REVIEWS

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The application of ecological stoichiometry to plant–microbial–soil organic matter transformations

Sophie Zechmeister-Boltenstern,[1,5] Katharina Maria Keiblinger,[1] Maria Mooshammer,[2] Josep Peñuelas,[3,4]
Andreas Richter,[2] Jordi Sardans,[3,4] and Wolfgang Wanek[2]

[1]*University of Natural Resources and Life Sciences Vienna, Institute of Soil Research, Department of Forest and Soil Sciences, 1190 Vienna, Austria*
[2]*University of Vienna, Terrestrial Ecosystem Research, Department of Microbiology and Ecosystem Science, 1090 Vienna, Austria*
[3]*CSIC, Global Ecology Unit CREAF-CSIC-UAB, Cerdanyoladel Valles 08193 Spain*
[4]*CREAF, Cerdanyoladel Valles 08193 Spain*

Abstract. Elemental stoichiometry constitutes an inherent link between biogeochemistry and the structure and processes within food webs, and thus is at the core of ecosystem functioning. Stoichiometry allows for spanning different levels of biological organization, from cellular metabolism to ecosystem structure and nutrient cycling, and is therefore particularly useful for establishing links between different ecosystem compartments. We review elemental carbon : nitrogen : phosphorus (C:N:P) ratios in terrestrial ecosystems (from vegetation, leaf litter, woody debris, and dead roots, to soil microbes and organic matter). While the stoichiometry of the plant, litter, and soil compartments of ecosystems is well understood, heterotrophic microbial communities, which dominate the soil food web and drive nutrient cycling, have received increasing interest in recent years.

This review highlights the effects of resource stoichiometry on soil microorganisms and decomposition, specifically on the structure and function of heterotrophic microbial communities and suggests several general patterns. First, latitudinal gradients of soil and litter stoichiometry are reflected in microbial community structure and function. Second, resource stoichiometry may cause changes in microbial interactions and community dynamics that lead to feedbacks in nutrient availability. Third, global change alters the C:N, C:P, and N:P ratios of primary producers, with repercussions for microbial decomposer communities and critical ecosystem services such as soil fertility. We argue that ecological stoichiometry provides a framework to analyze and predict such global change effects at various scales.

Key words: carbon use efficiency; growth rate hypothesis; homeostasis; litter decomposition; nitrogen turnover; nutrient recycling; phosphorus deficiency; soil enzymes; soil microbiology; substrate age hypothesis.

Introduction

Microorganisms are the primary decomposers of organic matter in terrestrial ecosystems. The chemical composition of the plant residues and organic matter in soil in turn affects microbial activity and microbial community structure and thus the decomposition rate (Aneja et al. 2006). Plant detritus (e.g., leaf litter, woody debris, dead roots) provides a major input of energy and nutrients for microbial decomposer communities (Wardle et al. 2004), beyond soil organic matter (SOM) itself. While stoichiometric element ratios (sensu stricto the element balance of the major nutrients C:N:P; all element ratios presented are molar [atomic] rather than mass-based ratios) diverge during leaf senescence and litter fall (Homann 2012), microbial processing narrows these ratios during litter decomposition and the build-up of SOM (Mooshammer et al. 2014*b*). The structure and function of microbial communities and predominating life strategies adapt to the altered resources. At the same time, they strongly influence the speed and direction of stoichiometric shifts of the resources during decomposition.

Since decomposer N and P requirements are high compared to concentrations in plant litter or detritus, these nutrients (we refer to N and P as nutrients, and consider C in its role as energy source) need to be

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[5] E-mail: sophie.zechmeister@boku.ac.at

immobilized by decomposers from their resources until the elements are enriched above a critical value. At that point, the decomposers switch to net nutrient mineralization, and net nutrient losses may occur (Berg and McClaugherty 2003, Moore et al. 2006, Parton et al. 2007). Decomposers therefore determine N and P recycling during decomposition.

Litter decomposition rates are controlled by soil organisms as well as by environmental conditions and the chemical composition of the litter. Cross-site and cross-litter investigations covering different biomes offer insights into the questions of litter decomposition along global gradients of climate and edaphic conditions (Trofymow et al. 2002, Smith et al. 2011). While many regulating factors of litter decomposition are well studied, it remains a challenge to separate effects of stoichiometry from environmental and organic chemistry effects (see Plate 1). In particular, feedback mechanisms between C:N:P ratios of different ecosystem compartments under varying environmental conditions deserve further analysis because these mechanisms will affect nutrient cycling in a changing world.

Applying the concept of ecological stoichiometry (EST) provides a new approach to tackle the challenge of predicting nutrient recycling in different habitats. In addition, it helps introduce general ecological theories into the field of microbial ecology, where they are strongly needed (Prosser et al. 2007). The theory of EST was originally developed for aquatic ecosystems, but is universally valid, and gained increasing attention for terrestrial ecosystems during the last decade (Austin and Vitousek 2012). Sterner and Elser (2002) demonstrated that stoichiometric constraints significantly influence microbial growth and nutrient cycling in terrestrial systems. Nitrogen and P play especially important roles in this concept because these elements are essential for organism structure and function (Elser et al. 1996), and they are often limiting. Scrutinizing C:N, C:P, and N:P ratios helps us to understand little-known mechanisms, such as resource allocation of organisms under nutrient-limiting conditions.

Ecological stoichiometry has been applied to different aspects of plant growth and development, physiological traits, and nutrient acquisition. Similarly, there is increasing interest in the role of stoichiometric regulation of soil organisms and their function (Mulder et al. 2013*b*). Connecting the "green and brown worlds" by examining the formation and decomposition of plant detritus via elemental stoichiometry is an upcoming issue with the potential to advance the understanding of both nutrient limitation and global change effects in terrestrial ecosystems. In this review, we inspect stoichiometric mechanisms regulating the C:N:P ratios of ecosystem compartments and of nutrient dynamics across different scales. Implementing this new knowledge, namely explicit stoichiometric linkages, into practical applications such as process-based mathematical models, can advance the prediction of future developments in a changing environment (Sistla et al. 2014).

When relating above- and belowground stoichiometry in a global context, we raise the following questions: (1) How do global gradients in climate and edaphic conditions affect plant and litter stoichiometry and decomposability? (2) What are the effects of variable resource stoichiometry on microbial community structure and function? (3) How does global change affect the mechanisms of plant and microbial nutrient cycling?

In order to answer these questions, we synthesize current knowledge on the linkage between above- and belowground stoichiometry. Our approach is to track down variations in stoichiometry from plant foliage to litter, from litter to microbes, from microbes to soil, and from soil back to plants. In order to shed light on our questions, we focus on global variations in soil nutrient status as well as in climate, which we consider to be the major factors behind latitudinal gradients of C:N:P stoichiometry. Processes such as nutrient resorption before leaf abscission, the microbial conversion of different fractions of plant detritus, and microbial community composition and its effect on decomposition rate all depend on the original nutrient status of the system. We argue, however, that this is not a unidirectional relationship, but that the microbial community displays several mechanisms of feedback on nutrient limitation. We demonstrate how understanding the biological regulation of C, N, and P cycles helps to predict future developments in light of rapid global change. Finally, we discuss whether evidence for a growing imbalance of element stoichiometry exists.

How do Global Gradients in Climate and Edaphic Conditions Affect Plant and Litter Stoichiometry and Decomposability?

The ratios of C:N:P in environments and organisms are intimately connected with ecological processes, from the structure of communities (Sterner and Elser 2002) to biodiversity (Sasaki et al. 2010). These connections have increased interest in studying the environmental factors that determine the C:N:P ratios of terrestrial plants (Sardans et al. 2012*b*). Plant N and P concentrations are strongly determined by the corresponding availabilities in soil, as observed in several studies that have compared sites with similar climates but different soil N and P concentrations (Vitousek 1998, Cardenas and Campo 2007). Despite their obvious and important role, soil N and P availabilities do not appear to be the only determinants of plant N:P ratios. Most studies conducted on a global scale have reported decreases in leaf N and P concentrations (with concomitant increases in leaf C:N and C:P ratios, as leaf C is relatively constant) and increases in N:P ratios as latitude decreases and as mean annual temperature (MAT) and mean annual precipitation (MAP) increase (McGroddy et al. 2004, Reich and Oleksyn 2004, Kerkhoff et al. 2005, Ordonez et al. 2009, Yuan and Chen 2009; see also Fig. 1 for N:P; Appendix:

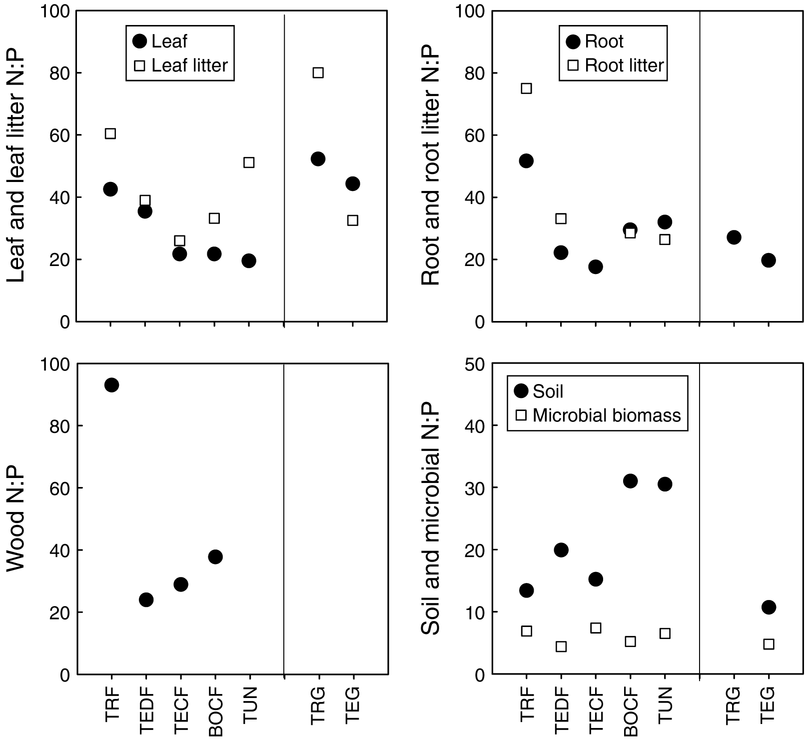

FIG. 1. Changes in ecosystem N:P stoichiometry across major biomes. The following biomes were targeted: tropical rain forests (TRF), temperate deciduous forests (TEDF), temperate coniferous forests (TECF), boreal coniferous forests (BOCF), tundra (TUN), tropical/C_4 grasslands (TRG), and temperate/C_3 grasslands (TEG). Vertical lines in each panel separate grassland biomes from the other biomes. All ratios are molar (atomic) ratios, and mass-based ratios were transformed to atomic ratios by dividing by the respective atomic masses. Data were compiled from the following sources: leaves (McGroddy et al. 2004, Reich and Oleksyn 2004, Wang et al. 2010), leaf litter (McGroddy et al. 2004, Yuan and Chen 2009, Brovkin et al. 2012), living fine roots (Gordon and Jackson 2000, Yuan et al. 2011), dead fine roots (Yuan et al. 2011), wood (Harmon et al. 1986, Martinelli et al. 2000, Weedon et al. 2009, Manzoni et al. 2010, Thomas and Martin 2012), soil organic matter (Xu et al. 2013), and soil microbial biomass (Xu et al. 2013). Most leaf stoichiometric ratios were taken from Wang et al. (2010); only those for TECF were obtained from McGroddy et al. (2004). Leaf litter ratios were mainly compiled from Yuan and Chen (2009); for TRG and TECF, they were taken from McGroddy et al. (2004) and Brovkin et al. (2012). Live-root stoichiometry was taken from root N, P, and N:P ratios (Fig. 2) and the mean C content (44.7%) in Yuan et al. (2011). Live-root stoichiometry of TEDF, TECF, and BOCF was averaged from data by Gordon and Jackson (2000). Dead-root N:P was estimated from mean latitudes of major biomes and the power function in Fig. 1 ($\mathrm{N:P} = 66.6 \times \mathrm{latitude}^{-0.42}$) of Yuan et al. (2011). No data were provided for C:N and C:P. Wood stoichiometry was taken as an average from data on TRF (Martinelli et al. 2000), TECF and TEDF (Harmon et al. 1986, Martinelli et al. 2000), and BOCF (Manzoni et al. 2010).

Fig. A1 for C:N and Fig. A2 for C:P). Moreover, plant N:P ratios and the corresponding plant-litter N:P ratios can vary strongly by several factors that affect the resorption process during leaf senescence (Aerts 1997*b*, Silla and Escudero 2006, Richardson et al. 2008, Reed et al. 2012, Mulder et al. 2013*b*) and that thereafter control the final litter stoichiometry, thus affecting its decomposability, soil trophic webs, and nutrient cycling (Zhang et al. 2008, Schneider et al. 2012, Schreeg et al. 2013).

Soil and climate gradients and the explanation of global trends in leaf stoichiometries

This relationship between latitude and leaf N:P ratio may be related to the substrate age hypothesis (SAH; Walker and Syers 1976), which claims that old tropical soils have a low capacity to release P from parental material (Table 1; Vitousek et al. 2010). In contrast, N-containing compounds available to plants are nearly absent from igneous and metamorphic rocks (Vitousek et al. 2010), and most terrestrial ecosystems are largely devoid of N as they begin their development (Walker and Syers 1976, Holloway and Dahlgren 2002). Nitrogen, though, accumulates over time by biological N fixation, when N fixers dominate in early stages of soil development, and/or by N deposition or biological N fixation from dispersed sources (Vitousek et al. 2010). The SAH therefore predicts young soils to be N limited, and as soils age, continued weathering, cation and P losses, and N inputs cause them to become N rich but P poor. This hypothesis is supported by several studies on nutrient cycling, soil and plant chemistry, and soil chronosequences from young to old soils (Richardson et al. 2005). They further confirm a general trend of increasing P limitation toward areas with a tropical climate (Reich and Oleksyn 2004, Elser et al. 2007,

Table 1. Brief explanation of commonly used terms in the framework of ecological stoichiometry.

Concept	Definition
Ecological stoichiometry (EST)	Balance of multiple chemical substances in ecological interactions and processes, or the study of this balance. Also sometimes refers to the balance of energy and materials (Sterner and Elser 2002).
Redfield ratio	Well-constrained molar ratio of C:N:P in planktonic biomass of 160:16:1; has advanced the knowledge of biological processes and cycling in marine ecosystems (Redfield 1958).
Substrate age hypothesis (SAH)	Younger soils at higher latitudes, rejuvenated by cyclic glaciations, have a higher capacity to release P from parental materials than do older tropical soils whose surface parental materials have long been leached and have consequently become depleted in P (Walker and Syers 1976, Vitousek et al. 2010).
Growth rate hypothesis (GRH)	Elevated demands for increased allocation to P-rich ribosomal RNA under rapid growth drives variation in the P content (and thus C:P and N:P ratios) of many biota (Elser et al. 2003).
Nutrient use efficiency	Amount of production per unit nutrient used (Bridgham et al. 1995). Microbes excrete nutrients that are present in excess in their substrates compared to their biomass composition by adjusting their element use efficiencies.
Homeostasis	Results in narrowing of variation in chemical content in an organism compared to the resources it consumes (Sterner and Elser 2002).
Consumer-driven nutrient recycling (CNR)	Homeostatic organisms regulate their elemental composition by retaining elements in which they are limited and releasing those in excess (Sterner and Elser 2002).
Threshold elemental ratio (TER)	Defines the transition of an ecological system from being controlled by energy flow (C) to being controlled by limiting nutrient flow (N or P; e.g., Urabe and Watanabe 1992, Anderson and Hessen 1995, Frost et al. 2006); sometimes also referred to as "breakpoint ratio" (e.g., Townsend et al. 2007).
Resource allocation theory	Enzyme production should increase when simple nutrients are scarce and complex nutrients are abundant (Allison and Vitousek 2005).
Overflow metabolism	Microbial respiration of C in excess of metabolic requirements (Russell and Cook 1995, Schimel and Weintraub 2003).

Note: All element ratios presented in this review are molar (atomic) rather than mass-based ratios.

Sardans et al. 2012*b*). Hence, the overall results suggest that P-rich bedrock and optimal climatic conditions for growth favor high leaf N and P concentrations (low C:N and C:P ratios) with low N:P ratios.

Ecological lifestyles and the explanation of global trends in leaf stoichiometries

Not only bedrock and climate influence leaf stoichiometries; plant species with different ecological lifestyles have different N and P concentrations and N:P ratios, and plants with higher growth rates typically have higher leaf N and P concentrations (lower C:N and C:P ratios) and lower leaf N:P ratios. These trends support the growth rate hypothesis (GRH; Table 1), which claims a relationship between growth rates and elevated demands for P for the synthesis of P-rich ribosomal RNA (Elser et al. 2000, Karpinets et al. 2006), the latter causing cytoplasmic N:P ratios to decline.

Globally, N:P ratios correlate negatively with growth rates (Sardans et al. 2012*b*). This is frequently observed when comparing plant species of different growth rates (Sterner and Elser 2002). Even though foliar N:P ratios tend to be higher toward tropical areas in a trend determined strongly by soil age, foliar N:P ratios are variable within each biome. This reflects variations in soil and topography, phylogenetic community composition, climatic conditions, and the ecological strategies and growth-rate capacities of the species. Within species, there is also a stoichiometric flexibility that has been related to species' lifestyles.

The differences in the concentrations and ratios of the elements as expressions of stoichiometric flexibility are greater (less homeostatic) in fast-growing species, with higher N and P concentrations and lower C:N, C:P, and N:P ratios than in slow-growing species (Yu et al. 2011). Aerts (1996) observed that the plant groups with less capacity to modify their resorption efficiency (plasticity) as a function of soil nutrient availability were evergreen shrubs and trees, the most slow-growing species.

Complementary hypotheses related to the GRH have been proposed to explain increases in plant nitrogen (N) and phosphorus (P) concentrations with latitude: temperature-driven variations in growth rate, where greater growth rates (requiring greater nutrient levels) are needed to complete growth and reproduction within shorter growing seasons in temperate than tropical climates (Kerkhoff et al. 2005, Kerkhoff and Enquist 2006, Lovelock et al. 2007). Supporting this, a recent meta-analysis with a 6800-record database reveals that mean photosynthetic tissue N and P increase (C:N and C:P decrease) with latitude in aquatic and terrestrial ecosystems, but P increases more rapidly, causing N:P to decline (Borer et al. 2013). This effect would be related to the decrease in growing-season length that makes photosynthetic tissues with high N and P concentrations and lower N:P ratios more important for sustaining rapid production and growth to take advantage of short favorable growth periods for biomass production (Borer et al. 2013). Most meta-analyses support the conclusion that leaf N and P increase from the tropics to the cooler

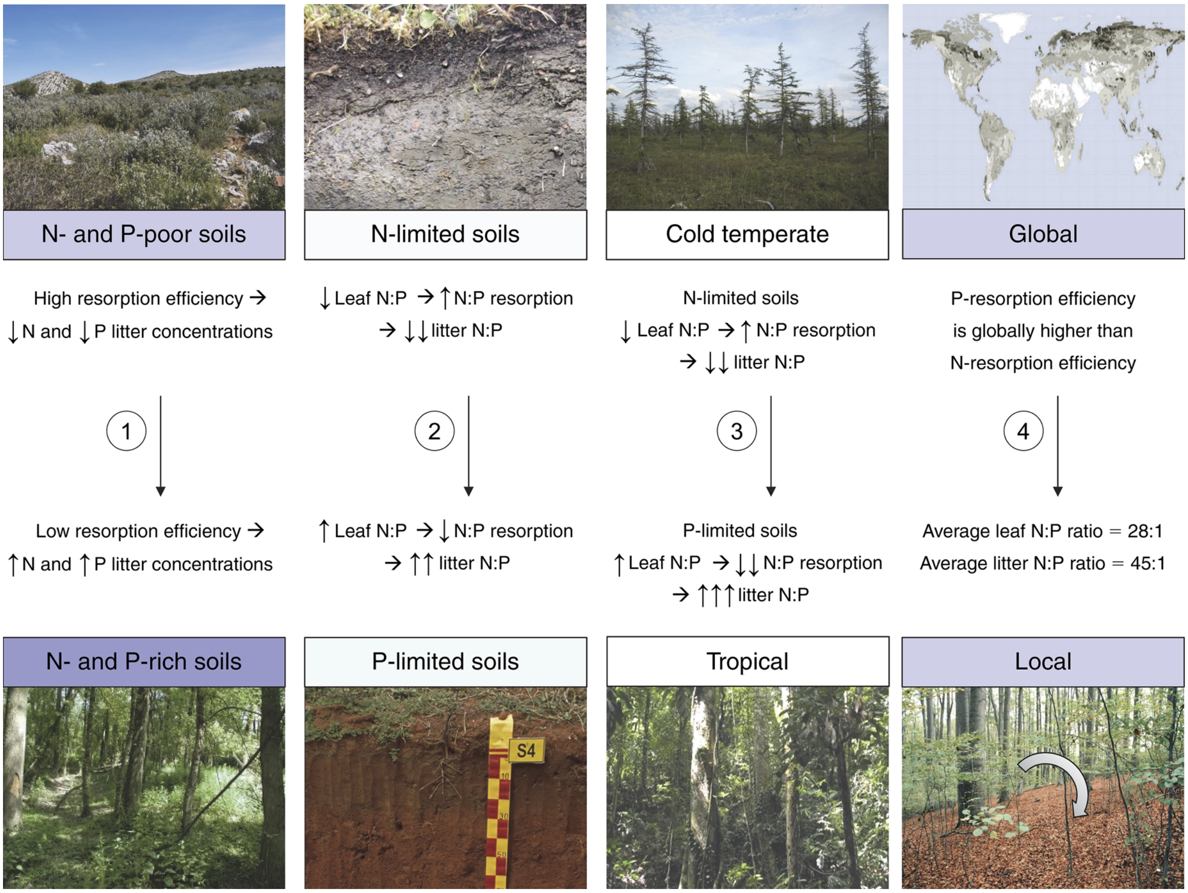

FIG. 2. Global trends and mechanisms of changes in N:P ratios from leaves to leaf litter. Up arrows indicate increases, down arrows indicate decreases, and number of arrows indicates magnitude of change. Numbers correspond to trends listed in *How do global gradients in climate and edaphic conditions affect plant and litter stoichiometry and decomposability?: Factors determining the differences in N and P concentrations and C:N:P ratios between leaves and leaf litter*. Photo credits (left to right, top to bottom): Josep Peñuelas, Andreas Richter, Jörg Schnecker, Sophie Zechmeister-Boltenstern, Martin Gerzabek, Wolfgang Wanek, Sophie Zechmeister-Boltenstern.

and drier mid-latitudes, and then plateau or decrease at high latitudes because of both the climate-related plant physiological stoichiometry and the biogeographical gradients in the frame of soil substrate age (Reich and Oleksyn 2004).

Factors determining the differences in N and P concentrations and C:N:P ratios between leaves and leaf litter

The key process that can generate differences between leaf and litter N and P concentrations and C:N:P ratios among and also within plant species is the leaf resorption efficiency (the percentage of leaf nutrients resorbed from leaves before leaf fall). Four general trends can be concluded from the literature when comparing the N and P concentrations and N:P ratios of leaves to those of leaf litter (Fig. 2). First, a greater fraction of foliar N and P are resorbed in nutrient-poor soil–plant systems (Aerts 1996, Richardson et al. 2005, Silla and Escudero 2006, Li et al. 2012, Lu et al. 2012). Second, N:P resorption ratios generally increase when the soil is N limited and generally decrease when the soil is P limited (van Heerwaarden et al. 2003, Zotz 2004). Third, foliar N:P resorption ratios on a global scale tend to increase with latitude and decrease with MAP and MAT, leading to a global trend to produce litter with very high N:P ratios toward the tropics (McGroddy et al. 2004, Reed et al. 2012; Fig. 1). Soils consequently tend to develop higher N:P ratios over time (Hedin et al. 2003). This third trend is related to the SAH, in the sense that, in general, as P becomes more limiting toward the tropics, plants decrease N:P resorption ratios. Fourth, despite the previous trends, P tends to be resorbed more than N on a global scale (Fig. 3), and this difference tends to be even higher in nutrient-rich sites, favoring leaves with lower N:P ratios and litter with higher N:P ratios (Mulder et al. 2013*a*).

The three first trends are related to the fact that plant species growing on soils with low nutrient availabilities have higher N and P resorption efficiencies than do

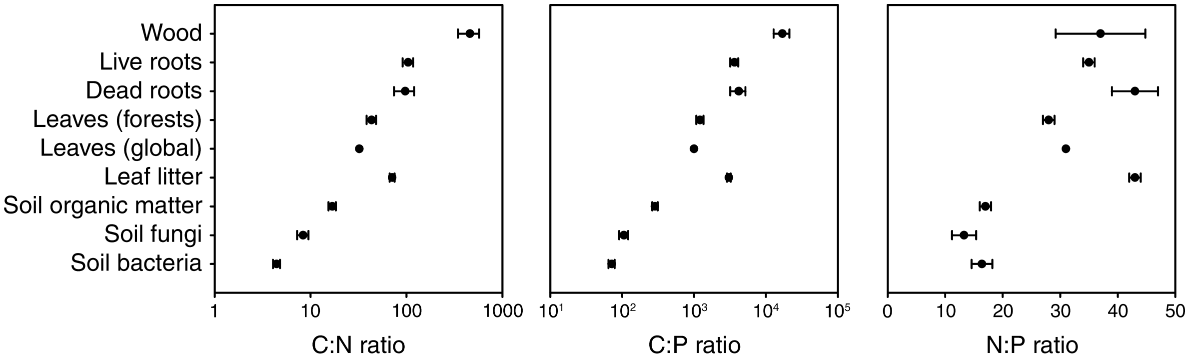

FIG. 3. Changes in global C:N:P ratios from live to dead plant materials, and convergence of C:N:P ratios from detrital pools toward soil organic matter and soil microbes. Data on global atomic C:N:P ratios were compiled or calculated from the following sources: wood (Harmon et al. 1986, Martinelli et al. 2000, Weedon et al. 2009), live and dead roots (Yuan et al. 2011), forest leaves (McGroddy et al. 2004), global leaves (Kattge et al. 2011), leaf litter (Yuan and Chen 2009), soil organic matter and soil microbial biomass (Xu et al. 2013), and fungi and bacteria (Mouginot et al. 2014*a*). Error bars show standard deviation.

species growing in richer soils (Aber and Melillo 1980, Aerts 1996, Côté et al. 2002, Martínez-Sánchez 2005, Richardson et al. 2005, Silla and Escudero 2006, Li et al. 2012, Lu et al. 2012), an effect related to a higher plant nutrient use efficiency, a longer nutrient mean residence time in plant biomass, and generally a more conservative use of nutrients when scarce (Aerts 1997*b*, Silla and Escudero 2006; Fig. 2). Plants growing in association with mycorrhizae and therefore having higher nutrient uptake rates resorb less N and P (Chuyong et al. 2000). Also, plants growing in dry areas resorb more N and P than do plants growing in wet areas (Sardans and Peñuelas 2013). Soils already low in nutrients thus receive even fewer nutrients from the litter (Kitayama et al. 2004, Kobe et al. 2005, Han et al. 2013), enhancing the recycling and nutrient use efficiency of plants with further feedback consequences on litter decomposition (Aerts and Chapin 2000). The N:P resorption ratio increases in N-limited soils, and the opposite occurs in P-limited soils (van Heerwaarden et al. 2003, Zotz 2004). By increasing P resorption, plants in P-limited soils thus produce litter with high N:P ratios, suggesting a limiting role of P for communities of soil-dwelling decomposers. The opposite occurs in N-limited soils (Fig. 2). Regardless, the differences in leaf and litter N and P concentrations and resorption efficiencies observed along soil N and P availability gradients are driven both by species-specific differences and also by the plasticity of individual species (Richardson et al. 2005).

The fourth trend indicates certain general asymmetric behaviors in N vs. P resorption and is consistent with most global meta-analyses that indicate broader ranges for P than for N resorption efficiencies (Mao et al. 2011, Vergutz et al. 2012). This trend is further corroborated by most experimental and observational studies (Kozovits et al. 2007, Hättenschwiler et al. 2008), despite the large variability of the results (Reed et al. 2012, Vergutz et al. 2012; Fig. 2). These meta-analyses observed that the proportional concentration of C and N relative to P is higher in litter than in leaves, 3007:45:1 and 1212:28:1, respectively (McGroddy et al. 2004), indicating a generally higher resorption efficiency of P than of N. At least two circumstances seem to underlie this asymmetry. One is the necessity to retain P in the ecosystem because soils tend to develop P limitation with age. A high efficiency of P resorption is the main mechanism for the retention of P by plants in ecosystems on P-poor soils, as observed in several tropical and temperate forests (Hättenschwiler et al. 2008, Richardson et al. 2008). Analyses of global data sets (McGroddy et al. 2004, Reed et al. 2012) show that leaf litter tends to have higher N:P ratios toward tropical areas (Fig. 1), in accordance with the SAH and the increasing role of P limitation (Fig. 2). The leaf N resorption/P resorption efficiency ratio of forests is close to 0.6 in tropical ecosystems and rises to 1 in temperate ecosystems (Reed et al. 2012). The second cause of this asymmetry would be related to the GRH. In fact, optimum climatic conditions for plant growth frequently coincide with high foliar N and P concentrations and with low N:P ratios in leaves (Reich and Oleksyn 2004, Kerkhoff et al. 2005, Yuan and Chen 2009, Sardans and Peñuelas 2013). In a meta-analysis of senescent leaves, Yuan and Chen (2009) observed that litter N concentrations increase from 10 to 15 mg/g and litter P concentrations decrease from 0.63 to 0.32 mg/g when MAP increases from 500 to 4000 mm, confirming the decreasing N resorption/P resorption ratio with increasing MAP as observed in other meta-analyses (Reed et al. 2012).

Convergence of C:N:P ratios of plant detrital inputs toward SOM and soil microbes during decomposition

Beyond the focus on leaf litter, which is due to its importance as a source of detrital input, and due to the wealth of available data, other dead organic materials are also important as a source of energy and nutrients for decomposer communities (Freschet et al. 2013). For instance, coarse woody debris (CWD) represents an important localized input of plant detritus in forests worldwide. CWD input rates vary widely, but contribute

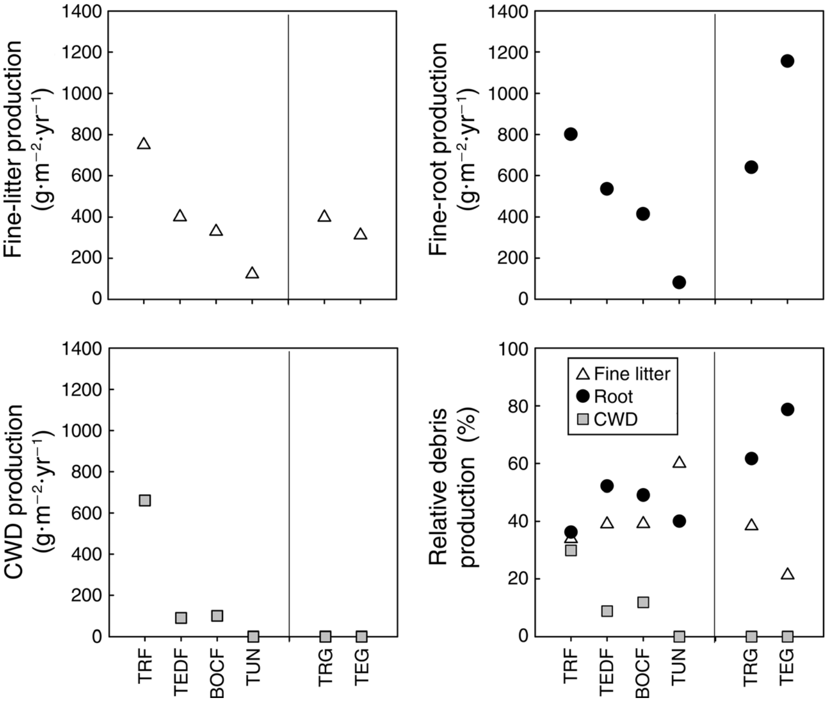

FIG. 4. Changes in plant debris production across major biomes (Fig. 1) and relative (percentage) contributions of fine-litter production, fine-root production, and coarse woody debris (CWD) production to total soil detritus inputs. Data for biome plant detritus production fluxes were compiled or calculated from the following sources: fine-litter production (Potter and Klooster 1997, Hui and Jackson 2006, Zhang et al. 2014), fine-root production (Hui and Jackson 2006, Finer et al. 2011*a*, *b*), and CWD production (Potter and Klooster 1997, Palace et al. 2008). Fine-litter and fine-root production fluxes in TUN were calculated from the single studies (Chapin et al. 1988, Sullivan et al. 2007, 2008, Campioli et al. 2009, Sloan et al. 2013). Fine-root production in mature terrestrial ecosystems was assumed to be equal to root death and therefore with annual input of dead roots, with no resulting accrual in root biomass.

between 10% (temperate forests) and 30% (tropical forests) to total plant detritus inputs to soil (Fig. 4). Compared to leaf litter (C:N:P of 3055:43:1) CWD has much higher C:N:P ratios (14 103:40:1) and markedly lower N and P concentrations (Harmon et al. 1986, Martinelli et al. 2000, Weedon et al. 2009) but similar N:P ratios (43:1 vs. 40:1, Fig. 3). Tropical wood has higher N:P ratios than temperate and boreal wood (Fig. 1), and therefore follows the same large-scale latitudinal pattern as leaf litter, conforming to the SAH (Table 1).

Fine-root production and turnover also represent a quantitatively highly important input of plant detritus to soils. Decomposing fine roots are a key energy source to soil microbes and a major pathway of nutrient flux in terrestrial ecosystems (Yuan and Chen 2010). Globally, fine-root production increases from the arctic toward the tropical biome, and contributes between 40% and 80% of total detrital soil inputs (Fig. 4). Root litter has high C:N:P ratios (4184:43:1; Fig. 3), with N:P ratios similar to leaf litter and CWD. Due to the limited data on root litter stoichiometry, it remains unclear if systematic differences exist between ecosystems and biomes, but a trend of increasing dead-root N:P ratios toward the tropics has been reported (Gordon and Jackson 2000, Yuan et al. 2011). On the other hand, N:P ratios of living fine-root biomass clearly differed between biomes, declining exponentially with latitude (Fig. 1), which again conforms to the SAH (Yuan et al. 2011). It has been a longstanding debate whether C and nutrient resorption occurs during fine-root senescence (Nambiar 1987). Only recently, mean root N (27%) and P (57%) resorption was demonstrated in tundra ecosystems (Freschet et al. 2010), leading to a weak increase in root-litter N:P ratios relative to living fine roots (Yuan et al. 2011; Fig. 3). However, it seems that root resorption efficiencies are much lower compared to those of leaves (Freschet et al. 2010).

In contrast to the large observed differences in C:N and C:P ratios between plant detritus pools, N:P ratios of these materials are relatively similar globally, ranging between 40:1 and 43:1 (Fig. 3). In addition, on a broad scale, N:P ratios are highly similar in resource-acquiring plant biomass pools (i.e., between leaves and living fine roots) as well as in their detritus pools (i.e., between leaf and root litter). This indicates a common functional nutrient stoichiometry of the live plant tissues (Yuan et al. 2011), and similarities in above- and belowground nutrient resorption processes.

Great differences have been observed when comparing C:N:P ratios of plant detritus, SOM, and soil microbial biomass (Fig. 3). Analyzing a data set of 186 observations, Cleveland and Liptzin (2007) observed atomic C:N:P ratios of 186:13:1 in soils and of 60:7:1 in soil microbial biomass. More recently, analyzing a data set of 3422 data points from around the world, Xu et al. (2013) reported average C:N:P ratios of 287:17:1 and 42:6:1 for soil and soil microbial biomass, respectively (Fig. 3). These global data analyses therefore suggest the following patterns: (1) The losses of N must be much higher than the losses of P (from an N:P ratio of ~40 in litter to 6–7 in microbes; Fig. 3) during detritus decomposition and SOM formation, and that globally, terrestrial ecosystems are adapted to retain more P than N. The fast turnover of microbes compared to plant tissue may be related to their high N and P concentrations (low C:N and C:P ratios) and low N:P ratios, suggesting that microbial biogeochemical processes will be one of the causes of the lower N:P ratios observed in soils compared to plant detritus, and thereby contribute to retaining proportionally more P than N in soils. (2) During organic matter decomposition, losses of C are much greater than those of N or P. This causes the C:N and C:P ratios of decomposing plant detritus to decline and converge toward SOM and soil microbial biomass (Fig. 3). As outlined in *What are the effects of variable resource stoichiometry on microbial community structure and function?: Mechanisms regulating microbial carbon and nutrient cycling in response to resource stoichiometry*, microbial C use efficiency (CUE) is expected to be low in C-rich resources such as plant detritus, causing large respiratory losses of organic C while nutrients are retained with higher efficiencies (Mooshammer et al. 2014*a*, *b*). In soils with low C : nutrient ratios, CUE is expected to be higher and microbes to become energy limited but less nutrient conservative. The convergence of detrital C:N:P toward SOM and soil microbes during decomposition (see patterns 1 and 2) is therefore based on microbial decomposition processes causing larger C than nutrient losses from decomposing organic matter (Manzoni et al. 2012). Moreover, the pattern is also reflected in the increasing contribution of microbial remains to decomposing organic matter and ultimately to SOM (Simpson et al. 2007, Miltner et al. 2012), and highlights the impact of microbial physiology on SOM formation and on its chemistry viz. stoichiometry. (3) The latitudinal trends in (C:) N:P ratios as found in plant biomass and plant detrital pools (Fig. 1; Appendix A: Figs. A1 and A2) are not reflected in SOM and soil microbial biomass (Xu et al. 2013). In contrast, soils show an inverse trend in (C:) N:P ratios from tropical forests toward tundra ecosystems, and neither the detritus nor the soil N:P trends are reflected in soil microbial biomass. Soil microbes are therefore largely, though not strictly, homeostatic in terms of C:N:P stoichiometry (Cleveland and Liptzin 2007, Sistla and Schimel 2012, Hartman and Richardson 2013, Xu et al. 2013, Li et al. 2014). In EST, homeostasis relates to the physiological regulation of organism biomass stoichiometry, where in strict homeostasis, variable resource stoichiometry has no effect on organism stoichiometry (Sterner and Elser 2002). Mechanisms of homeostatic regulation are discussed in *What are the effects of variable resource stoichiometry on microbial community structure and function?: Mechanisms regulating microbial carbon and nutrient cycling in response to resource stoichiometry* and by Mooshammer et al. (2014*b*). Despite microbes being largely homeostatic, the soil microbial biomass shows relative flexibility in its C:N:P, and significant differences have been found between biomes and ecosystem types (Hartman and Richardson 2013, Xu et al. 2013, Li et al. 2014). The increase in soil N:P ratios (and in C:N and C:P) from low- to high-latitude ecosystems is paralleled by increases in surface SOM content (0–15 cm depth; Xu et al. 2013). Soil N:P increases from low- to high-humic soils (Appendix: Fig. A3), and therefore positively scales with SOM content (Hartman and Richardson 2013). As forest floor and organic soils are high in organic matter that is less microbially decomposed, they are also more closely related to plant detritus with high C:N, C:P, and N:P ratios compared to mineral soils with strongly decomposed organic materials that are stoichiometrically more closely related to microbial remains (Appendix: Fig. A3). The same trend, decreases in soil C:N:P with decreasing SOM content and increasing microbial processing of this organic matter, was also found with increasing soil depth (Tian et al. 2010). C:N:P ratios of detritus and SOM therefore closely reflect the degree of microbial decomposition of organic matter.

Synthesizing the latest outcomes of biogeochemical research, we conclude that microbes worldwide encounter different concentrations and stoichiometric ratios of C, N, and P, depending on climate, soil type, and soil age. Global latitudinal gradients display higher N:P ratios of plant tissues and litter (but not in soils and soil microbes) toward the tropics, indicative of decreasing plant P availability at low latitudes. Microbially mediated decomposition of plant detritus causes C:N:P ratios to decline and converge toward SOM and ultimately microbial biomass. Changes in C:N:P ratios cause feedback effects on the decomposition process and on nutrient recycling, but is it possible to predict the sequel for the microbial community, their physiology, and competitive strategies?

What Are the Effects of Variable Resource Stoichiometry on Microbial Community Structure and Function?

Stoichiometry and the decomposition rates of different plant materials

Microbial decomposition of plant detritus results in the breakdown and respiratory use of organic C as well as in the mineralization and recycling of nutrients. The nutrient status of ecosystems strongly affects nutrient concentrations and the stoichiometry of plant detritus. To what extent do these stoichiometric differences feed back on decomposition rate and hence on nutrient recycling? Can we detect major differences in decomposition rate between different types of plant detritus?

Leaf litter decomposes much faster than wood, with a global mean k value of 0.58 $g \cdot g^{-1} \cdot yr^{-1}$ for leaf litter (Zhang et al. 2008) and 0.05–0.1 $g \cdot g^{-1} \cdot yr^{-1}$ for dead wood (Weedon et al. 2009). Globally, root litter decomposes slightly faster (0.83 $g \cdot g^{-1} \cdot yr^{-1}$; Silver and Miya 2001) than leaf litter, which is not necessarily the case when root and leaf litter decomposition are studied at the same site, e.g., Freschet et al. (2012). These tissue-specific differences in decomposition can be caused by differences in a wide array of chemical and structural traits, or different environmental conditions under which the studies were undertaken. More generally, decomposition of plant detritus is driven by multiple factors, of which soils, climate, decomposer communities, and litter quality are the most important (Berg and McClaugherty 2003). Litter quality is a broad term including chemical variables such as C chemistry (lignin and carbohydrate content, secondary compounds), element contents (N, P, Ca, K, etc.) and their ratios (C:N, C:P, N:P, lignin : N), and structural variables such as tissue density and surface : volume ratio.

Climate has been implicated as the most important direct control on litter decomposition, with variable results from multi-site experiments where litter of the same species was decomposed; in tropical sites, MAP was most important (Powers et al. 2009), while in temperate and boreal sites, MAT played the key role (Trofymow et al. 2002). However, two recent meta-analyses clearly showed that climate is less rate limiting compared to litter quality. The meta-analysis by Zhang et al. (2008) demonstrated that litter quality explained 73% of the variability in decomposition rate across plant species and types of plant tissues while MAT and MAP accounted for a maximum of 30%, some part of which was caused by collinearity between climate and litter-quality parameters. Similarly, Cornwell et al. (2008) cite a sixfold range in decomposition rates of litter from the same species decomposing in very different climate conditions (Parton et al. 2007), but found an 18-fold range in decomposition rates of leaf litter of different species decomposing at the same site.

Which litter trait is most important in controlling decomposition globally? Structural parameters have been shown to be important determinants of wood decomposition, such as the diameter of the decomposing wood piece (analogous to surface area : volume ratio) and tissue density (wood density; van Geffen et al. 2010, Pietsch et al. 2014), and leaf litter decomposition was shown to be negatively affected by leaf mass per area (Cornwell et al. 2008, Pietsch et al. 2014). Low surface area : volume ratios and high tissue densities decrease the accessibility to the decomposer community and their extracellular enzymes, and increase recalcitrance.

The relative importance of C chemistry, element contents, and element stoichiometry as determinants of litter decomposition varies from study to study, depending on decomposition environment and tissue type. Carbon chemistry, such as lignin and tannin content, lignin : carbohydrate, and lignin : N ratios, has been implicated as a major factor negatively affecting litter decomposition (Melillo et al. 1982, Hättenschwiler and Jorgensen 2010, Talbot and Treseder 2012). Litter element contents, particularly N and P, strongly positively affect the decomposition rate of dead wood (Weedon et al. 2009), root litter (Silver and Miya 2001), and leaf litter (Cornwell et al. 2008). However, essential cations such as Ca, Mg, and K also exert strong positive controls on the decomposition of dead roots (Silver and Miya 2001) and across all types of plant detritus (Zhang et al. 2008), and therefore shall be included in a stoichiometric view of litter decomposition.

The importance of litter stoichiometry for decomposition has also been investigated across the full breadth of autotrophic detrital tissues, ranging from unicellular algae to trees; detrital C:N and C:P ratios were strongly negatively related to decomposition rates (Enríquez et al. 1993). In our data compilation of detrital C:N:P and decomposability across leaf litter, root litter, and CWD, we found a strong curvilinear response of litter decomposition rate to C:N and C:P, but not to N:P (Fig. 5). This indicates that decomposition of plant detritus is nutrient but not energy (C) limited, given the necessary investment of (C and) N into extracellular enzymes by decomposer microorganisms and based on the high demand of microbial decomposers for N and P to build and maintain biomass. Moreover, decomposition nearly halts above C:N ratios of 100 and C:P ratios of 4000, pointing to C : nutrient thresholds at which nutrient limitation outrivals any other environmental or chemical factor (Fig. 5). One emerging question is whether C:N (C:P) effects are really stoichiometric or only reflect the effect of N (P) on nutrient-limited litter decomposition where organic C is in excess and litter C concentrations are relatively invariable (40–50%). Therefore litter N (P) content is strongly negatively related to litter C:N (C:P), and it is ambiguous whether nutrient contents or C : nutrient ratios are the primary agent affecting litter decomposition. In regression models testing for N (P) and C:N (C:P) effects, nutrient contents sometimes explain a larger fraction of variance in decomposition rate (Zhang et al. 2008), sometimes C : nutrient ratios are better explanatory variables (Silver and Miya 2001, Weedon et al. 2009). It is therefore likely that true C:N and C:P effects are smaller compared to direct nutrient effects on litter decomposition. The strong correlation between detritus N and P across a broad scale of plant tissues (Enríquez et al. 1993), and similar slopes of litter decomposition with litter N or litter P indicate that litter N:P does not vary much across different plant materials and environmental conditions, compared to C : nutrient ratios (see also Fig. 3). Accordingly, litter N:P may not significantly

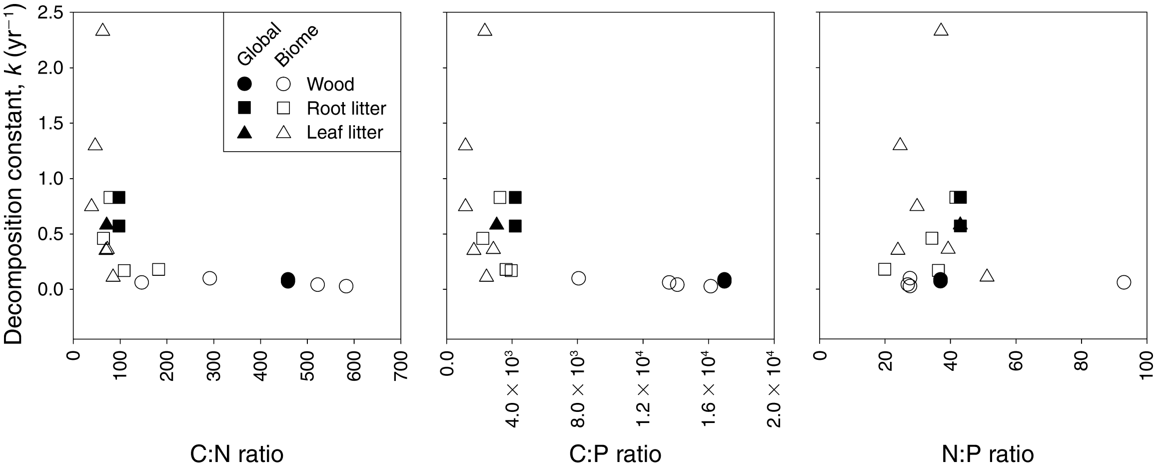

FIG. 5. Effects of C:N:P stoichiometry of plant detritus on its decomposition rate. Decomposition rate is given as decomposition constant k ($g \cdot g^{-1} \cdot yr^{-1}$); stoichiometric ratios are molar. Circles represent wood, rectangles root litter, and triangles leaf litter data; solid symbols are global means and open symbols are biome means. Wood data are shown as global, tropical, temperate/boreal, angiosperm, and gymnosperm averages, root litter data as global, broadleaf, conifer, fine-, and coarse-root averages, and leaf litter data as global, tropical, temperate, broadleaf forest, coniferous forest, and tundra averages. Data were from the following sources: C:N:P stoichiometry (Harmon et al. 1986, Aerts 1997*a*, Martinelli et al. 2000, Silver and Miya 2001, Zhang et al. 2008, Yuan and Chen 2009, Kang et al. 2010, Yuan et al. 2011); decomposition (Harmon et al. 1986, Aerts 1997*a*, Silver and Miya 2001, Zhang et al. 2008, van Geffen et al. 2010).

affect decomposition rates (Enríquez et al. 1993) compared to N and P concentrations.

Structural and chemical parameters are often tightly related. For instance, for leaf litter, mass loss was negatively related to leaf mass per area, lignin content, and polysaccharide content, and positively related to litter N and P across 818 plant species (Cornwell et al. 2008). Moreover, this set of litter traits is highly coordinated in leaves (termed the leaf economics spectrum) and reflects the plant species' ecological strategy, i.e., being slow-growing, long-lived, and nutrient-conservative, or vice versa (Wright et al. 2004). The leaf economics spectrum therefore has a strong "influential afterlife, affecting the rate of decomposition" (Cornwell et al. 2008). Furthermore, decomposition rates of leaves, fine roots, and fine stems were recently demonstrated to be coordinated across species globally (Freschet et al. 2013). Similarly wood and leaf litter decomposability of >300 tree species was positively correlated and related to plant functional traits along the leaf and wood economics spectrum. The covariation of structural and chemical litter traits along a plant economics spectrum hinders the study of the importance of single traits, though plant mutants with altered cellulose or lignin content and lignin structure have helped investigate mechanisms and feedbacks of these traits on decomposition (Talbot and Treseder 2012). Also, comparative studies focusing on leaf litter from one plant species with similar structure and C chemistry but different C:N:P stoichiometries can overcome this handicap (Manzoni et al. 2010, Keiblinger et al. 2012). For instance, faster decomposition rates have been measured with lower leaf litter N:P ratios than with higher ones (Schneider et al. 2012). This shows that besides nutrient limitation of microbial decomposers of plant detritus, a certain relative proportion of nutrients is crucial for high decomposer activity, an activity expressed as enzyme and respiratory activities (Schneider et al. 2012).

We conclude that (1) litter chemistry outrivals environmental drivers of litter decomposition rates, (2) nutrient concentrations, specifically litter N and P, have a strong positive effect on litter decomposition rates, which may exceed the effect of stoichiometry, i.e., litter C:N:P ratios, and that (3) globally, litter nutrient concentration, litter C quality (lignin content), and structural features covary, making individual controls on microbial communities and decomposition processes difficult to tease apart.

Mechanisms regulating microbial carbon and nutrient cycling in response to resource stoichiometry

Besides environmental factors, resource stoichiometry can limit microbial activity, thereby governing ecosystem-level C and nutrient flow (Sterner and Elser 2002). Given that microbial stoichiometry is the basis for the nutrient requirements of decomposer communities, the stoichiometric imbalance between resource and microbial biomass reflects a limitation of microbial activity by a particular nutrient. For example, heterotrophic microorganisms in plant litter are thought to be limited by N or P, whereas microbial communities decomposing SOM are expected to be C limited, because (simplistically) the progressively lower C:N or C:P ratios from litter to organic soil, and further to mineral soil, correspond to a decreasing C availability in relation to

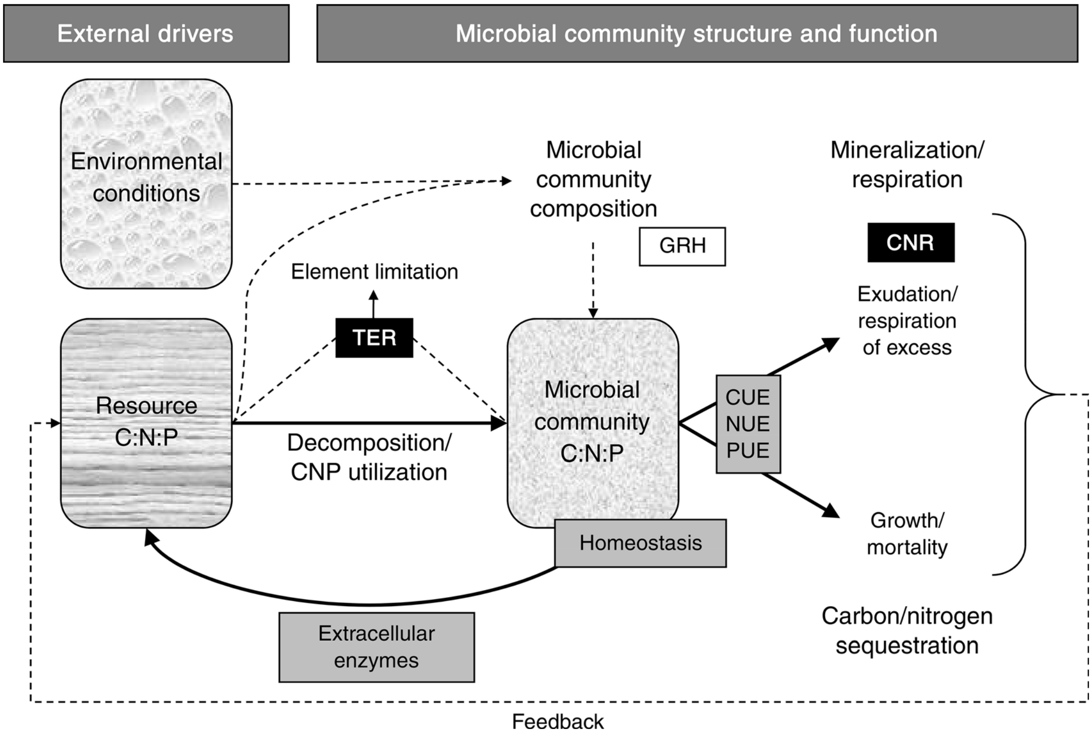

Fig. 6. Proposed effects of resource stoichiometry and environment on microbial community structure and function. Major concepts of ecological stoichiometry and important microbial features are indicated: threshold element ratio (TER), consumer-driven nutrient recycling (CNR), growth rate hypothesis (GRH), homeostasis, extracellular enzymes, C use efficiency (CUE), N use efficiency (NUE), P use efficiency (PUE), mineralization and respiration, and growth. Solid lines indicate processes/fluxes, while dashed lines indicate influences/controls. Black boxes indicate central hypotheses of ecological stoichiometry related to microbial biogeochemical processes (TER and CNR), the open box indicates another important hypothesis not directly related (GRH), and gray boxes indicate parameters and processes underlying stoichiometric responses of microbial communities to elemental imbalances.

N and P (increasing C limitation). Such different elemental limitations for microbial growth have distinct implications for individual microbially mediated C and nutrient fluxes, leading to feedbacks on nutrient availability (Fig. 6). The most prominent examples are the release of excess C via overflow respiration under nutrient limitation (Tempest and Neijssel 1992) and the release of excess N as ammonium contributing to N mineralization flux under C (or another element than N) limitation (Schimel and Weintraub 2003). A differential recycling of C and nutrients (N or P) as a consequence of imbalance between resource stoichiometry and microbial nutrient demand results in disparate C : nutrient release ratios and is termed the consumer-driven nutrient recycling theory (CNR; Sterner 1990, Elser and Urabe 1999, Sterner and Elser 2002). The CNR theory proposes that the balance of the stoichiometry of resource and consumer and their element use efficiency, such as CUE, directly determines the ratios of nutrient recycling. A key assumption for CNR is that consumers are (strictly) homeostatic (Sterner and Elser 2002). Soil microbial communities exhibit a large degree of stoichiometric homeostasis, which they maintain by adjusting (1) their element use efficiency (to release elements in excess and optimize the use of limiting elements) and (2) their extracellular enzyme production (to mobilize resources to meet their elemental demand; Mooshammer et al. 2014*b*). These are the underlying mechanisms of the CNR theory (Fig. 6), and are discussed in the framework of the threshold elemental ratio (TER). The CNR theory is intimately linked to the TER that represents an indicator of relative nutrient limitation, providing a tool to understand constraints on microbial growth by different nutrient availabilities in the environment. TER is commonly integrated in decomposition models to predict microbial C and nutrient fluxes as a function of resource stoichiometry (e.g., Manzoni and Porporato 2009, Moorhead et al. 2012, Averill 2014).

TER is defined as the elemental C : nutrient ratio at which the control of microbial metabolism switches from energy (C) to nutrient (N or P) supply (e.g., Urabe and Watanabe 1992, Anderson and Hessen 1995, Frost et al. 2006, Doi et al. 2010). Thus, a certain nutrient becomes limiting for growth when resource C : nutrient ratios are greater than TER. Because TER links microbial biomass stoichiometry and element use efficiencies, it may vary by the extent to which microbial homeostasis is maintained in relation to variations in external resource supply. In practice, TER can be estimated from the transition from net nutrient immobilization to net nutrient mineralization during organic matter decomposition, i.e., the critical C:N or C:P ratio (or $TER_{C:N}$ or $TER_{C:P}$). Usually, $TER_{C:N}$ for terrestrial decomposers is thought to be relatively constant around a molar ratio of 23–47 (e.g., Berg and McClaugherty 2003, Moore et al. 2006, Parton et al. 2007). For forest floor organic matter, a critical C:P molar ratio of 1420 has been reported (Saggar et al. 1998). Plant litter, however, is almost always rich in C compared to nutrients and, thus, terrestrial litter decomposition is considered to be N or P limited rather than C limited. In the case that plant litter has a C:N and C:P ratio above the microbial $TER_{C:N}$ and $TER_{C:P}$, respectively, we can adapt the TER concept to the transition from microbial N to P limitation. The $TER_{N:P}$ or critical N:P ratio for decomposition was proposed to range between a molar ratio of 20 and 33 (Aerts 1997*a*, Smith 2002). Notably, Güsewell and Freeman (2005) found that litter decomposition was always P limited for litter with molar N:P ratio above 49, but could be N or P limited with lower N:P ratios. Although litter decomposition is considered to be nutrient limited (N or P), it is often limited by low C quality (Ågren et al. 2001, Bridgham and Richardson 2003). The consequence of high recalcitrance of organic matter for $TER_{N:P}$ was illustrated by Sinsabaugh and Follstad Shah (2011) in the context of the GRH and their reinterpretation of the results of Güsewell and Gessner (2009). That study found that increasing the nutrient supply to the plant litter decomposers increased mass loss rates and shifted community composition, and thereby the $TER_{N:P}$ of microbial decomposers decreased from a molar ratio of 100 to 4. According to the GRH, increasing resource supply promotes faster growth, which increases biomass P relative to N (Sterner and Elser 2002). The resulting higher P demand then shifts the $TER_{N:P}$ toward a lower N:P ratio. In turn, in plant litter with low C quality, a significant fraction of essential elements (N in particular) are bound in recalcitrant molecules, reducing nutrient availability. As organic matter recalcitrance increases, nutrient supply effectively declines. Consistent with the GRH, microbial growth rates and biomass P decrease and consequently $TER_{N:P}$ increases due to lower microbial P demand. The $TER_{N:P}$ thus is, among other factors, strongly dependent on plant species composition, which determines C quality, N:P ratio, and initial N and P concentration.

The TER concept integrates the metabolic theory of ecology (MTE), which describes ecological organization in thermodynamic terms, and the EST, which describes ecological organization in terms of elemental resource availability (Sterner and Elser 2002, Brown et al. 2004, Allen and Gillooly 2009). Extracellular enzyme activities (EEA) represent an intersection of MTE and EST because enzyme expression is a product of cellular metabolism specifically regulated by environmental nutrient availability. The application of EEA through TER has become an emerging conceptual framework of ecoenzymatic stoichiometry (Sinsabaugh et al. 2008, 2009, Sinsabaugh and Follstad Shah 2011, 2012). By using the activities of β-1,4-glucosidase (BG), β-1,4-N-acetylglucosaminidase (NAG), leucine aminopeptidase (LAP), and acid (alkaline) phosphatase (AP), Sinsabaugh et al. (2009) observed a mean global ratio of C:N:P acquisition, ln(BG):ln(NAG+LAP):ln(AP), of approximately 1:1:1. This consistent, nearly 1:1:1 ratio of enzymatic activities was proposed to represent the equilibrium between the stoichiometry of microbial biomass and organic matter and the microbial element use efficiencies. Based on this, Sinsabaugh and Follstad Shah (2012) developed a biogeochemical equilibrium model that predicts microbial CUE from the stoichiometry of microbial biomass and organic matter, and the ratios of EEAs under conditions of multiple resource limitation by combining kinetics of enzyme activity, MTE, and EST.

Both TER and CNR are a function of microbial element use efficiency (ratio of element invested in growth over total element uptake), such as CUE, nitrogen use efficiency (NUE), and phosphorus use efficiency (PUE; Fig. 6; Sterner and Elser 2002). Microbes can regulate their element use efficiencies according to their nutrient demand, such that they release elements in excess depending on their C and nutrient demand (e.g., respiration, N mineralization). Microbial CUE has been the focus of many studies in biogeochemistry, and its stoichiometric and environmental control and importance within the TER concept has been recently reviewed by Manzoni et al. (2012) and Sinsabaugh et al. (2013). By contrast, we have only little knowledge on the regulation of microbial NUE as well as PUE, although they have been taken into account in some theoretical and conceptual models of organic matter decomposition (e.g., Manzoni and Porporato 2009) or stoichiometric models, in which they are often assumed be constant (Sinsabaugh and Follstad Shah 2012). Mooshammer et al. (2014*a*) have recently demonstrated, however, that microbial NUE increased with increasing resource C:N ratio and that the C:N imbalance between resource and microbial biomass was also compensated for by adaptations in NUE and not solely by CUE, as usually assumed. In other words, resource C:N imbalance inversely affects CUE and NUE (Fig. 7). In the framework of TER, we expect that microbial CUE reaches a maximum (Sinsabaugh et al. 2013) below the $TER_{C:N}$ when microbial communities are C-limited and N is in excess, accompanied by a concomitant decrease in NUE. In contrast, above the $TER_{C:N}$, microbes are expected to be N limited, while C is in excess, and NUE should consequently reach a maximum accompanied by down-regulation of CUE. Such integration of variable microbial nutrient use efficiencies has the potential to facilitate further development and application of CNR and TER to advance

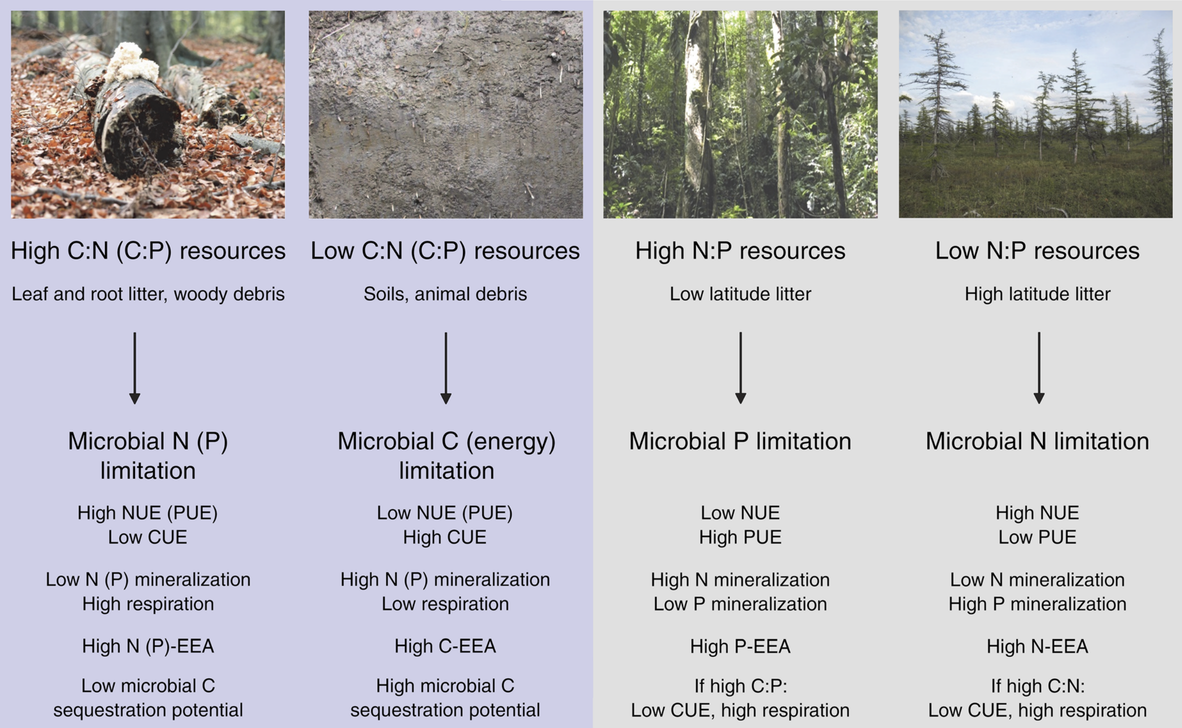

Fig. 7. Hypothetical effects of plant litter and soil C:N:P on microbial processes; CUE, NUE, PUE, C (N, P)-acquiring extracellular enzyme activity [C (N, P)-EEA]. Photo credits (left to right): Alexander Bruckner, Andreas Richter, Wolfgang Wanek, Jörg Schnecker.

our understanding of microbially mediated nutrient fluxes as a response to nutrient limitation.

In addition to adjustments in element use efficiencies, microbial communities can also mobilize resources to meet their elemental demand by producing specific extracellular enzymes in order to alleviate limitations by a particular element. The resource allocation theory proposes that microbial communities maximize their productivity by optimizing their allocation of resources in the production of extracellular C-, N-, and P-acquiring enzymes, i.e., increased investment of C and available nutrients into enzymes mining for limiting nutrients (Sinsabaugh and Moorhead 1994). Phosphatase activity has been shown to be inversely related to inorganic P availability and to be highly responsive to changes in local nutrient conditions (Olander and Vitousek 2000, Treseder and Vitousek 2001, Allison et al. 2007, Marklein and Houlton 2012). Phosphorus additions thus suppress phosphatase activity, whereas N additions enhance phosphatase activity, suggesting that microbes may allocate excess N to phosphatase enzymes (Olander and Vitousek 2000, Marklein and Houlton 2012). Whereas the inverse relationship between phosphatase activity and P availability is well supported across scales, there is no such simple relationship between N-acquiring EEAs and N availability at the ecosystem scale (Sinsabaugh and Follstad Shah 2012). This relationship may be masked by the fact that N acquisition from organic matter (1) is more complex than P acquisition, and (2) organic N represents not only an important N resource but also a C resource. Organic P is generally attached by ester bonds, which are easily broken down through hydrolytic phosphatase enzymes (Vitousek and Howarth 1991), allowing microbes to deconstruct organic phosphorus-containing compounds and take up inorganic phosphate without the associated C. By contrast, N-acquisition strategies are linked to the C-substrate preferences of particular taxa, because N is distributed among several classes of organic polymers as well as humic substances (McGill and Cole 1981). Microbial utilization of organic N may have different implications for C and N mineralization fluxes, as one would predict from simple stoichiometric models, assuming that microorganisms have substrate-specific CUE, which influences their substrate preferences. For example, if C from N-containing substrates was used with a higher efficiency than C from C-only substrates, microbes would use C more efficiently by preferentially utilizing the N-containing substrate, which would increase N mineralization. In addition, it must be kept in mind that microbes that are N limited may not be able to allocate resources to extracellular enzymes, as enzymes themselves are N-rich substances that need to be released to the environment and are thus lost for the organism. If microorganisms become severely limited by N, it is likely that they will become dormant until new resources become available (Blagodatskaya and Kuzyakov 2013).

Overall, the TER concept is established as a simple but applicable tool for predicting microbial C and nutrient fluxes. However, even the simple relationship between resource stoichiometry and mineralization fluxes as predicted by CNR theory has not yet been explicitly tested for terrestrial microbial communities. Another important mechanism underlying decomposition and nutrient cycling is the taxonomic composition of the microbial community. Different microorganisms have different enzyme capabilities, and metabolic and stoichiometric characteristics. Certainly, for an accurate representation of stoichiometric relationships in biogeochemical models, we need to account for microbial community dynamics, which have the potential to influence C and nutrient flow driven by a microbial community response to resource stoichiometry (Kaiser et al. 2014).

Stoichiometric requirements of microbial groups and feedbacks on nutrient availability

Decomposition rate is not only affected by chemical composition but also by turnover rates, cell size, life history, and shifts in community composition in response to resource stoichiometry. Here we raise the following questions: (1) To what extent are microbial communities related to the nutrient status of the ecosystems? (2) Do global gradients of microbial communities exist? (3) What are the feedbacks of microbial colonization on the substrate stoichiometry?

Resource stoichiometry (C:N:P) affects which microorganisms dominate the decomposition process and the extent to which N or P limits growth. Nutrient-poor organic matter is usually dominated by fungi because their nutrient requirements and metabolic activity are lower than in bacteria (Güsewell and Gessner 2009). This explains the lower P requirements of fungi vs. bacteria (Güsewell and Gessner 2009). Fungal dominance also relates to the higher N:P ratios at which fungi become P limited, whereas bacteria become P limited at lower N:P ratios (Appendix: Table A1). Besides the ability of fungi to provide enzymes for the degradation of more complex C-rich substrates, which are usually poor in nutrients, their lower P requirement is probably another explanation for fungal dominance in the decomposition of litter types with higher N:P ratios (Wardle et al. 2004). Within fungi there appear to be differences within phyla, e.g., within the phylum of *Ascomycota*, *Chaetothyriomycetes* were related to decomposition in resource-poor environments, while *Leotiomycetes* and *Sordariomycetes* were related to decomposition in resource-rich environments (Strickland et al. 2009, Schneider et al. 2012). Within bacteria, *Acidobacteria* and *Actinobacteria* were associated with resource environments of lower quality (Strickland et al. 2009). Especially for the *Actinobacteria*, there is relatively little known about their ecological attributes, but they have a filamentous growth form similar to fungi and therefore are presumed to have the ability to effectively scavenge nutrients. Gram-negative bacteria are favored in soils with high organic matter content (Fierer et al. 2003, Bray et al. 2012) and nitrogen availability (Hossain et al. 2010, Bray et al. 2012). Thus, higher-quality litters tend to be dominated by Gram-negative bacteria while fungi and Gram-positive bacteria are more prevalent on litters of lower quality.

We have summarized recent findings on how resource stoichiometry favors colonization by certain phylogenetic groups, but it also affects life strategies. When organisms have limited access to essential nutrients, natural selection within populations will favor individuals that are most effective at acquiring these nutrients (Strickland and Rousk 2010). Limiting nutrients can be assimilated from the resources through the production of extracellular enzymes. This strategy has costs and benefits that are related to organism life strategies (Allison 2012). With slower growth and turnover rates, *K*-strategists invest more into decomposition of C-rich substrates and have higher cellular C:N ratios. With faster growth and turnover rates, *R*-strategists have a larger amount of N- (and P-) rich ribosomes and also higher mortality rates, resulting in a higher N demand over time (Kaiser et al. 2014). Thus, *r*-strategists are favored at low substrate C:N ratios, and *K*-strategists are favored at high substrate C:N ratios. Similar to the separation of microbes into *r*- and *K*-selected organisms (Fierer et al. 2007, Strickland and Rousk 2010) is the differentiation into opportunistic microorganisms, which are characterized to use broadly different pools of organic matter, and show high growth rates as they have a high affinity to soluble substrates (Moorhead and Sinsabaugh 2006), and "miners," which are characterized by the use of lignin as a substrate, and grow rather slowly (Moorhead and Sinsabaugh 2006, Hättenschwiler et al. 2011).

Resource quality and nutrient availability promote the establishment of certain phylogenetic as well as physiological groups; in addition, the type of microbial interactions with each other and with plants can be affected. Thrall et al. (2007) hypothesized that mutualistic associations most likely arise in nutrient-limited environments and parasitic associations are most likely in high-fertility environments, i.e., under nutrient surplus. At high enzyme-production rates, the community changes toward cheaters (organisms who do not synthesize enzymes but take up product; Allison 2005), and the community that produces a broad spectrum of enzymes declines. Taxa that produce few or no enzymes (cheaters) can survive or even accumulate to high abundances when enzyme production by miners is high. When total enzyme production is low, it seems to be advantageous for microbes to produce a broad range of enzymes, and remains still favorable as cheater populations increase (Allison 2012). Positive associations tend to reduce the selection for a distinct suite of enzymes, by taking up monomers provided by other microbes. These community dynamics were related to rates of litter decomposition. Low rates of enzyme production resulted in linear increases in litter decomposition rates, while high rates of enzyme production led to a saturation of decomposition rates (Allison 2012). While cheating is an antagonistic relationship between microbes, different trends of interactions with plants can also be observed.

Mycorrhizal fungi have developed especially efficient P-uptake strategies. This promotes the proportion of mycorrhizal fungal hyphae, increasing the N:P ratio of the microbial biomass in P-deficient systems. Mycorrhizal fungi deliver P to their host plants, even though they have higher tissue P concentrations and lower N:P ratios (ectomycorrhizae biomass N:P ratio 11.3; Appendix: Table A1; Wallander et al. 2002, 2003) than plants. This is probably because their superior P acquisition allows them to readily satisfy their own needs, creating a surplus that can be used in C-for-P trade (Johnson 2010). These examples illustrate how fungi can deal with higher resource stoichiometries and feedback on the nutrient status of the ecosystem by lowering N:P ratios for plants.

In boreal forests, which are typically N limited, ericoid mycorrhizal fungi can also deliver simple organic N compounds to their host plants (Näsholm et al. 1998). In contrast, arbuscular mycorrhizae (AM) in the tropics are highly efficient P mobilizers. Ericoid mycorrhizae dominate cold and wet environments that contain high C:N litter, and ectomycorrhizae dominate ecosystems containing litter with intermediate C:N ratios. AM occur in warmer ecosystems containing lower C:N litter, which is more easily mineralized but tends to be P limited (Johnson 2010). Generally, across large latitudinal gradients, there appears to be a strong relationship between litter quality, the humus that arises from it, and the predominant form of microbes (saprotrophs or mycorrhizae) that exploit soil resources (Read 1991). These global patterns of different types of mycorrhizae illustrate how fungi can reduce N limitation in boreal areas and P limitation in the tropics.

We conclude that (1) microbial communities respond to the nutrient status of the ecosystem on a phylogenetic level as well as by life strategy. Some saprotrophic fungi and bacteria with hyphal growth use their advantage of easier access to external N and P and thrive under nutrient-poor conditions as miners. (2) Global gradients from N limitation in boreal forests to P limitation in the tropics are reflected by different forms of mycorrhizae. (3) In the examples mentioned, microbial groups help alleviate N and P limitations.

How Does Global Change Affect the Mechanisms of Plant and Microbial Nutrient Cycling?

Enhanced CO_2

Under rising atmospheric CO_2, plant C:N and C:P ratios generally increase in C_3 plants, but not in C_4 plants (Sardans et al. 2012*a*). A recent meta-analysis of atmospheric CO_2 enrichment experiments at concentrations projected for the coming decades revealed overall increases in leaf C:N and C:P ratios (22% and 38%, respectively) in C_3 plants (Sardans et al. 2012*a*). These increases in plant C : nutrient ratios translate to higher soil C : nutrient ratios, despite the usual absence of observed effects on soil fertility (Sardans and Peñuelas 2012). Moreover, recent studies give strong evidence that increasing atmospheric CO_2 induces higher foliar N:P ratios (AbdElgawad et al. 2014, Yang et al. 2014).

PLATE 1. The stoichiometry of litter decomposition is affected by climate change as investigated at the experimental site Lehrforst Rosalia, Lower Austria. Photo credits: Sonja Leitner.

By affecting plant stoichiometry, enhanced CO_2 affects microbial turnover rates in the soil, theoretically resulting in slower decomposition and reduced N availability. However, the water status of an ecosystem largely determines the CO_2 impact on mineralization (Garten et al. 2009). To be specific, the effects of enhanced CO_2 on soil N availability depend on the balance between enhanced microbial N mineralization and increased N demands by plants (Reich et al. 2006). This, in turn, is affected by water availability. For instance, N_2O emission (indicating N overflow metabolism) was enhanced in CO_2 enrichment experiments in humid grasslands (e.g., Regan et al. 2011), but reduced or unchanged in similar experiments in semiarid shortgrass steppe (Mosier et al. 2002) and desert (Billings et al. 2002). Likewise, enhanced N mineralization was observed under enhanced CO_2 and warming in northern, moist ecosystems (Bengtson et al. 2012). The authors explain these results as increased belowground C allocation by root exudates. This stimulated the growth of microbial biomass with a C:N ratio of 7.8, triggering a priming effect leading to SOM decomposition (Bengtson et al. 2012). We therefore assume that N availability can even be stimulated by enhanced CO_2 under the condition that soil moisture and temperature are not limiting microbial activity. This is in line with global model predictions claiming that on the decadal time scale, CO_2-stimulated plant growth will attenuate, and the effect of increased inorganic N mineralization due to climate change will tend to overwhelm the plant N uptake rate (Xu et al. 2012). If this holds true, then the combination of increased CO_2 and warming would even increase N availability, provided that there is sufficient soil moisture.

N eutrophication

Anthropogenic N eutrophication is a current driver of global change that is severely affecting the C:N and N:P ratios of soils and terrestrial plants (Sardans et al. 2012*a*, Peñuelas et al. 2013*a*). Two contrasting situations exist. In areas with intense pastoral activity and use of animal slurry as fertilizer, the N:P ratios of soils have decreased (Arbuckle and Downing 2001, Peñuelas et al. 2009). Cropland is heavily and continuously fertilized with livestock wastes that have N:P ratios of ~3:1, when crop requirements are generally 10:1 or more (Gilliam 1995, McFarland and Hauck 2004). The P-fixing capacity of the soil is thus exceeded (Gilliam 1995), producing even lower N:P ratios over time. This is because P is less soluble than N and therefore tends to accumulate in soil more than N does (Gilliam 1995, McFarland and Hauck 2004).

On a global scale, the continuous increase of N:P ratios of all types of inputs resulting from human activities leads to a progressive global increase in plant-available N:P ratios (Peñuelas et al. 2012, 2013*a*). Anthropogenic applications of P from mineral fertilizers, livestock slurry, and manure reach 22–26 Tg P/yr and have been nearly constant since 1989 (see detailed information in Peñuelas et al. [2012, 2013*a*]). In contrast, global anthropogenic inputs of N, including reactive N from fossil fuel combustion, industrial N fertilizers, and biological fixation of atmospheric N_2 by cultivated leguminous crops and rice, are 208–216 Tg N/yr and continue to increase (Peñuelas et al. 2012). Unlike N, P is not volatile, so very little P is redistributed from cropland to nearby natural terrestrial ecosystems. For example, the atmospheric molar N:P deposition ratio is currently 44–47 over land, approximately twice the molar ratio in terrestrial plants (22–30). Over the oceans it is 114–370, which considerably exceeds the Redfield ratio (Peñuelas et al. 2013*a*). Projections of future N emissions suggest an expansion of the area with high anthropogenic N deposition and high deposited N:P ratios from the populated temperate regions of the Northern Hemisphere into tropical regions (Lamarque et al. 2010, Hietz et al. 2011, Peñuelas et al. 2013*a*). Available studies show a 25% average decrease in foliar C:N ratios in response to simulated experimental N deposition (Sardans et al. 2012*a*). Even though N inputs accelerate P cycles (Marklein and Houlton 2012) and reduce the abundance of N_2 fixers, these inputs are frequently insufficient to equilibrate plant N:P stoichiometry and to prevent an increase in the N:P ratios of organisms and ecosystems. N deposition therefore increases the N:P ratios of terrestrial plants. This potentially alters the species composition of communities, reduces the community of N_2 fixers in the soil, and reduces species diversity (Sardans et al. 2012*a*, Peñuelas et al. 2013*a*). We can expect that plant and litter N:P ratios will increase in the short term in areas with continuous loadings of high N:P ratios. Moreover, species with high leaf and litter N:P ratios will be favored in the medium to long term, with further consequences on soil trophic webs (Peñuelas et al. 2012, 2013*a*, Sardans et al. 2012*a*). We can also expect that N saturation will decrease N resorption and increase the litter N:P ratio, thus altering the role of P limitation in soil trophic webs (Kozovits et al. 2007, Jacobson et al. 2011).

Because of stoichiometrically coupled C and N cycles, N eutrophication affects C sequestration in soils, which constitute the largest terrestrial C pool. Increasing N inputs to natural ecosystems promote plant growth and hence also increase C inputs to the soil litter layer. At the same time, trees invest a smaller fraction of C into root growth and exudates, the latter potentially inhibiting mycorrhizal fungi and rhizosphere-inhabiting bacteria (Högberg 2010, Högberg et al. 2010, Luo and Zhou 2010). This leads to uncertain consequences for long-term C sequestration.

Warming and drought

Elevated concentrations of atmospheric greenhouse gases have changed the global climate, raising Earth's surface temperature by 0.74°C in the past century and changing the intensity of precipitation in several areas of the world (IPCC 2007). Most studies suggest that warming and drought increase plant C:N and C:P ratios in currently warm-dry and temperate-dry ecosystems by mechanisms associated with water conservation and increased nutrient use efficiencies (Sardans et al. 2012*a*). These effects can be even higher if warming and drought coincide and if the atmospheric concentration of CO_2 continues to rise (Sardans et al. 2012*a*). Such changes in C:N:P stoichiometry are accompanied by other changes in leaf chemistry. These include increases in the concentrations of K, cellular osmolytes (including sugars and amino acids), and secondary metabolites that are normally C-rich anti-stress compounds such as phenolics (Rivas-Ubach et al. 2012). These effects are also frequently associated with reduced water uptake by plants (Peñuelas et al. 2013*b*), with decreased activity of soil enzymes, and with reduced availability of N and P (Sardans and Peñuelas 2012). Under more arid conditions, increases in litter C:N and C:P ratios (Sardans et al. 2012*b*) and slow returns of nutrients from leaf litter to soil are expected and have already been observed (Saura-Mas et al. 2012).

The effects of warming on C:N and C:P ratios at high latitudes, however, are less clear. This suggests a strong dependence on the richness of soil nutrients and on interactions with other drivers of global change, such as N deposition (Aerts et al. 2012). Some studies report lower plant C:N ratios after increases in nutrient uptake associated with higher soil biological activity and nutrient availability (Welker et al. 2005, Aerts et al. 2009). In a recent meta-analysis, Aerts et al. (2012) calculated an increase in C:N ratios in the litter of subarctic flora in response to warming. Recent studies are providing continuous evidence that increasing drought and warming raise plant N:P ratios (Dijkstra et al. 2012, Yang et al. 2013). The several potential implications, including changes in soil processes, warrant future research.

Soil C mineralization shows higher temperature sensitivity than N mineralization, and the latter is more dependent on soil moisture (Beier et al. 2008). The results suggest that C and N cycles respond asymmetrically to warming, which may lead to progressive N limitation and thereby acclimation in plant production. The microbial C and N cycles are also coupled via oxygen consumption. This means that temperature can indirectly affect microbial N turnover by stimulating soil respiration: this will promote anaerobic conditions in moist soils, thereby accelerating N losses via denitrification (Veraart et al. 2011, Butterbach-Bahl et al. 2013). Soil warming by 4°C in a mountain forest did not significantly affect microbial biomass or community composition, but it did increase soil respiration by 40% and significantly reduce CUE of microbes (Schindlbacher et al. 2011). Nonetheless, the stimulating soil warming effect on decomposition was offset by prolonged summer droughts (Schindlbacher et al. 2012). This supports our expectation that warming in combination with arid conditions will slow down nutrient cycling between plants, litter, and soil.

From this, we deduce that global change effects on the stoichiometry of nutrient recycling largely depend on the soil water status (see Plate 1). This holds true for enhanced CO_2 as well as for nitrogen inputs to ecosystems; likewise the impacts of global warming on plant C:N and C:P ratios, and soil C sequestration may be obscured by moisture conditions.

Conclusions

This review demonstrates that a stoichiometric perspective facilitates interpretation of the linkage between above- and belowground systems, the so-called green and brown worlds. In answer to our question (1), we found evidence that latitudinal gradients of stoichiometry do exist, but with different trends for plant tissue and litter and soil organic matter and microbial biomass. This apparent paradox can be solved by looking into plant and microbial physiology in the light of stoichiometric concepts, which allow for positive and negative feedback effects on substrate N and P availability. Foliar N and P are resorbed less at N- and P-rich sites and under optimal climatic conditions than at N- and P-poor sites. Thus, lower litter nutritional quality coincides with nutrient-poor sites and nonoptimal climatic conditions, constituting a positive feedback with negative consequences for the soil trophic web. Plant nutrient resorption efficiency is higher on nutrient-poor soils. The lower nutrient concentration in litter results in reduced decomposition rates, nutrient release, and energy and matter transfer to the other trophic levels. Moreover, compared to N, P shows higher variability in resorption efficiency and higher resorption sensitivity to nutrient availability, features that are very important for P conservation in plants and for final litter N:P stoichiometry. Sites exhibiting litter low in N and P tend to show microbial nutrient immobilization during decay (question 2). This leads to a forest floor depleted of available nutrients and perpetuates nutrient deficiency for plant growth. However, standing crops of undecomposed litter progressively slow down mineral leaching and soil erosion and hence help conserve nutrients in ecosystems, i.e., a negative feedback on N and P depletion. In addition, the microbial decomposition process triggers a convergence of C:N:P ratios due to the largely homeostatic nature of microbes. On a microbial-community level, microbial groups such as bacterial and fungal miners with hyphal growth and specific types of mycorrhizae alleviate N- and P- limitations, respectively, and thereby help lower stoichiometric constraints for plants. Besides these explanations, other underlying mechanisms of latitudinal trends in stoichiometry are complex, involving chemical and physical stabilization processes of organic debris, and strong impacts of climate, which opens up a vast field of future research. In particular, the interactive effects of different global change drivers demand a better understanding, as well as microbial element use efficiencies and their temperature and moisture sensitivities.

We report that many studies on aspects of global change suggest that warming, drought, and CO_2 enrichment increase plant C:N and C:P ratios by mechanisms associated with water conservation and increased nutrient and water use efficiency (question 3). These increases in plant C : nutrient ratios translate to higher topsoil C : nutrient ratios, slowing down nutrient recycling and microbial SOM decomposition. Under moist conditions, opposite effects can be expected to be triggered by priming and enhanced mineralization processes under high CO_2 and warming. We therefore suggest introducing stoichiometric regulation of the growth and activity of plants as well as soil microorganisms into process-based models and linking these with regionalized climate scenarios which include future rainfall patterns (Sistla et al. 2014). Better knowledge of stoichiometric regulation of N and P availability under predicted temperature/moisture regimes will help better understanding future nutrient cycling in a changing world.

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SUPPLEMENTAL MATERIAL

Ecological Archives

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