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Global Change and the Soil Microbiome: A Human-Health Perspective

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The importance of the gut and the soil microbiomes as determinants of human and ecosystem health, respectively, is gaining rapid acceptation in the medical and ecological literatures. This suggests that there is a wealth of highly transferable knowledge about the microbial ecology of human and non-human ecosystems that is currently being generated in parallel, but mostly in isolation from one another. I suggest that effectively sharing this knowledge could greatly help at more efficiently understanding and restoring human health and the functioning of ecosystems, which are currently under wide-spread pressure. I illustrate this by comparing the effects of nitrogen deposition on ecosystem carbon sequestration with unhealthy dietary habits and human disease. The deposition of N, a key nutrient for plant growth, may increase carbon sequestration (equivalent to obesity) through several mechanisms, including a reduction in the ability of soil microbes to process organic matter, which some argue could help mitigate climate change. However, this usually results in a degradation of ecosystem health and, thus, cannot represent a real solution. Similarly, human obesity is linked to an alteration of the composition and functioning of microbial communities inhabiting the gut, which is often attributed to unhealthy dietary habits, including ingesting high amounts of simple sugars and processed foods. Finally, I advocate for the explicit recognition of the many commonalities between the functioning of the gut and ecosystems and a broader multidisciplinary collaboration among experts in ecology and human health, including the engineering of soil microbial communities designed *ad-hoc* to restore ecosystem health.

Keywords: carbon sequestration, climate change mitigation, ecosystem health, human health, microbiome, nitrogen deposition, probiotics, synbiotics

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NITROGEN DEPOSITION AND CARBON SEQUESTRATION IN A CHANGING CLIMATE

It has been widely proposed that atmospheric nitrogen (N) deposition could help mitigate climate change by increasing the rates of carbon (C) sequestration in terrestrial ecosystems (Knorr et al., 2005; Reich et al., 2006; Yue et al., 2016). Two commonly observed responses are typically proposed as mechanisms: first, a greater amount of N usually implies a higher capacity for plant growth, which would result in a greater amount of C retained within the system (Magnani et al., 2007; de Vries et al., 2009; Laubhann et al., 2009). Of course, for this to be true, it is necessary that the increase in the rates of C uptake and accumulation exceed the C emission rates, whatever the main route by which the latter happens, including plant and/or microbial respiration and changes in fire dynamics due to an excess of biomass accumulation (Dezi et al., 2010; Fenn et al., 2010). The second main mechanism is linked to a reduction in decomposition rates, particularly of recalcitrant organic matter, which would, therefore, accumulate within the system (Knorr et al., 2005; Waldrop and Zak, 2006). Otherwise, this accumulated C may be lost to the atmosphere in the form of CO_2 after being respired by soil microorganisms (Janssens et al., 2010). Of course, the relative importance of these mechanisms depend on how plant communities and soil microorganisms respond, directly and indirectly, to the additional inputs of N which, in any case, usually ends up resulting in a disruption of the interaction between these two key components of the ecosystem (Liu et al., 2014).

THE NEED FOR A NEW PERSPECTIVE

In this article, I will adopt a human health perspective, hardly used in the discipline of global change ecology, to substantiate why atmospheric N deposition cannot represent a positive (i.e., healthy) alternative to mitigate climate change. In the medical literature, it is now widely recognized that human beings are like ecosystems (in fact, some consider us as living ecosystems) in which the eukaryotic cells that form part of our bodies and the prokaryotic cells that live in and on us are deeply interconnected, whereas the enormous importance of our microbiome to human health is also increasingly gaining acceptation (Bengmark, 1998; Berendsen et al., 2012; Ha et al., 2014; Alivisatos et al., 2015; Tilg and Adolph, 2015; Blaser, 2016; Blaser et al., 2016). The fact that many modern diseases, including conditions of the nervous and circulatory systems, skin and heart and allergies (including atopic dermatitis and food allergies), are directly caused by alterations in the microbial communities that live in our interior and exterior is also gaining rapid acceptation (Ha et al., 2014; Tilg and Adolph, 2015; Chang et al., 2016; Tang and Lodge, 2016). In this sense, the word ecosystem is widely used in the current literature of integrative medicine and gastroenterology. However, the opposite does not frequently happen in ecology [i.e., (cautiously) comparing ecosystems with the human body], despite the wealth of knowledge in the medical and human health literature that we, as ecologists, could apply in, for example, issues related to understanding the functioning (i.e., metabolism) of ecosystems and plant-soil-microbe interactions subjected to human pressure (Berendsen et al., 2012; Blaser et al., 2016; **Table 1**; **Figure 1**). Therefore, I will finally defend the need to approach problems in ecology from a more multidisciplinary, fresher perspective.

WHY NITROGEN DEPOSITION CANNOT BE THE SOLUTION TO CLIMATE CHANGE

The reason why I think that a temporary, N deposition-induced increase in the rate of C sequestration will not contribute to mitigating climate change in the long term is equivalent to the reason of those that argue that an increase in obesity rates in human populations derived from a diet rich in simple sugars and processed food and the consequent alteration of their microbiome will not successfully and permanently solve any public health problem of today's societies. Ingesting large amounts of simple sugars, processed foods, sugary drinks and saturated fats is definitely better than starving, but that does not mean that it is a healthy practice. And the same happens with N deposition and C sequestration. In ecosystems where N is still a limiting nutrient, which is quite common worldwide (LeBauer and Treseder, 2008), an increase in the availability of N can increase ecosystem productivity to levels comparable to human obesity (Tian et al., 2016), but that does not mean that the ecosystem is healthier and, therefore, that this will result in a long-term benefit (Bobbink et al., 2010; Jones et al., 2014). In this sense, a healthy ecosystem may be defined here as a highly multifunctional ecosystem that can maintain an adequate supply of services, at least as compared to a previously defined reference state.

In medicine, the term dysbiosis refers to changes in the composition of the microbiome that are not beneficial to the individuals, including a loss of abundance and diversity of beneficial microorganisms and increased number of pathogens, and that result in the development of a condition (Ha et al., 2014; Tilg and Adolph, 2015). This term could also be used to describe ecosystems that are dysfunctional due to alterations of their microbial communities. In this sense, it has been repeatedly shown through experimental studies and meta-analyses that increased N deposition is typically associated with changes in soil microbial communities (usually related to a decrease in abundance and biodiversity; Treseder, 2004, 2008; Ramirez et al., 2010; Zeng et al., 2015), reduced ecosystem functionality (alterations of energy metabolism; Waldrop and Zak, 2006; Treseder, 2008; Liu et al., 2014) and short- to mid-term increases in C sequestration, especially in aboveground biomass, but also in the soil and roots (comparable to obesity, as previously mentioned; Xia and Wan, 2008; Yue et al., 2016). Given that metabolic disorders and obesity in humans are clearly associated with a deterioration in the health status of individuals that may even result in cases of fatality due to chronic diseases, sudden death or, quite commonly in the natural world, to increased sensitivity to other environmental stresses (Mathur and Barlow, 2015; Monteiro et al., 2015), I think that we would do well to be cautious when we consider, perhaps naively, the potential benefits of a N that, after all, is the result of the atmospheric pollution derived from our activities (Gruber and Galloway, 2008).

THE "DECEPTIVELY SIMPLE" SOLUTION

The connections between human health, disease, and the microbiome, especially in the case of the gut, are becoming increasingly apparent and are attracting the public attention, especially because of the high social cost of unhealthy dietary habits and lifestyles and the "deceptively simple" solution of the problem (Mathur and Barlow, 2015; Tilg and Adolph, 2015; Blaser, 2016). In the case of both people and ecosystems, (i) ensuring a healthy supply of nutrients derived from the breakdown and cycling of unprocessed food/organic matter, (ii) minimizing the use of antibiotics (particularly those associated

TABLE 1 | Characteristics associated with healthy and unhealthy guts and ecosystems.

Characteristics associated with a healthy gut	Impacts associated with an unhealthy diet	References	Characteristics of healthy soils and ecosystems	Impacts associated with nitrogen deposition	References
Higher bacterial diversity and abundance that are able to metabolize more food sources and provide essential molecules such as vitamins, hormones, etc.	Functionally and compositionally impoverished gut communities	Thomas et al., 2014	Higher microbial diversity and abundance	Functionally and compositionally impoverished soil communities	Leff et al., 2015; Berg et al., 2017
Protection against disease through the stimulation of the immune system. More longevous individuals	Disease (obesity, diabetes, depression, inflammation etc.). People die younger	Berendsen et al., 2012; Ha et al., 2014; Thomas et al., 2014; Alivisatos et al., 2015; Tilg and Adolph, 2015; Xu et al., 2015; Blaser, 2016	Higher stability and resistance to disturbance	Die-back due to long-term N toxicity, altered fire regimes, pest outbreaks, less tolerance to frost, heat waves, etc.	Bobbink et al., 2010
Lean phenotype	Obese phenotype	Joyce and Gahan, 2014	Rapid processing, transformation and stabilization of litter inputs in the long-term soil pool	Accumulation of intact and partially decomposed leaf litter (i.e., carbon accumulation)	Knorr et al., 2005
High-energy feeling	Low-energy feeling	Umu et al., 2013	Higher ecosystem functionality and supply of key services such as air and water purification, food resources for pollinators, protections against extreme events such as floods, heat waves, etc.	Lower functionality and reduced supply of key services	Costanza et al., 1997; Jones et al., 2014
Well-trained immune system. No medication required. This is also associated with a smaller social cost	Weak immune system. Medication is very often required to treat diverse conditions. Development of drug-resistant strains. Higher social cost	Round and Mazmanian, 2009; Blaser, 2016	High ability to self-regenerate. No or very little management required. No extra cost involved	Management required, including applying herbicides, weeding, etc. High monetary cost	Costanza et al., 1997; Chiquoine et al., 2016
Higher Bacteroidetes to Firmicutes ratio	Lower Bacteroidetes to Firmicutes ratio	Mathur and Barlow, 2015	Higher fungal to bacterial biomass and activity ratio. Higher abundance and diversity of mutualistic mycorrhizal strains	Lower fungal to bacterial ratio. Less mutualistic mycorrhizal strains	Frey et al., 2004; Treseder, 2004; Waldrop et al., 2004; de Vries et al., 2006; Wallenstein et al., 2006

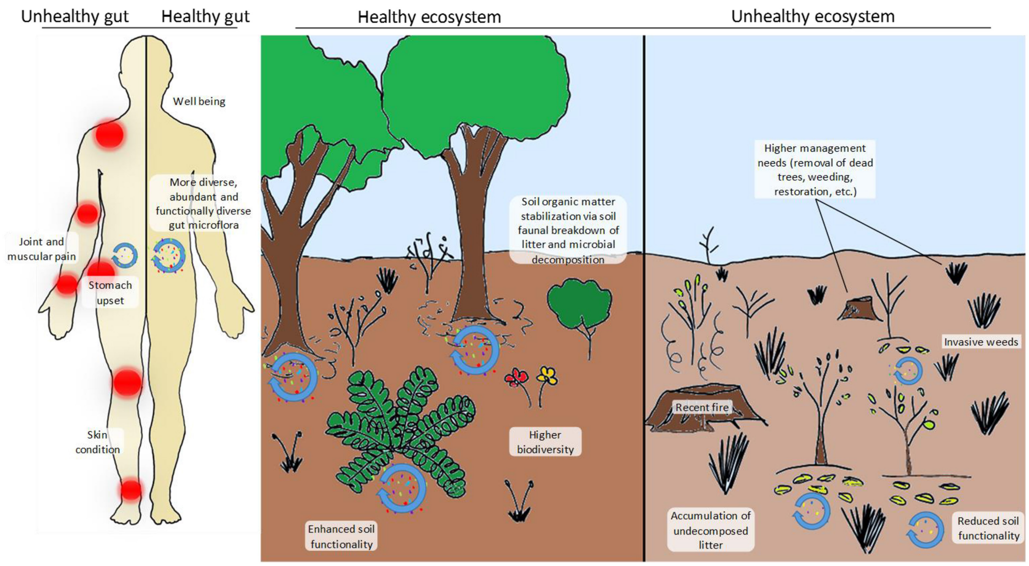

FIGURE 1 | Comparison between a healthy and an unhealthy gut (left-hand side panel) and a healthy and an unhealthy ecosystem (right-hand side panel). In the case of the human individual, his/her gut microbiota is less diverse ("red" microbes are completely absent), less abundant and contains more pathogenic taxa ("yellow" microbes). The individual with the healthy gut has a more functional and more abundant microbiota that provides him/her with essential nutrients, hormones, amino acids, etc. and stimulates his/her immune system. A healthy gut is also less prone to become infected by pathogens and can process toxic compounds (i.e., detoxify) more easily. The disturbed (i.e., unhealthy) ecosystem shown here has recently been affected by a devastating fire fuelled by the accumulation of N-loving exotic grasses that have altered the natural fire dynamics of the system. Facilitated by the altered fire dynamics, the system has also become chronically dominated by weedy grasses, therefore requiring intensive (and costly) management practices (dead tree removal, weeding and restoration), also posing a threat to nearby human populations and their properties. Biodiversity (in terms of microbial, faunal and plant communities) is remarkably higher in the healthy ecosystem, which also has a higher potential to process organic matter inputs and stabilize them in the long-term soil pool. In contrast, undecomposed or partially decomposed litter accumulates on the functionally impoverished soil of the unhealthy ecosystem. This pattern is in agreement with reported observations of higher soil carbon sequestration under increased nitrogen deposition scenarios due to the inhibition of soil enzymes and the reduction of microbial biomass but poses relevant questions such as: Is this type of N deposition-induced carbon sequestration desirable? And, does it really represent a long-term (or even short-term) solution?

with the livestock industry in the case of ecosystems; Park and Choi, 2008) and chemicals (including herbicides and pesticides in the case of ecosystems) that destroy the microbiome, unless this is strictly necessary, and (iii) promoting practices that favor the system's ability to self-regenerate, something that living systems do wonderfully well, and that increase its resilience against pathogens and extreme events could be part of the solution, if not all, of the problem.

Of course, there are opportunities to aid in the recovery of our damaged and degraded ecosystems as well as there are possibilities to recover the lost or damaged intestinal flora (Brudnak, 2002; Sheth et al., 2016). This can be achieved by the use of properly designed probiotics or fecal transplants or, in the case of ecosystems, inocula assembled in the lab from pure cultures or soil samples obtained in the field from healthy ecosystems (Bowker, 2007; Chiquoine et al., 2016; Wubs et al., 2016) in conjunction with a balanced nutrient supply (i.e., organic matter inputs, the equivalent to prebiotics; Mathur and Barlow, 2015; Sheth et al., 2016). In this sense, the concept of synbiotics (i.e., synchronous administration of probiotics and prebiotics) could represent a particularly promising benchmark borrowed from the human health literature to successfully restore degraded ecosystems (Tang and Lodge, 2016) and, thus, the human probiotics industry has an opportunity to play a key role in this development.

CONCLUDING REMARKS

Recognizing and understanding the similarities and deep connections between the gut and the belowground world, where roots are the equivalent to our gut and the rhizosphere is the gut microflora (Berendsen et al., 2012) can help us advance the understanding of ecosystems by leaps and bounds through the search of similar microbial indicators of disease (e.g., Bacteroidetes to Firmicutes ratio in humans; Mathur and Barlow, 2015) and, therefore, to implement quick and successful measures in ecosystem management rather than relying, perhaps naively, on that the very same thing that caused climate change (i.e., pollutant emissions to the atmosphere) will also be part of the solution. From here, I advocate for the development of a new field of research that specifically aims at recognizing and make practical use of the profound links between the functioning of the gut and the ecosystems that extend beyond our bodies and that benefits from a truly multidisciplinary collaboration among experts in the areas of global change ecology and human health.

AUTHOR CONTRIBUTIONS

The author confirms being the sole contributor of this work and approved it for publication.

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