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Nutrient limitation of soil microbial processes in tropical forests

TESSA CAMENZIND,[1,2,5] STEPHAN HÄTTENSCHWILER,[3] KATHLEEN K. TRESEDER,[4] ANIKA LEHMANN,[1,2]
AND MATTHIAS C. RILLIG[1,2]

[1] *Institute of Biology, Freie Universität Berlin, Altensteinstr. 6, 14195 Berlin, Germany*
[2] *Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), 14195 Berlin, Germany*
[3] *Centre d'Ecologie Fonctionnelle et Evolutive (CEFE), UMR 5175, CNRS, Université de Montpellier, Université Paul-Valéry Montpellier, EPHE, 1919 route de Mende, 34293 Montpellier Cedex 5, France*
[4] *School of Biological Sciences, University of California, Irvine, California 92697 USA*

Abstract. Soil fungi and bacteria are the key players in the transformation and processing of carbon and nutrients in terrestrial ecosystems, yet controls on their abundance and activity are not well understood. Based on stoichiometric principles, soil microbial processes are expected to be limited by mineral nutrients, which are particularly scarce in often highly weathered tropical forest soils. Such limitation is directly relevant for the fate of soil carbon and global element cycles, but its extent and nature have never been assessed systematically across the tropical biome. Here, we address the relative importance of nitrogen, phosphorus, and other nutrients in limiting soil microbial biomass and process rates in tropical forests. We conducted an in-depth literature review and a meta-analysis of the available nutrient addition experiments in tropical forests worldwide. Our synthesis showed predominant and general phosphorus limitation of a variety of microbial processes across tropical forests, and additional nitrogen limitation in tropical montane forests. The apparent widespread microbial phosphorus limitation needs to be accounted for in the understanding and prediction of biogeochemical cycles in tropical forests and their future functioning. Other mineral nutrients or carbon may modify the importance of phosphorus, but more experimental studies are urgently needed.

Key words: meta-analysis; mineral elements; nitrogen; nutrient limitations; phosphorus; soil microbes; tropical forests.

INTRODUCTION

Soils are a key component of the global carbon (C) cycle because they represent the major terrestrial pool of organic carbon (C; Post et al. 1982, Jobbagy and Jackson 2000). Contrary to previous ideas, environmental and biological factors more strongly control soil C dynamics than do the molecular structure of soil C compounds and soil physical parameters (Ryan and Law 2005, Davidson and Janssens 2006, Schmidt et al. 2011). This paradigm shift emphasizes the need to understand how environmental conditions and soil microbes interact to affect soil C dynamics. Such understanding is particularly important in the face of ongoing changes in climate and biological diversity. In particular, it can help improve model predictions of future soil C storage and release in response to these changes (Pansu et al. 2010, Townsend et al. 2011, Bonan et al. 2013).

Microorganisms have an important role in ecosystem processes in general, and the C cycle in particular (Tiedje et al. 1999, Nannipieri et al. 2003, Bardgett and van der Putten 2014). Soil fungi and bacteria represent an astounding diversity of biochemical capacities for the breakdown of organic compounds, which makes them a key component in soil processes and ecosystem functioning (Bardgett et al. 2008, Wall et al. 2012). Free-living heterotrophic microorganisms as well as plant mutualists (e.g., mycorrhizal fungi, N-fixing bacteria) drive C dynamics, nutrient mining from mineral soil, nutrient transformations and mineralization, and greenhouse gas emissions from soils (Potter et al. 1996, van der Heijden 2008, Trivedi et al. 2016).

Microorganisms are often discussed as being primarily limited by C availability (Demoling et al. 2007, Kamble and Baath 2014), and yet the bodies of all soil microorganisms share the characteristic of narrower nutrient to C ratios compared to that of their plant-derived resources (Cleveland and Liptzin 2007, Manzoni et al. 2010, Mooshammer et al. 2014). The microbial community as a whole can adjust its stoichiometry, to a certain

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[5] E-mail: tessac@zedat.fu-berlin.de

degree, toward that of plant resources (Fanin et al. 2013). Even so, stoichiometric constraints may lead to nutrient limitation by nitrogen (N), phosphorus (P), or other nutrients (Elser et al. 2007, Kaspari and Yanoviak 2009, Townsend and Asner 2013, Kaspari and Powers 2016). Because soil microorganisms can take up these nutrients from soil, the extent of nutrient limitation depends on soil fertility. Nutrients such as P, potassium (K), calcium (Ca), or magnesium (Mg) decrease steadily with ongoing rock weathering and soil development (Walker and Syers 1976, Vitousek and Sanford 1986). Nitrogen is an exception, since it is largely absent in parent rock and tends to accumulate over time via biological N fixation and atmospheric deposition (Gorham et al. 1979, Vitousek and Farrington 1997). Tropical ecosystems harbor some of the oldest and most nutrient impoverished soils. In particular, biologically available P can be extremely scarce in these old tropical soils, because P tends to diminish over time by depletion, runoff and occlusion (Walker and Syers 1976, Dalling et al. 2016) and is not readily accessible to plants and microbes. Soil P depletion with soil development has been documented along the Long Substrate Age Gradient in Hawaii (Crews et al. 1995, Chadwick et al. 1999), and substantial differences in soil P concentrations depending on soil age occur across the Amazon basin (Quesada et al. 2010). Global trends in leaf stoichiometry also suggest that P limitation of plant growth is greater at lower latitudes (McGroddy et al. 2004, Reich and Oleksyn 2004). Phosphorus limitation is thought to be particularly relevant in lowland tropical forests, since theory predicts a negative correlation of soil age with elevation (Walker and Syers 1976). This elevational pattern was partly confirmed from plant growth responses to experimental nutrient additions (Tanner et al. 1998, Homeier et al. 2012, Fisher et al. 2013), though other factors like topography or bedrock properties are also important (Quesada et al. 2010, Werner and Homeier 2015). Together, these lines of evidence suggest that P can be a limiting resource in tropical soils for autotrophs and heterotrophs alike. The role of other mineral, often rock-derived elements, which are depleted in old soils, has received less attention so far. Interestingly, recent experimental studies in tropical forests suggest limitation by elements other than N and P for certain ecosystem processes (Barron et al. 2009, Wright et al. 2011, Kaspari and Powers 2016), challenging the traditional view of N- vs. P-limitations explaining ecosystem productivity (Elser et al. 2007).

Soil microbial communities play key roles in ecosystem functioning, especially because microbe-mediated mineralization of organic material contributes a large part of available nutrients for plant growth (Brearley et al. 2003, Cleveland et al. 2013) and they help reduce nutrient losses from ecosystems through leaching or occlusion by permanent binding in geochemical sinks (e.g., aluminum or iron oxides; see Olander and Vitousek 2004, De Araujo et al. 2015). As such, the microbial nutrient pool is important due to its comparatively high turnover rate, which increases the probability of plant uptake (Schimel and Bennett 2004). A growing number of studies focusing on topics related to soil microorganisms and their relation to nutrient availability in the tropics (Fig. 1) demonstrate an increasing awareness of the key role of soil microorganisms in the functioning of ecosystems and the provision of ecosystem services. However, a synthetic assessment of the available data and their integration into a general conceptual framework of microbial nutrient limitations is currently missing. We set out to achieve this here by summarizing the available studies on microbial nutrient limitations in tropical forest soils, and we carried out a meta-analysis on the consequences of experimental N and P additions on microbially driven processes in tropical forests. This is a complex subject to tackle due to multiple nutritional constraints on microorganisms, the important heterogeneity in geology, climatic conditions, and other environmental aspects of tropical ecosystems, and due to the tremendous phylogenetic and functional diversity of microorganisms. Nevertheless, and despite the varying methodologies used in the studies reviewed

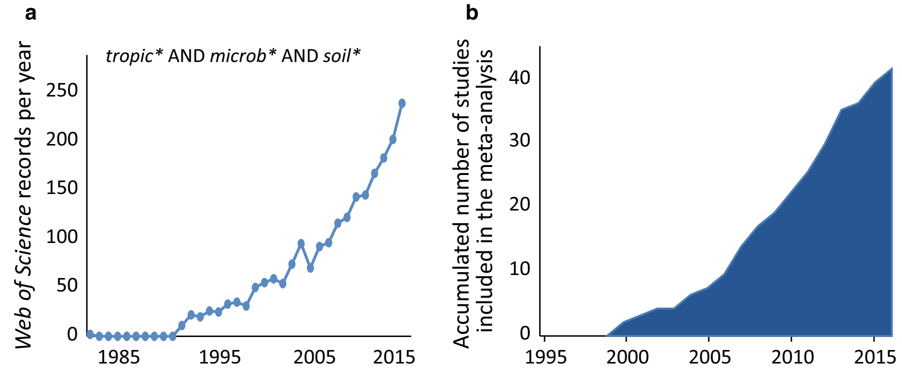

Fig. 1. Overview of publication records in the last decades on the topic of soil microorganisms in tropical systems. In (a), the number of hits in a *Web of Science* search string are displayed; (b) displays the cumulative number of studies sorted by year, which report on responses of microbial abundance or processes in tropical forest soils in response to N and P additions (as included in the meta-analysis).

here, our synthesis reveals clear evidence of a fundamental importance of P limitation in many tropical systems, but also shows that some other frequently neglected mineral elements may have a role in soil microbial processes in the tropics.

CURRENT EVIDENCE FOR P LIMITATION AT LOWER LATITUDES

A growing body of literature compares nutrient dynamics among different biomes as part of global reviews or meta-analyses, especially using simple elemental stoichiometry (Elser et al. 1996), so far mainly focusing on N and P. Although not all of these studies show a clear latitudinal pattern (Vergutz et al. 2012, Ostertag and DiManno 2016), potentially related to heterogeneity within biomes (Townsend et al. 2008, Vergutz et al. 2012, Ostertag and DiManno 2016), they provide strong evidence of P limitation of plant growth in tropical regions. For example, Sardans et al. (2012) describe a general increase in soil and plant N:P ratios from high-latitude boreal and temperate ecosystems towards tropical ecosystems. Likewise, observations of foliage and litter C:N:P ratios at large spatial scales indicate a shift from N- to P-limitation of plant growth from high to low latitudes (Aerts 1997, McGroddy et al. 2004, Reich and Oleksyn 2004). In line with this, foliar nutrient resorption in tropical trees provides striking evidence of plant P limitation in tropical forests (Hättenschwiler et al. 2008, Yuan and Chen 2009, Reed et al. 2012). These observations are further supported by the results of N and P nutrient manipulation experiments and their consequences for net primary productivity (Tanner et al. 1998, LeBauer and Treseder 2008, Li et al. 2016, Sayer and Banin 2016).

Similar to the large-scale comparisons of plant leaf stoichiometry, Cleveland and Liptzin (2007) summarized data on microbial stoichiometry at the global scale. They showed highly constrained soil and microbial C:N:P ratios in general, and, based on the N:P ratios reported in the few studies from the tropics, evidence of microbial P limitation in the tropics in particular. Li et al. (2014) also showed higher microbial N:P ratios at lower latitudes in a global analysis. In combination with high litter and mineralization N:P ratios (the average N:P released from decomposing substrates) found in tropical areas, Marklein et al. (2016) and Cleveland et al. (2013) argue for an increased P demand of microbial decomposers. Likewise, nutrient release patterns and immobilization dynamics in a litterbag experiment covering different biomes indicated that decomposers in tropical regions tended to be more P limited compared to other biomes (Manzoni et al. 2010). Because enzymes released by the soil microbial community reflect elements for which microbes currently forage, the stoichiometry of enzyme activity provides a good indicator for relative microbial limitation. Indeed, global comparisons of soil enzyme stoichiometry suggest increasing P limitation with decreasing latitude (Sinsabaugh et al. 2008, Waring et al. 2014).

These global comparisons among different biomes reveal general trends and patterns, but it should be noted that there is substantial heterogeneity in soil types and fertility within the tropics and that not all tropical soils are systematically poor in P (Kitayama et al. 2004, Cleveland et al. 2006, Quesada et al. 2010). Still, a meta-analysis across 113 tropical sites covering a wide range of soil types and fertility by Cleveland et al. (2011) reports positive effects of soil P availability on net primary productivity, but also on decomposition and soil respiration rates. Another study across different lowland tropical forest sites showed a negative correlation of litter P concentration with the thickness of the litter layer suggesting higher decomposition rates with higher litter P concentrations (Kaspari and Yanoviak 2008). On the other hand, the meta-analysis on factors controlling leaf litter decomposition in tropical forests conducted by Waring (2012) reported a large amount of unexplained variation and only little impact of litter nutrient concentrations on decomposition; this was possibly due to other factors such as soil fauna and secondary metabolites not accounted for in her analysis. Indeed, leaf litter decomposition in a lowland tropical forest of French Guiana was driven by larger soil fauna and correlated well with condensed tannin but not with P concentrations despite very low soil P concentrations (Coq et al. 2010).

Collectively, the accumulated evidence over the last 10 years from large-scale analyses suggest that tropical ecosystems are generally more P limited than ecosystems at higher latitudes, although there is considerable heterogeneity within the tropics that should not be neglected. Phosphorus limitation appears to transcend different trophic levels and affects plants as well as soil microorganisms.

EFFECTS OF EXPERIMENTAL N AND P ADDITIONS ON SOIL MICROBIAL ABUNDANCE AND PROCESS RATES: A META-ANALYSIS

Stoichiometric patterns as well as correlations among nutrient contents and ecosystem processes give valuable insights into potential element restrictions of organismal growth and activity (Cleveland et al. 2011, Kaspari 2012). However, "limitation by a nutrient is shown if the rate of an ecosystem process is increased by addition of that nutrient, and strictly speaking it can only be determined experimentally" (Tanner et al. 1998, Sayer and Banin 2016). Therefore, we conducted an in-depth literature search (for details, see Appendix S1) to collect studies that evaluated the effects of nutrient additions on soil microbial abundance and/or microbe-driven process rates in tropical forests across the globe. Studies presenting results of experimental nutrient additions for at least one microbial response variable that were conducted in soils of undisturbed tropical forests were included. We considered both, field experiments and experiments under controlled laboratory conditions as long as the latter used soil from undisturbed tropical forests. With these selection criteria we found a total of 42 studies on the impacts of N and P additions from 34 different study sites (Figs. 1, 2; Appendix S1: Table S1), analyzing microbial response variables of eight distinct response categories (soil microbial biomass, soil microbial respiration, decomposition, free-living N-fixation, N mineralization, net nitrification, soil methane uptake, and P immobilization). However, there were not enough studies evaluating microbial responses to additions of individual elements other than N or P to run a meta-analysis, and we refer to those studies separately below. Details of the meta-analysis, including search terms, data extraction, minimization and control for publication/plot bias, detailed statistical methods and graphical illustrations are given in Appendix S1. Briefly, results are based on a random-effects meta-analysis using the package metafor (Viechtbauer 2010) in R version 3.1.2. (R Core Team 2014). Effects of tested moderators were analyzed by omnibus tests of model coefficients (Viechtbauer 2010).

The studies included here cover the neotropical region quite well (Fig. 2), whereas only few areas of the paleotropics were included. In addition, those latter studies were concentrated in one research area in southeastern China (Chen et al. 2016*a*) and one site in Borneo (Kitayama et al. 2004). Afrotropical studies found with our search string only included disturbed or agriculturally used sites (e.g., Ilstedt and Singh 2005, Teklay et al. 2006). Some study sites featured in the data set several times (Fig. 2), but for different response variables, methodologies or time points. These long-term multidisciplinary experiments (e.g., Vitousek and Farrington 1997, Wright et al. 2011, Liu et al. 2013) represent an important source of data for this review, and the risk of disproportionate influence of these experimental plots was controlled by sensitivity analyses, which were not only conducted for separate study IDs, but also for plot IDs when applicable (Appendix S1: Figs. S1–S5; Andrade-Linares et al. 2016, Zheng et al. 2016).

Overall, P additions had a significantly positive effect on soil microbial abundance and activity, N additions had neutral effects, whereas the concurrent application of N and P also resulted in positive responses. These findings support the hypothesis that P is the main limiting element in tropical forests (Walker and Syers 1976, Vitousek 1984). The results are also in line with the generally high P demand for high ribosome densities in microbial biomass (Elser et al. 1996, Hartman and Richardson 2013), explaining the positive effects of P on soil microbial activity also reported in some cases from other biomes (Sundareshwar et al. 2003, Craine et al. 2007, Su et al. 2015). The combined N and P additions showed fairly similar effect sizes to the addition of P alone (Fig. 3), indicating that P alone drives the response with no apparent evidence of N and P co-limitation. However, in some individual studies a combined addition of P and N showed stronger effects than just P additions (e.g., Vitousek and Hobbie 2000*b*, Reed et al. 2011, Fanin et al. 2016). By contrast, responses to N additions were overall neutral, but also negative in the case of lowland forests (Fig. 3) and for certain response variables (Fig. 5). In extratropical biomes, N additions have previously been observed to stimulate microbial processes in a few cases (e.g., Hu et al. 2001, Sistla et al. 2012), but negative effects of N addition are more frequent (Treseder 2008, Kamble et al. 2013, Zhou et al. 2014). Toxic effects have been discussed as the main reason for the negative effects of N addition, for example by changing the osmotic potential (Broadbent 1965), decreasing the pH (Kaspari et al. 2008, Kamble et al. 2013) or by the formation of more recalcitrant compounds (Treseder 2008).

In contrast to the negative effects observed in lowland forests (<1,000 m above sea level), N additions had

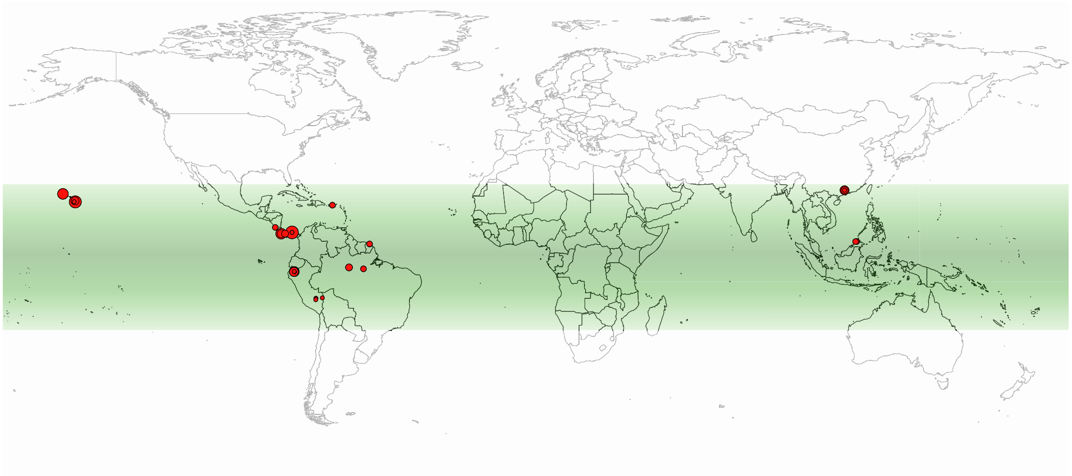

Fig. 2. Map of study sites included in the meta-analysis. Dot sizes relate to the number of experiments included per site (see Appendix S1: Methodological descriptions and Table S1). Green marked areas display the tropical region.

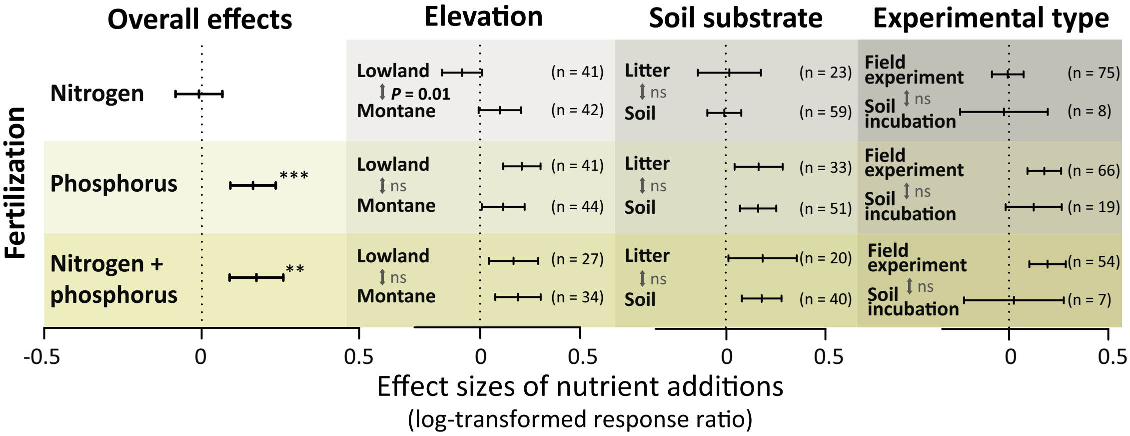

FIG. 3. Responses of soil microbial abundances and process rates to nitrogen (N) and phosphorus (P) additions. The effects of tested moderators, elevation, soil substrate, and experimental type are also evaluated. Bars represent the mean estimates given by random effects meta-analysis, as well as lower and upper boundaries of the respective 95% confidence intervals. Asterisks indicate significant deviations of effect sizes from zero (**$P < 0.01$, ***$P < 0.001$).

positive effects in montane sites (>1,000 m above sea level; Fig. 3). This result is in line with theory predicting that P should be in low supply in highly weathered lowland forests, whereas N should be limiting in younger soils of montane sites (Walker and Syers 1976, Tanner et al. 1998, Hedin et al. 2009). This categorization is quite coarse, since elevation does not consistently correlate with soil age (Vitousek and Farrington 1997, Wolf et al. 2011) and topographic patterns and small-scale heterogeneity may play a predominant role (Hättenschwiler et al. 2008, Brechet et al. 2009, Werner and Homeier 2015). Nonetheless, the pattern across the different study sites covered in our analysis is clear (Fig. 3). In addition, linear correlations between effect sizes and the elevation of study sites support the increasingly positive N effect with elevation (Fig. 4), which is in line with stoichiometric shifts in microbial enzymatic activity along an altitudinal gradient in Peru (Nottingham et al. 2015). In contrast to the clear distinction of microbial responses to N addition between lowland and montane tropical forests, there was only a (non-significant) trend for different responses to P addition (Figs. 3, 4). We would have expected a clearer difference of more positive P effects in lowland than in montane tropical forests because of the predicted stronger P limitation in older soils. Elevation is not entirely equivalent to soil age, thus, using soil age as a category in our analyses might yield clearer results. Since soil age data were rarely provided in the studies, we tried to run our models with other soil variables instead, but did not find a correlation between effect sizes of nutrient additions and total soil P concentration, nor with any other of the investigated soil parameters (N:P and C:N ratio, pH, see Appendix S1: Table S2). Potentially, available data on total soil element concentrations given on a soil weight basis do not sufficiently reflect nutrient deficiency at the sites and more specific predictor variables will be needed in future studies (e.g., consistently measured plant-available P data or nutrient levels on an area basis).

We also evaluated potential differences in the results from soil vs. litter measurements and field vs. lab studies, but we found no effects (Fig. 3). Resource stoichiometry and the structure of microbial communities differ quite substantially between soil and leaf litter (Fanin et al. 2012, Smith et al. 2015), with differential responses to nutrient additions expected (Fanin et al. 2012). Nevertheless, across the entire data set evaluated here, the relative limitations by N and P on microbial processes were similar in soil and litter, which may be explained by the fact that plant litter stoichiometry mirrors the available soil nutrient pool (Werner and Homeier 2015, Marklein et al. 2016). Concerning experimental setups, incubation experiments with isolated soils may better deal with potentially confounding indirect effects in field settings, such as changes in plant litter traits (Vitousek and Hobbie 2000*b*, Sayer et al. 2012), and may more accurately represent the immediate microbial response to nutrient additions. Thus, despite a comparatively small number of lab experiments, the fact that they show similar positive microbial responses to P additions under more controlled conditions strengthens our finding of microbial P limitation.

While allowing a general assessment of the effects of N and P additions on soil microbial parameters, pooling the different microbial response variables into a single effect size may hide important information about the heterogeneity of soil microbial nutrient limitations among functional groups. In total there were eight categories of soil microbial abundance and process rates that were measured in the studies included (Fig. 5; Appendix S1: Table S1). The high variability of soil microbial functioning must be considered in the discussion of microbial nutrient limitations (van der Heijden 2008), since certain processes are mediated by only a small subset of microbes in soil and may not reflect the

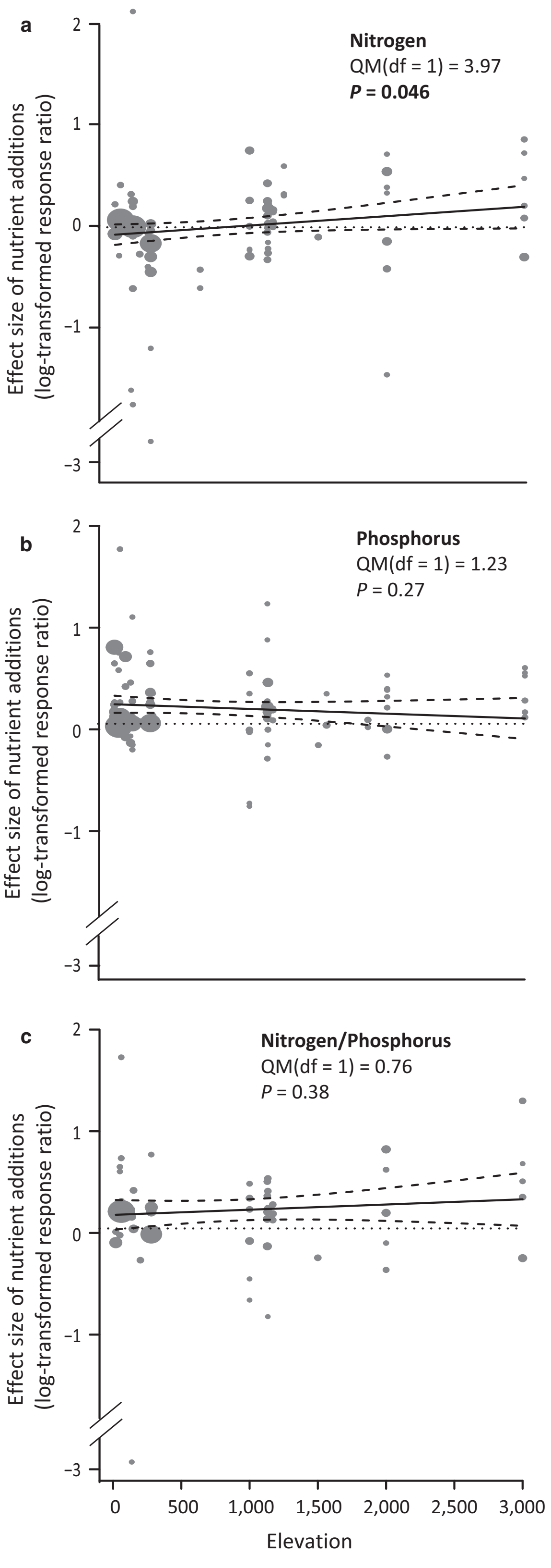

FIG. 4. Correlation of effect sizes (of soil microbial abundances and activity in response to nutrient additions) with elevation for (a) nitrogen, (b) phosphorus, and (c) the addition of both nutrients are displayed. Solid lines indicate mean estimates, respective dashed lines 95% confidence intervals. Dot sizes relate to weights (inverse of effect size variance). Test statistics of the moderator Altitude are given by QM (test statistic for the Wald-type test of model coefficients) and corresponding *P* values.

response of the entire soil microbial community (Moore et al. 2005, Bardgett and van der Putten 2014). Interestingly, the different microbial parameters showed consistently positive responses to P additions with no significant deviations among effect sizes of single variables (Fig. 5). In contrast, responses to N additions differed significantly in their direction with some negative and some positive effects (Fig. 5), resulting in overall neutral responses (Figs. 3, 5). The consistent responses of several microbial process rates and also of microbial biomass to P additions suggest a general P limitation in tropical forests across highly diverse soil microbial communities and various processes they drive. On the other hand, responses to N additions clearly depended on the specific microbial response variable (Fig. 5). The rather broad parameters such as biomass, respiration and litter decomposition, to which the majority of microorganisms contribute, showed overall neutral effects, shifting to more positive responses in montane sites (data not shown). By contrast, analyses of the more specific N-cycling processes resulted in effect sizes that differed from zero. The negative effects on free-living N fixation may indicate a decrease in competitive advantages of N-fixing organisms due to increased inorganic N supply (Matson et al. 2015). The responses of soil N mineralization and nitrification rates to inorganic N inputs are quite complex and require individual interpretations based on associated parameters, e.g., the type of N fertilizer added, responses of net primary production and associated N sinks and further variables important for N cycling (Zak et al. 1990, Silver et al. 2001, Houlton et al. 2006). These partly divergent microbial responses to N additions, also depending on concurrent P limitations, may result in highly complex and barely predictable shifts in nutrient cycles in response to increased N deposition in the future, a topic that needs to be addressed by specific experimental and modelling approaches (Phoenix et al. 2006, Wieder et al. 2015).

Differences in experimental approaches and methodology may also account for variability within the data set. For example, at the Barro Colorado Island research site in Panama, where several studies were conducted (Appendix S1: Table S1), Kaspari et al. (2008) and Milton and Kaspari (2007) reported different P effects on cellulose decomposition depending on how P was added. Cellulose decomposition was enhanced with regular and

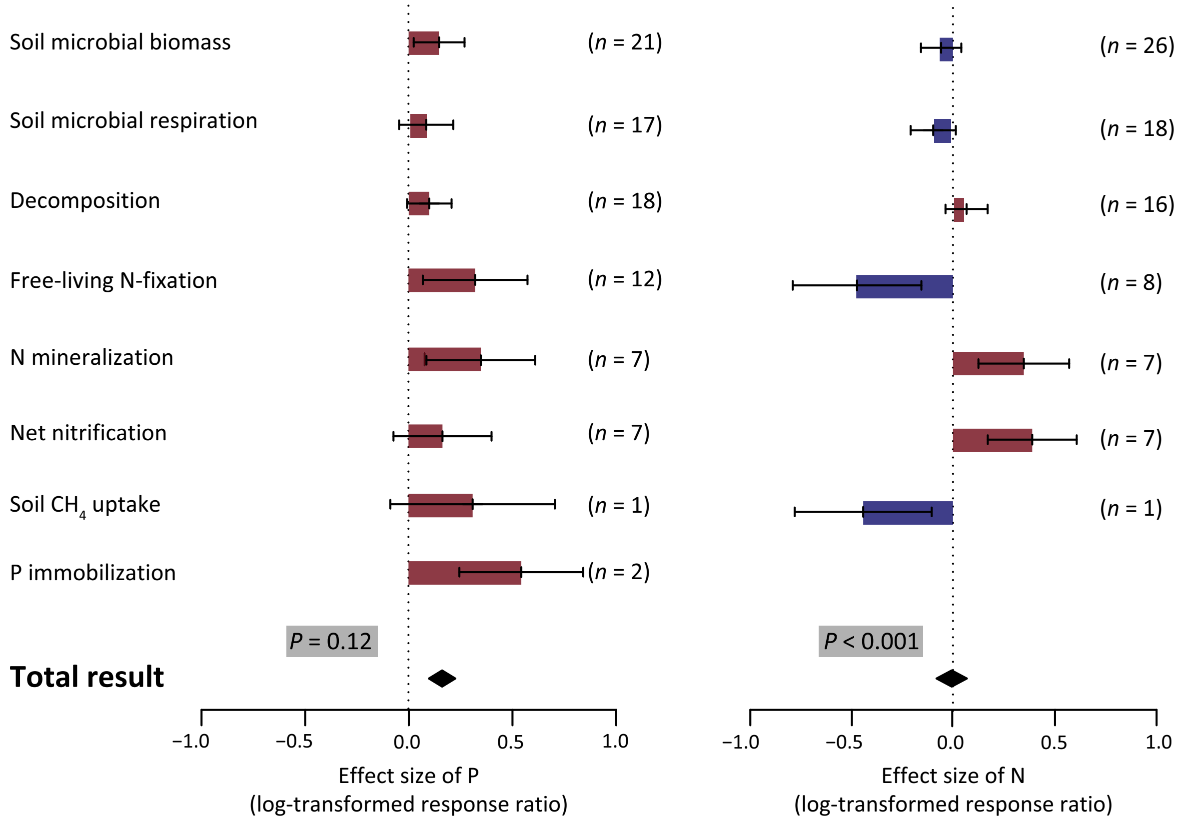

FIG. 5. Responses of different soil microbial response variables to phosphorus (P) and nitrogen (N) additions. Bars illustrate the mean estimate given by meta-analysis, error bars the respective 95% confidence intervals, positive responses are indicated by red, negative ones by blue color; effect sizes are significantly positive or negative if their 95% confidence intervals do not overlap the zero line (dashed line). The number of respective trials are indicated in brackets. *P* values represent differences between soil microbial response variables. They result from statistical tests of the moderator "response category" analyzed by omnibus tests of model coefficients; *P* values < 0.05 are significant.

constant P fertilization in the long term (Kaspari et al. 2008), whereas short-term nutrient pulses did not have any effects (Milton and Kaspari 2007). Also, the way a particular response variable is measured and analyzed can change the results: When microbial biomass measurements were integrated over an entire season (Turner and Wright 2014), the results differed compared to a single one-time sampling at the same site (Sayer et al. 2012), which is also relevant since seasonality represents an important factor shown to influence microbial responses to nutrient additions (Cleveland et al. 2004, Cleveland and Townsend 2006). Additionally, their sampling was conducted after two more years of nutrient applications. However, when we specifically considered these differences in experimental protocols in our analyses we did not observe any significant relation of effect sizes with experimental type, experimental duration or the amount of fertilizer added (Fig. 3; Appendix S1: Figs. S6, S7).

The element itself and the form in which it is applied likewise have important impacts on observed results, and direct comparisons among elements need to be done cautiously (Sayer and Banin 2016). Conceptually, nutrient limitation is referred to when there are apparent microbial demands for the added element (Tanner et al. 1998). However, the addition of N can also affect other soil properties beyond its availability, especially by soil acidification and associated changes (Chen et al. 2015, Riggs and Hobbie 2016) as also reported in some studies included in our meta-analysis (e.g., Corre et al. 2010, Cusack et al. 2010, Chen et al. 2016*a*). Such detrimental side effects on soil microbial activity may mask microbial N limitations. By contrast, only neutral or positive but no negative effects following P additions were reported in this data set. Additionally, the fate of N is very different from that of P once added to the soil, since N may be rapidly lost through leaching and gaseous emissions (Hall and Matson 1999, Corre et al. 2010, Velescu et al. 2016), whereas P will be less available by geochemical sorption, though kept in the system for longer periods (Olander and Vitousek 2004). These differential effects must be considered in the interpretation of nutrient manipulation experiments, also in light of shifts in stoichiometric ratios by the addition of multiple elements (Cleveland and Liptzin 2007, Kaspari 2012).

In summary, with our meta-analysis of N and P addition experiments in tropical forests, we provide the first quantitative synthesis of soil microbial responses that strongly suggests a general microbial P limitation. Experimental P additions consistently caused significant positive effects on a range of different soil microbial parameters in lowland and montane sites. At higher elevations, there was also an indication for N limitation, since we observed a switch from negative to positive N effects from lowland to montane tropical forests, supporting theoretical predictions of elevation-associated differences in soil age. Nevertheless, it is important to note that the interpretation of N addition effects may be influenced by concurrent chemical changes in soils following fertilizer inputs, which potentially counteract stimulating N effects on microbial activities and growth.

Tropical Soils as a Non-Liebig World

The agricultural concept of Liebig's law of the minimum predicts that plant productivity is limited by a single element, a concept that has been extended to other organismic groups and ecosystem processes. However, a growing body of literature reports that the levels of limitation by several elements are so close together that in reality most ecosystems are co-limited by two or more elements (Elser et al. 2007), and that relative limitation changes dynamically at short temporal scales (Fanin et al. 2016). Moreover, in the physically and chemically heterogeneous soil matrix that provides a multitude of microhabitats for a functionally diverse microbial community, the limiting elements may differ at very small spatial scales resulting in co-limitation by two or more elements at larger spatial scales (Townsend and Asner 2013, Fanin et al. 2015, Kaspari and Powers 2016). Accordingly, while P was the single most important factor in our meta-analysis, N also increased microbial process rates in montane tropical forests, which suggests P and N co-limitation. Furthermore, although N and P have been reported as the main limiting elements in ecosystems worldwide (Elser et al. 2007, Harpole et al. 2011), other nutrients may play an important role especially in tropical regions (Kaspari et al. 2009, Wright et al. 2011, Wullaert et al. 2013).

Only few studies evaluated the effects of nutrients other than N and P. These include some long-term experiments, where a mixture of different micronutrients was added as an additional treatment (Hawaii K, Ca, Mg, S, Fe, Mo [Vitousek and Hobbie 2000*a*]; Panama Ca, Mg, S, Fe, Mo, Cu, B, Mn, Zn [Barron et al. 2009]; French Guiana K, Ca, Mg, S, Fe, Mo, Cu, B, Mn, Zn [Barantal et al. 2012, Fanin et al. 2012]), making it impossible to assign potential effects to a particular element. These studies reported positive and negative effects of micronutrients on litter decomposition in Panama (Kaspari et al. 2008) and in French Guiana (Barantal et al. 2012), respectively, and negative effects on soil microbial activity in French Guiana (Fanin et al. 2012). Free-living N_2 fixation was stimulated by micronutrients in Panama as well as in Hawaii (Vitousek and Hobbie 2000*a*, Barron et al. 2009). Interestingly, Barron et al. (2009) conducted a follow-up experiment to isolate the specific micronutrient driving this response, and they identified it to be molybdenum (Mo), a key component of the nitrogenase enzyme, an element that also typically occurs at very low concentrations in weathered old tropical soils. Implementing a separate Mo fertilization experiment they were able to show that Mo added alone resulted in increased nitrogenase acetylene reduction activity, and even provided evidence that observed positive effects by P additions were related to Mo traces found in the applied P fertilizer. Wurzburger et al. (2012) and Reed et al. (2013) also reported positive Mo effects in interaction with P on free-living N_2 fixation.

Other studies reported variable effects of different nutrients on different soil processes, which might be specific for particular sites with conspicuous soil types and soil chemistry. For example, Powers and Salute (2011) reported that P and zinc (Zn) fertilization stimulated decomposition, possibly because Zn represents an important co-factor in microbial enzymes (Wackett et al. 2004). Kaspari et al. (2008) found that K limits cellulose decomposition and Luizao et al. (2007) showed evidence of positive S and K effects on soil microbial respiration rates. Correlating leaf litter nutrient contents with corresponding decomposition rates may provide further evidence, e.g., in the studies by Santiago (2010) and Waring (2012) who revealed a potential impact of Ca, Mg, and K.

Tropical forests with highly weathered soils and that are far away from the coastline may also face sodium (Na) shortage as proposed in the sodium ecosystem respiration hypothesis (Kaspari et al. 2014). However, Na limitation is particularly important for soil animals (Kaspari et al. 2009, 2014, Clay et al. 2015, Jia et al. 2015), whereas microorganisms may be less affected. In a decomposition experiment manipulating fauna access experimentally by using litterbags with either 5 or 0.2 mm mesh, decomposition was only enhanced by Na additions in the presence of fauna (Jia et al. 2015). Similarly, microbial respiration and fungal abundance in litter did not respond to Na additions (T. Camenzind et al., *unpublished data*).

Besides the impact of the availability of macro- and micronutrients, soil conditions like pH (Pansu et al. 2010), O_2 availability (Liptzin et al. 2011, Hall et al. 2015), and moisture conditions (Yavitt et al. 2004, Turner and Wright 2014) play an important role, which altogether results in a complex interplay of site-specific soil factors regulating microbial processes. Given this complexity, the clear effect of P addition detected here across very different tropical forest ecosystems is even more striking and supports the generality of P limitation despite very different environmental conditions and soil types. Still, the importance of other elements as (co-) limiting factors cannot be assessed at the moment due to a lack of experimental evidence. More specific approaches designed to evaluate the effects and interactions of other elements are strongly needed ("embracing all twenty-five elements required to build an organism," Kaspari and Powers 2016).

The Role of Carbon Availability

In general, soil microbes are discussed in the literature as being primarily limited by C availability (Ekblad and Nordgren 2002, Demoling et al. 2007, Kamble and Baath 2014), though few authors claim the direct limitation of other elements than C based on experimental results (Hu et al. 2001, Cleveland et al. 2002, Kaspari and Yanoviak 2008, Chen et al. 2016*b*). Unlike nutrients, C is overabundant in essentially all soils of the different tropical forest ecosystems discussed here, with C:nutrient ratios largely exceeding those of soil microbial biomass (Cleveland and Liptzin 2007). This stoichiometric mismatch between soil organic matter (SOM) and microbial biomass is commonly interpreted in favor of predominating nutrient over C limitation in microbial heterotrophs (Cherif and Loreau 2007, Manzoni et al. 2010, Mooshammer et al. 2014). However, soil C is a highly heterogeneous pool of a vast diversity of different C compounds, and only a very small fraction of this C is readily accessible for microorganisms. This could lead to a limitation of soil microbial growth by C (energy) despite the large total quantity of C (Ekblad and Nordgren 2002, Demoling et al. 2007, Kamble and Baath 2014). Experimental tests of the relative importance of C vs. nutrient limitation are difficult to design, simply because there is no straightforward way to manipulate C availability. Microbial responses depend strongly on the kind of organic C compounds added to the soil and may differ among groups of microorganisms (Schutter and Dick 2001).

There are a few tropical studies that have attempted to manipulate C availability along with nutrient additions. For example, Cleveland et al. (2002) added glucose and P alone or in combination to a range of soils from Costa Rica that differed in background P availability. Glucose always increased microbial respiration, whereas P alone had no or small effects. However, the glucose effect strongly increased with a simultaneous P addition in soils with low P concentration, but not in those with already a comparatively high P concentration. These results suggest that C is the primary limiting resource for microbial activity. Such immediate responses to glucose are not surprising and increased respiration rates should be interpreted cautiously as they may only show short term stimulations of the metabolism of an unchanged microbial biomass rather than increased microbial growth (Reischke et al. 2015). Also, such energy pulses may favor only fast-growing lineages, and the observed differences may not well represent the whole microbial community (Chen et al. 2008, Sullivan and Hart 2013).

Microbial co-limitation by C, N, and P was shown in a montane forest site of Ecuador, as indicated by a fully factorial experiment analyzing the effects of glucose, N and P additions on microbial biomass and respiration (Krashevska et al. 2010). Interestingly, bacteria were primarily limited by P, whereas fungi responded to either addition of C only or a combined addition of all three elements. These distinct responses of bacteria and fungi suggest that different groups of microbes can be limited by different elements or combinations of elements under otherwise identical environmental conditions.

Using cellulose rather than glucose to address the question of relative limitation by C, N, and P availability, Fanin et al. (2015) reported a considerable increase in microbial biomass (fungi and bacteria likewise) and activity in response to P addition after two years of fertilization in the soil of a rainforest in French Guiana. This positive P effect, however, was amplified with a simultaneous addition of cellulose that was interpreted as co-limitation by P and C. In the same fertilization experiment, the relative effects of cellulose, N and P on litter decomposition was evaluated (Barantal et al. 2012, Fanin et al. 2012). They reported increased litter decomposition and substrate induced respiration measured in litter with a combined addition of N and P, with C additions only strengthening this effect in the presence of fauna. However, they also showed that the dissolved organic carbon content found in litter further enhanced the positive NP effect. In fact, when testing initial litter quality effects on decomposition without any nutrient addition, Hättenschwiler and Jorgensen (2010) reported that the concentration of easily accessible C compounds correlated best with litter mass loss with no effects of litter nutrient stoichiometry (see also Hättenschwiler et al. 2011).

The limited number of experiments on the effects of C addition in tropical forests suggests that soil microbial communities may indeed respond with greater biomass and activity to an increased availability of an accessible C source. Depending on the study site, the effect size of C addition was more or less important than that of P addition, and in the two lowland forest studies C and P clearly affected microorganisms interactively. Although there are not enough data for a general conclusion, this suggests that irrespective of potential microbial C limitation in tropical soils, P availability still has a significant effect on microbial functioning in lowland tropical forest soils.

Embracing the Complexity of Soil Microbial Nutrient Limitations in Future Studies

The assessment of soil microbial nutrient limitations is challenging as the functioning of soil microbial communities depends on a multitude of interacting environmental factors and methodological choices are manifold. Soil must still be seen as a "black box" (Nannipieri et al. 2003, Amador 2012), though covering a huge diversity of organisms with heterogeneous ecosystem functions (Whitman et al. 1998, Curtis et al. 2002). Thus, the application of meta-analytical approaches may overcome and summarize these complex data sets and provide ubiquitous conclusions (Koricheva et al. 2013), but also partly mask underlying complexity, which is highly relevant for deeper insights into ecosystem processes. In the following, we discuss factors adding potential biases and complexity to the interpretation of nutrient limitations, but also solutions reported in the literature and guidance for future research.

Methodological approaches

Regarding methodologies, the assessment of microbial processes is typically based on indirect measurements, e.g., O_2 consumption, nitrogen transformations or decomposition (Vitousek and Hobbie 2000*b*, Krashevska et al. 2012, Baldos et al. 2015). The latter, for example, represents a highly relevant ecosystem process that can be quantified relatively easily. However, it is not only affected by microbial activity but also by physical degradation and to a varying amount by macro- and mesofauna (Wall et al. 2008, Powers et al. 2009, Garcia-Palacios et al. 2013). Barantal et al. (2012) assessed the contribution by fauna to observed effects using different mesh sizes, showing a similar direction of responses in decomposition to N, P, and C additions, though the P and N+P effect was much stronger in the presence of fauna. Thus, considering the interaction of biotic and abiotic factors affecting measured response variables is crucial to identify individual responses of the group of interest as well as its relations to other ecosystem components.

Indirect effects via changes in vegetation dynamics

Plants respond to nutrient additions via shifts in root abundance, mycorrhizal associations, root C sequestration, or stoichiometric patterns in litter, even as a short-term response (Homeier et al. 2012), affecting microbial processes in turn (de Graaff et al. 2006, Wardle et al. 2015). Such indirect plant-driven effects are especially important to consider in field experiments. They can be addressed, for example, with common-garden approaches or experimental litter additions/removals allowing to control for indirect effects via changes in litter production and nutrient contents (Vitousek and Hobbie 2000*a*, *b*, Sayer et al. 2007, 2012, Kaspari et al. 2008). However, the potential impact of changing abundance of roots and/or root traits has so far not been addressed, even though it is well known that nutrient additions affect fine root biomass, root:shoot ratios, root turnover rates, and exudation (e.g., Gower and Vitousek 1989, Wright et al. 2011, Homeier et al. 2012, Zhu et al. 2013), which in turn influences microbial community composition and activity (Singh et al. 2004, Mark et al. 2005, Bais et al. 2006). This interrelation of primary production and soil microbial activity in response to altered nutrient regimes has rarely been assessed systematically, and its functional implications at the ecosystem level must be addressed more specifically with appropriate experimental designs and statistical exploitation of existing data (Garcia-Palacios et al. 2015, Wardle et al. 2016).

Microbial N mining hypothesis

Vitousek and Hobbie (2000*b*) reported that higher N and P uptake by microbes did not always translate into increased decomposition rates. Thus, despite the fact that microbes were apparently nutrient limited, it did not change the measured microbial process. This apparent paradox is addressed in the microbial N mining hypothesis, which states that an increased availability of mineral N requires less investment into the breakdown of organic material for N acquisition (Craine et al. 2007, Condron et al. 2010). This may even be an explanation for some negative effects observed following N additions (Hagedorn et al. 2003, Hartman and Richardson 2013), though there is no indication for this phenomenon in our data set when considering overall effects (Fig. 5). In the case of P, there is no evidence for P mining effects so far (Sinsabaugh and Moorhead 1994, Craine et al. 2007). These findings underline the necessity to understand geochemical and biological impacts of the added element and its relation to the measured response variables in more detail.

High functional and phylogenetic diversity in soils

Soils harbor a tremendous functional and phylogenetic diversity of microorganisms (Roesch et al. 2007, van der Heijden 2008), but our understanding of the interplay of different microbial groups in the context of nutrient limitation is currently very limited. Depending on the measured processes, only a part of soil microbial diversity is included in the assessment of treatment effects, and the interpretation of presented response variables partly only refers to a specific functional group of microorganisms. Different groups may have varying nutrient demands as shown for bacteria and fungi (Keiblinger et al. 2010, Krashevska et al. 2010), which also have different functional roles in soil (Rousk and Baath 2007, Paterson et al. 2008). Thus, changes in microbial community composition within functional guilds (Kaspari et al. 2010, Camenzind et al. 2014), but also among them (Liu et al. 2013, Fanin et al. 2016) will feed back on responses to nutrient additions (Leff et al. 2012). Very broad parameters like soil microbial biomass or respiration are useful for assessing the response of the whole microbial community, whereas analyses of specific functional or taxonomic groups reveal essential information on group-specific demands, which remain poorly understood in tropical forests (Kaspari et al. 2010, Schappe et al. 2017). Few studies specifically analyzed shifts in fungal, bacterial, and mycorrhizal community composition in response to nutrient additions (Kaspari et al. 2010, Camenzind et al. 2014). More frequently, the microbial community was analyzed based on phospholipid fatty acid markers, which consistently showed shifts in community composition and fungal:bacterial ratios following nutrient additions (Balser 2001, Krashevska et al. 2010, 2013, Cusack et al. 2011, Liu et al. 2013).

Soil heterogeneity

Tropical soils represent a highly heterogeneous environment with strong small- and large-scale spatial heterogeneity (Lodge et al. 1994, Brechet et al. 2009). This heterogeneity is an important source of variability in field experiments, and it also renders broader generalizations based on results from single studies difficult. On the one hand, such complexity and site-specific characteristics of respective study systems must be considered carefully in the interpretation of individual experiments addressing nutrient limitations of soil microbial processes (Cleveland et al. 2002, Kitayama et al. 2004). On the other hand, more consistent assessments of soil data (e.g., available P) and their correlation with microbial responses to nutrient additions at different sites will permit the identification of nutrient limitation thresholds, and with that improve predictions for global modeling approaches (Ptacnik et al. 2010, Reed et al. 2015). Adding more study sites, especially from the underrepresented paleotropics (Fig. 2), will further improve such quantitative syntheses as presented here.

Conclusions and Perspectives

We provide clear evidence that P limitation of microbial communities in tropical forest soils appears to be general. Individual properties of microbial communities and the processes they drive, however, differ in the extent of P limitation, and there is an apparent additional N limitation in montane tropical forests. The few studies that have addressed the importance of other, less explored mineral nutrients or of C availability for soil microbial processes indicate that several resources may interactively affect soil microbes. However, the lack of systematic assessments of other elements and especially their interactive effects currently impedes general conclusions. The identity of limiting resources and their interactions can also vary among different groups of soil microbes like bacteria and fungi, and perhaps among other groups at finer taxonomic resolution (Keiblinger et al. 2010). Frequently observed shifts in soil microbial community composition following nutrient additions support this assumption (Balser 2001, Liu et al. 2013, Camenzind et al. 2014) and indicate complex functional responses following nutrient inputs, though the number of available studies is low.

Our review also highlights some major knowledge gaps that should be addressed in future studies. Besides N and P, additional elements and especially their interactions should be investigated in more detail (Kaspari and Powers 2016). Among these are certainly Zn, K, S, or C, which can potentially have strong impacts (Fig. 6). For this purpose, the development of standardized experimental protocols implemented at various tropical sites may be useful, since results will be directly comparable among different areas that allows also to account

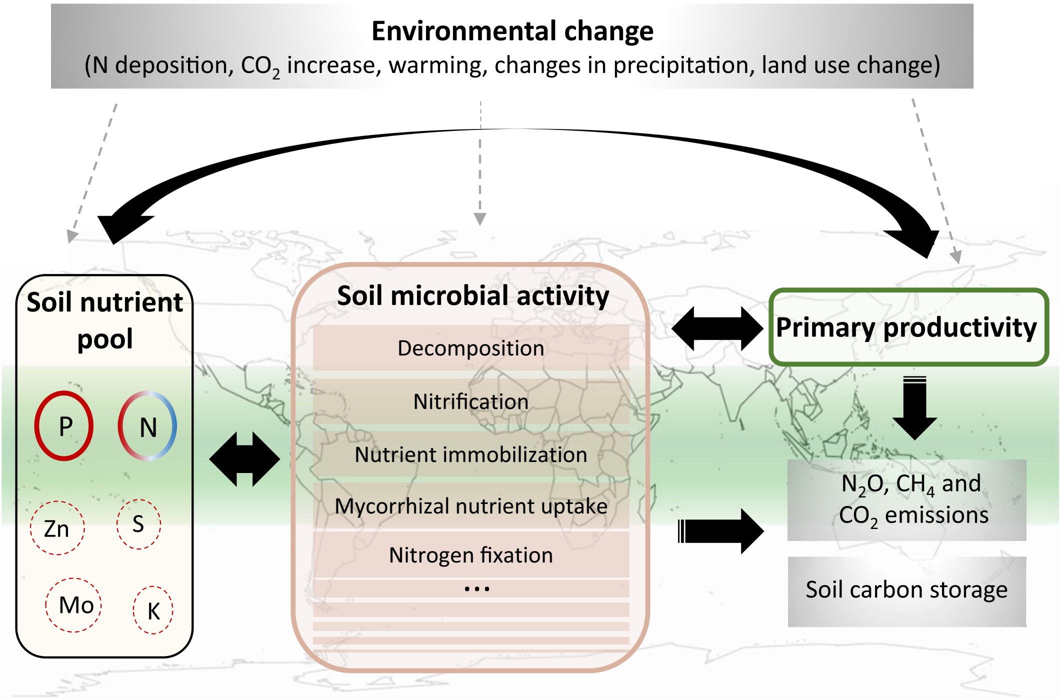

Fig. 6. Schematic overview of the complex interaction among soil nutrients, microbial activity, ecosystem processes and environmental drivers in tropical forests. Red circles indicate elements observed to positively affect microbial activity in nutrient addition experiments, blue negative, and dashed lines refer to preliminary findings that are not yet possible to generalize due to the low number of studies conducted.

for soil heterogeneity within the tropics and for context dependent effects of nutrient additions. Short-term experiments at small scales similar to those by Cleveland et al. (2002), Kitayama et al. (2004), or Powers and Salute (2011) provide a suitable model for that. By contrast, nutrient manipulation experiments designed over sufficiently large temporal and spatial scales permit to quantify and separate direct nutrient effects on soil microbial activity from plant-driven indirect effects via changes in plant traits and soil organic matter input. The relative importance of these two different pathways of nutrient addition effects on soil microbial functioning must be further explored based also on already existing multidisciplinary experiments of appropriate scope by using state-of-the-art statistical tools (see for example Wardle et al. 2016, Sayer et al. 2017). Such analyses will improve predictions on interactions among plant and soil microbial responses to shifting nutrient regimes, as well as the interdependency with other trophic groups, for example soil fauna. In addition, methodological advances of deep-sequencing approaches may be used to reveal insights into differential responses of distinct soil microbial taxa or functional groups to nutrient additions (Kaspari et al. 2017). A combination of the most recent molecular techniques with functional assessments of the microbial community may be particularly rewarding for the understanding of how resource availability and microbial community structure and function are interconnected (Su et al. 2015, Waring et al. 2016).

Such knowledge on the nature of resource limitation regarding the abundance and activity of soil microorganisms is fundamental for understanding ecosystem functioning, and how it is affected by changing environmental conditions. Anthropogenic activities will affect nutrient dynamics and limitations in tropical ecosystems (Galloway et al. 2008, Bonan and Levis 2010), though in turn ecosystem responses to environmental change will also depend on existing soil nutrient limitations (Fig. 6). A microbial community limited by P might not respond as predicted to increased atmospheric CO_2 concentrations or warming (Körner 1998, Mack et al. 2004), with far-ranging consequences for soil C storage and ecosystem-scale C fluxes (Hu et al. 2001, Craine et al. 2007). Likewise, responses in primary productivity highly depend on soil microbial processes, especially with respect to nutrient supply (Vandecar et al. 2009, Cleveland et al. 2013). Joint analyses of both components, plants and soil microorganisms, and their relations in response to nutrient additions are rare, though mutual interferences will occur, for example in the case of divergent responses to N additions (Elser et al. 2007, Treseder 2008).

Tropical trees depend not exclusively on soil microbial mineralization for their nutrition, but also on the activity of mutualistic microorganisms such as N_2-fixing bacteria and arbuscular mycorrhizal fungi (Nasto et al. 2014, Corrales et al. 2016). Microbial mutualists are situated at the interface of plants and soil and they also respond positively to P additions, as indicated from the few available studies (Vitousek 1999, Treseder and Allen 2002, Wurzburger and Wright 2015, Camenzind et al. 2016). However, interpretation of these findings is complex since the plant also regulates the extent of symbiotic association as a function of soil nutrient availability (Treseder and Allen 2002, Johnson 2010). These mutualistic associations play important roles in tropical ecosystems for primary productivity and carbon dynamics, and altered activities may have major impacts on plant growth, plant community dynamics and ultimately on ecosystem processes (Janos 1980, Hedin et al. 2009, Averill et al. 2014).

Collectively, this literature review highlights the relevance of microbial nutrient limitations in an ecological context and identifies knowledge gaps that urgently need to be addressed in future studies. The first quantitative synthesis of nutrient addition effects on soil microbes in tropical forests presented here indicates P availability as a key factor in the understanding of microbe-driven processes. Such P control needs to be taken into account for a mechanistic understanding of the functioning of tropical ecosystems and how their biogeochemical cycles develop under future global change.

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