-dependent selection may vary with environmental factors such as predators (Meyer and Kassen, 2007): the steeper the slope of the frequency-dependent fitness, the more persistent a rare species will be, but at the cost of remaining rare (Yenni et al., 2012).

Bacteriophages and protists often show frequency-dependent predation and tend to over-consume abundant prey species (Jousset et al., 2009; Winter et al., 2010), preventing them from dominating the community and creating space for rare species (Rodriguez-Valera et al., 2009; Figure 1d). Finally, rarity may be driven by changes in abiotic conditions, as rare species are more sensitive to environmental fluctuations and more prone to extinction (Gastón, 2008). Current abrupt changes linked to human activity, such as global change and intensive land use, may thus have a deep impact on the rare biosphere and associated ecosystem functions (Rodrigues et al., 2013). Monitoring changes in relative abundances or activities of rare microbes might then serve as an early warning system of environmental change (Chambers et al., 2016).

Ecological relevance of rare species

Rare species are increasingly recognized as drivers of key functions in terrestrial and aquatic ecosystems, as well as host-associated microbiomes (Figure 2; Table 1). Their functional importance may be due to effects that are disproportionately large given their abundance or via the provision of insurance effects. This may seem counter-intuitive given the expected high functional redundancy in microbial communities (Rousk et al., 2009); with many species sharing similar functions, rare species should not be necessary for maintaining function. Species that are considered functionally non-relevant under a given environmental condition may become important under changing conditions by providing necessary traits or acting as partners in new interspecific interactions (Shade et al., 2014; Fetzer et al., 2015). We propose that rare species offer a pool of genetic resources that may be activated under the appropriate conditions. This may provide insurance effects (Yachi and Loreau, 1999), as at least one species will perform a given process under a given environmental condition. Different processes vary in their sensitivity to the loss of rare species (Peter et al., 2011) with specialized functions, like pollutant degradation (Dell’Anno et al., 2012), particularly affected.

Research on the ecological importance of rare species is still in its infancy, but empirical evidence that the rare biosphere is involved in many microbial-driven processes is accumulating (Figure 2). Below, we highlight three areas in which rare microbes could be particularly influential.

Biochemical processes—nutrient cycling and pollutant degradation

Some nutrient cycling processes provide illustrative typical examples of the disproportionate effects of rare microbes. Low-abundance green and purple sulfur bacteria were found to be highly active
 Removal of rare microbes in activated sludge and freshwater greatly reduced the capacity to degrade pollutants and toxins (Dell’Anno et al., 2012; Hernandez-Raquet et al., 2013; Delgado-Baquerizo et al., 2016). Rare species probably offer the required gene pool to catalyze complex degradation processes, a hypothesis supported by observations that pollutants are often degraded by species falling below the detection limit in pristine samples (Giebler et al., 2013).

The role of rare species in the breakdown of organic matter is far less clear. Some studies found no consistent relationship between bacterial diversity and litter decomposition, concluding that a low number of species sufficed for efficient decomposition (Griffiths et al., 2001; Franklin and Mills, 2006). Other studies, however, highlighted that rare species may speed up decomposition (Salonius, 1981), especially the degradation of recalcitrant organic matter such as chitin and cellulose (Peter et al., 2011; Jimenez et al., 2014).

Community assembly
Experimental removal of rare species resulted in an increased establishment of new species (Van Elsas et al., 2012; Vivant et al., 2013), suggesting that rare species occupy a key niche and slow down invasive species establishment. A recent study demonstrated that rare species are vital in controlling invasions into soil communities by unwanted (for example, pathogenic) microbes (Mallon et al., 2015), suggesting that rare microbes may play an important role in biotechnological applications such as hygiene or crop protection.

Microbiome—host health
Rare species have been detected within the microbiomes of diverse hosts, from the rhizosphere (Nuccio et al., 2016) to human lungs (Guss et al., 2011), and evidence suggests that they can be critical to microbiome functionality and thus host health. Low-abundance plant-associated microbes are for instance involved in the production of antagonistic volatile compounds that protect the host plant against pathogens (Hol et al., 2015b). Further, removing rare species from an agricultural soil led to a higher plant biomass, albeit at the cost of a reduction of defense compounds against above-ground herbivores (Hol et al., 2010), suggesting that rare microbes can fine-tune the balance between host growth and defense.

In the human lung, a high diversity of low-abundance bacteria is associated with a reduced severity of bacterial infection in individuals with cystic fibrosis (van der Gast et al., 2011). Conversely, rare species may contribute to pathogenesis, as shown by the initiation of periodontal disease by low-abundance species that trigger changes in the oral microflora (Hajishengallis et al., 2011). Several

**Table 1 References for processes or functions which are supported by rare microbes**

| Process or function | References |
|---------------------|------------|
| **Biochemical processes** | |
| Sulfate reduction | Pester et al., 2010 |
| | Loy and Pester, 2010 |
| | Steger et al., 2011 |
| Methane consumption | Bodelier et al., 2013 |
| Carbon cycling | Franklin et al., 2001 |
| Substrate use | Matos et al., 2005 |
| | Hernandez-Raquet et al., 2013 |
| | Mallon et al., 2015 |
| Straw decomposition | Griffiths et al., 2001 |
| | Baumann et al., 2013 |
| Nitrogen cycling | Griffiths et al., 2004 |
| Nitrification | Mu et al., 2008 |
| Denitrification | Philippot et al., 2013 |
| Fixation | Hua et al., 2015 |
| Pollutant degradation | Sanchez et al., 2004 |
| 2,4,6-trichlorophenol | Dell’Anno et al., 2012 |
| Petroleum hydrocarbons | Giebler et al., 2013 |
| Phenanthrene mineralization | Hernandez-Raquet et al., 2013 |
| Triclosan, microcystin-LR | Delgado-Baquerizo et al., 2016 |
| **Community assembly** | |
| Resistance to invasion | Yan et al., 2015 |
| | Garland et al., 1999 |
| | Matos et al., 2005 |
| | Van Elsas et al., 2012 |
| | Vivant et al., 2013 |
| | Mallon et al., 2015 |
| Resilience | Griffiths et al., 2004 |
| | Tardy et al., 2014 |
| **Microbiome** | |
| **Human health** | |
| Lung infection | Van der Gast et al., 2011 |
| Periodontal disease | Hajishengallis et al., 2011 |
| Gut microbiota | Stecher et al., 2013 |
| **Plant health** | |
| Plant biomass, herbivores | Hol et al., 2010 |
| Plant biomass | Hol et al., 2015a |
| Plant pathogens | Hol et al., 2015b |

Background information for Figure 2.

keystone species in freshwater and crucial for nitrogen and carbon uptake (Musat et al., 2008). Similarly, Pester et al. (2010) found that the most important sulfate reducer in peatland was a rare bacterium with only 0.006% relative 16 S rRNA gene abundance. Denitrification also likely relies on rare species. A decrease of 75% of the measured species richness reduced soil denitrifying activity by a factor of 4–5 fold (Philippot et al., 2013), suggesting that dominant species cannot carry out this process alone.

Microbial communities play a key role in the degradation of organic compounds, including pollutants and the insurance provided by rare species can therefore contribute to ecosystem resilience to anthropogenic pollution. Organic pollutant degradation involves complex metabolic pathways shared across different species (Fuentes et al., 2014).
studies have further identified low-abundance pathogens in clinically relevant samples (Guss et al., 2011; Bittinger et al., 2014).

 Whilst rare species have traditionally received little attention from a clinical or biotechnological perspective, a better understanding of their ecology, and impact on microbiome function, may provide new tools to predict, and enhance, health effects of host-associated microbiomes.

**Mechanisms behind disproportional effects of rare microbes**

Here, we discuss three, non-mutually exclusive, mechanisms that may explain the high importance of rare microbes for ecosystem functioning: enhanced species activity, increased community functional diversity and community-wide species interactions.

**Rare microbes can be more active than the abundant ones**

In marine ecosystems, conditionally rare bacterial taxa tend to be more active when rare (Campbell et al., 2011). In fluctuating conditions, a rare taxon could be disproportionally active due to continuous regrowth. However, growth may not necessarily be responsible for this increased activity; *Desulfosporosinus* species, for instance, remain at low abundance despite increasing their ribosome content under activating conditions (Hausmann et al., 2016). A similar observation was reported for protists in lakes, where some species were always rare and yet highly active (Debroas et al., 2015). These examples utilized rRNA:rDNA ratios as a proxy for activity. Similar results have been observed using respiration as a proxy for bacterial activity. Rare species appear to sustain community activity; similar sized communities with rare microbes were shown to have higher respiration than communities with fewer rare microbes (Dimitriu et al., 2010). Thus, rare yet highly active microbes can contribute more to ecosystem functioning than expected based on their abundance, akin to some macroorganisms, such as rare but active predators or pollinators (Herrera, 1989).

**Rare species represent a vast functional gene pool**

Collectively, rare microbes represent a huge genetic pool and, as such, contribute to the metabolic potential of the community. Many microbial species are auxotrophs, that is, they need to obtain certain vitamins or amino acids from other organisms in their environment (Helliwell et al., 2013). Secretion of such compounds as metabolic waste by other microbes can greatly improve overall community function (Mee et al., 2014). Further, metabolism of complex products requires a large set of enzymes, which are often not present in a single organism. Potentially toxic by-products may thus accumulate if not further degraded by other organisms (Haruta et al., 2009). Dimitriu et al. (2010) measured activities of several enzymes involved in the degradation of organic material and concluded that more diverse bacterial communities harbor a greater set of functions due to the functional differences between species. They suggest that rare species are likely to be functionally dissimilar from abundant ones and therefore are likely to offer complementary, or unique, metabolic pathways to support community function. This high functional diversity of rare species can also be found in macroorganisms, for example, Amazonian fish, rainforest trees and tropical birds (Leitão et al., 2016).

**Rare microbes enhance functionality of abundant microbes**

Microbial physiology can be strongly influenced by the presence of other microbial species (Garbeva et al., 2011). Accordingly, the presence of rare microbes could induce metabolic responses in more abundant microbes, implying that rare microbes have indirect effects on ecosystem functioning. A comparison of communities containing and not containing rare species showed that bacterial communities including rare species strongly reduced fungal growth via production of antifungal volatiles (Hol et al., 2015b), suggesting that rare bacteria either produce or trigger dominant bacteria to synthesize these compounds. Similarly, for mammals the presence of a single predator can impact the behavior and physiology of a herd of prey. Another example of rare microbes influencing abundant microbes stems from the work of Low-Décarie et al. (2015), who showed that rare microbes rescued whole communities from lethal stress, possibly via horizontal gene transfer. Horizontal transfer of genetic material can also be found in animals and plants (Panaud, 2016), but occurs more frequently between microbes and probably has a larger role in microbial communities.

**Experimental and technological approaches**

Rare microbe research is a rapidly emerging field. Given the obstacles to exploring rare microbes and the rapid advances in experimental approaches, we provide a condensed summary of methods and strategies that can be employed to address the most pressing questions in this field (Table 2, see also Reid and Buckley, 2011; Lynch and Neufeld, 2015).

Synthetic communities are a powerful approach to test potential causes of rarity, such as order of arrival (Fukami and Morin, 2003), or density-dependent microbial interactions. Studies that manipulate species’ abundances can directly examine the impact of rare microbial species on community functionality. The use of flow cytometry, selecting for small cells before cultivation, could increase the likelihood
Table 2 Overview of the research questions and general approaches in the study of rare microbes

| Research questions | Method | Critical issues | Options | References |
|--------------------|--------|----------------|---------|------------|
| Synthetic communities | Order of arrival | Vary order of arrival to test priority effects | Cultivation dependent | Selective/spatially structured media | Fukami and Morin, 2003 |
| Density-dependent effects | Vary abundances to test effects of rare species | Cultivation dependent | Cell separation via microfluidic or flow cytometry | Zhang et al., 2009 |
| Manipulation of natural communities | Removal | Consequence of rare species loss | Dilution-to-extinction | Equal biomass in all treatments | Philippot et al., 2013; Mallon et al., 2015; Hol et al., 2015a,b; Delgado-Baquerizo et al., 2016 |
| | Enrichment | Responders to changing conditions | Salinity, dry–rewet, predation, pollution, nutrient amendments | Molecular methods for composition (DNA) and activity (RNA) | Incubation period for recovery of biomass | DNA normalization; improve coverage rare biosphere via single-cell genomics |
| In situ | Microbial population dynamics | Time series | Availability of data sets | Increase sampling | Shade et al., 2014 |
| | Genome recovery of rare species | Single-cell genomics | Selection of target | Labeling via FISH | Podar et al., 2007; Freilich et al., 2011 |
| | Function of rare species | SIP; Nano-SIMS | Low throughput | Combine with single-cell analysis | Musat et al., 2008; Pester et al., 2010 |

Abbreviations: FISH, fluorescence in situ hybridization; SIMS, secondary ion mass spectrometry; SIP, stable isotope probing.
Conclusion

Rare microbes may represent the hidden backbone of microbial communities, and our aim was therefore to increase awareness of and stimulate research on these rare ecosystem players. Rare taxa may vary in their ecological relevance and methods are becoming increasingly available to (1) assess relatively active taxa, (2) isolate them and (3) empirically determine their influence on community functioning. We summarized how rare microbes are important for several ecosystem processes and discussed the mechanisms by which these disproportional effects may become manifest. Future studies should further investigate the life-history traits that enable such widespread yet low-abundance existence. It may be important to determine the fraction of rare microbes that are active and dormant in order to predict functional consequences of rare species loss. We propose that including rare microbes in future investigations will improve our understanding of microbial community functioning, and help explain the buffering capacities of ecosystem against environmental change.

Conflict of Interest

The authors declare no conflict of interest.

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Author contributions

AJ and WHGH initiated the workshop where the ideas for this synthesis were developed. All participants of the workshop contributed ideas and text. AJ and WHGH compiled the first draft and all authors contributed substantially to revisions.

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