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Mineralization ratios of nitrogen and phosphorus from decomposing litter in temperate versus tropical forests

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ABSTRACT

Aim Terrestrial ecosystems sequester about 25% of anthropogenic CO_2 emissions annually; however, nitrogen (N) and phosphorus (P) limitation of plant productivity and microbial functioning could curtail this key ecosystem service in the future. Our aim is to address variations in nutrient resupply during decomposition – especially whether the N:P ratio of nutrient recycling via mineralization varies within and across diverse forest biomes.

Location Global forest ecosystems.

Methods We compiled data on *in situ* litter decomposition experiments (leaf, wood and root) from the primary literature to examine the relationships between net N and P mineralization across temperate versus tropical forests world-wide. We define net nutrient mineralization ratios as the average N:P released from decomposing substrates at a given ecosystem site.

Results We show that net N and P mineralization are strongly correlated within biomes, suggesting strong coupling between N and P recycling in forest ecosystems. The net N:P of leaf-litter mineralization is higher in tropical forests than in temperate forests, consistent with latitudinal patterns in foliar and leaf-litter N:P. At the global scale, the N:P of net mineralization tracks, but tends to be lower than that of litter N:P, pointing to preferential P (versus N) mineralization in forest ecosystems.

Main conclusions Our results do not support the view that there is a single, globally consistent mineralization N:P ratio. Instead, our results show that the N:P of net mineralization can be predicted by the N:P of litter, offering a method for incorporating P into global-scale models of carbon–nutrient–climate interactions. In addition, these results imply that P is scarce relative to microbial decomposer demands in tropical forests, whereas N and P may be more co-limiting when compared with microbial biomass in the temperate zone.

Keywords
Decomposition, mineralization, nitrogen, nutrient cycling, phosphorus, stoichiometry.

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INTRODUCTION

Nitrogen (N) and phosphorus (P) are necessary for life, yet these elements are scarce relative to the demands of most terrestrial organisms; hence the full production capacity of the biosphere is generally constrained by the availability of N and P (Vitousek & Howarth, 1991; LeBauer & Treseder, 2008; Vitousek *et al.*, 2010). Organisms in natural ecosystems rely heavily on nutrients released during the decomposition of organic matter, a process known collectively as nutrient mineralization. Mineralization
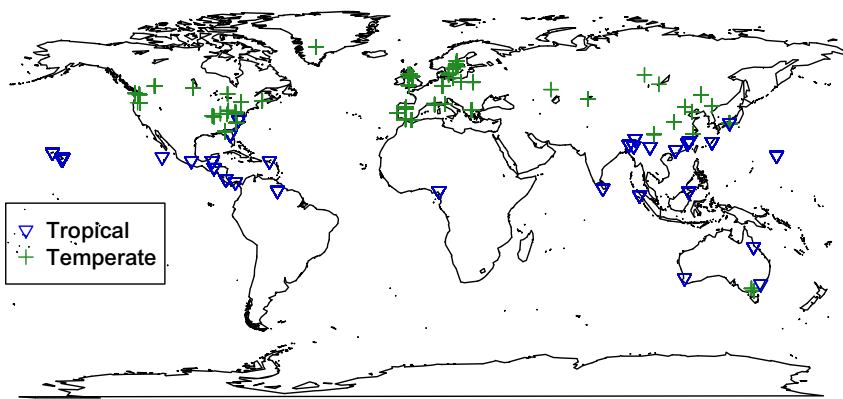
Figure 1 Map showing the sites included in the synthesis. Triangles indicate tropical forest sites while plus signs indicate temperate forest sites.

regenerates nutrients at a much faster rate than external inputs of either N or P in ecosystems; consequently, the conversion of organically bound N and P to biologically available forms fuels most of Earth's terrestrial and aquatic productivity (Eppley & Peterson, 2002; Cleveland *et al.*, 2013). Identifying global patterns of net mineralization is therefore critical to an improved understanding of how nutrients regulate plant CO_2 capture and terrestrial feedback to climate change (Hungate *et al.*, 2003; Thornton *et al.*, 2007; Gerber *et al.*, 2009; Wang & Houlton, 2009; Zaehle *et al.*, 2014). Here, we use data synthesis to examine patterns of net N and P mineralization across a range of globally distributed forest sites (Fig. 1), which allows us to develop and apply the concept of terrestrial nutrient mineralization ratios.

Scientists have for decades used N:P (the nitrogen–phosphorus ratio) of ecosystem pools to examine relationships between nutrient supply and demand in terrestrial and aquatic primary producers (Sterner & Elser, 2002; Elser *et al.*, 2007). In his benchmark paper of 1934, Alfred Redfield showed that the molar N:P of inorganic nutrients was *c.* 16/1 across ocean basins, matching that of marine organic matter (Redfield, 1934, 1958). This 'Redfield ratio' has provided a theoretical framework for a wide variety of marine studies and key insights into how the marine biosphere interacts with the global carbon (C) cycle and climate system (Omta *et al.*, 2006). The concept of nutrient mineralization ratios, which is defined as the N:P released from decomposing substrates over the time course of decomposition, is a useful way to estimate the relative biological utilization of nutrients (Anderson & Sarmiento, 1994). Also, nutrient mineralization ratios in the ocean have been used to understand patterns of N fixation, denitrification (Gruber & Sarmiento, 1997; Deutsch *et al.*, 2001) and nutrient limitation of marine phytoplankton (Deutsch & Weber, 2012).

Terrestrial ecologists have questioned the occurrence of Redfield-type relationships on land, resulting in the discovery of coherent patterns in the N:P of live and dead plant pools (Gordon & Jackson, 2000; McGroddy *et al.*, 2004; Reich & Oleksyn, 2004), plant resorption (Reed *et al.*, 2012; Sistla & Schimel, 2012; Vergutz *et al.*, 2012), soil microbial biomass (Cleveland & Liptzin, 2007; Xu *et al.*, 2012) and extracellular enzymes (Sinsabaugh *et al.*, 2009) across terrestrial ecosystems. In addition, previous analyses have shown negative correlations between litter decomposition rate and both litter C:N

and C:P (Parton *et al.*, 2007; Zechmeister-Boltenstern *et al.*, 2015). Stoichiometric studies have provided new insights into terrestrial nutrient limitation and the relationships between the nutrient status of organisms and environmental variation at large spatial and temporal scales (Vitousek, 1984; Zechmeister-Boltenstern *et al.*, 2015). For example, the average N:P of foliar, wood and root pools is higher in tropical than in temperate ecosystems (McGroddy *et al.*, 2004; Reich & Oleksyn, 2004), while the average N:P of resorption is higher in temperate than tropical forests (Reed *et al.*, 2012; Sistla & Schimel, 2012; Vergutz *et al.*, 2012). These observations suggest that temperate forest productivity is widely N-limited and tropical forest productivity widely P-limited, consistent with ecosystem-based theories for geographical patterns of terrestrial nutrient limitation (Walker & Syers, 1976; Vitousek & Sanford, 1986; Vitousek *et al.*, 2010).

We suggest that an examination of the N:P of mineralization from decomposing litter pools will complement our growing understanding of large-scale patterns in terrestrial ecosystem N:P. Litterbags (with leaf, wood or root litter) or tethered leaves have been used for decades to examine rates of decomposition and nutrient mineralization from decaying biomass pools across an array of ecosystem sites. In such experiments, a given mass of substrate and its corresponding nutrient content is tracked over the time-course of litter decomposition, thus resulting in an estimate of net nutrient immobilization and mineralization *in situ* (Swift *et al.*, 1979). Although this approach does not consider the nutrients recycled from pools of soil organic matter and may exclude larger members of decomposer community, litter is a globally important and often rapidly cycling nutrient reservoir that is ultimately converted to soil in terrestrial ecosystems.

Our approach compares net mineralization N:P with initial litter N:P, thereby increasing our understanding of interactions between substrate chemistry and the resupply of nutrients to vegetation. Our study differs from previous research which has evaluated C:N controls on patterns of net N mineralization (Parton *et al.*, 2007) without assessing P (Parton *et al.*, 2007; Manzoni & Porporato, 2009), or where N:P of net mineralization has been examined in the absence of information about initial litter N:P (Manzoni *et al.*, 2010). In addition, a global biogeochemical model has recently simulated system-

atic increases in the N:P of net mineralization from temperate to tropical ecosystems (Cleveland *et al.*, 2013), consistent with litter N:P patterns (McGroddy *et al.*, 2004; Reich & Oleksyn, 2004); however, this prediction is yet to be tested empirically. By exploring empirical relationships between substrate N:P and mineralization across forests, we seek to inform our growing understanding of global-scale nutrient cycling, biological stoichiometry and comparisons between land and ocean biogeochemistry.

Here, we examine the N/P of net mineralization during litter decomposition across temperate versus tropical forests, including an analysis of leaf, wood, root and total litter N:P, by compiling data from litter decomposition experiments across a globally distributed set of sites (Fig. 1). We examine the relative strength of two competing hypotheses. The first hypothesis (H1) is that N and P are mineralized in proportion to their concentrations in decaying litter, similar to results from the marine biosphere (Redfield, 1934, 1958). At its extreme, this hypothesis predicts a strict 1:1 relationship between substrate N:P and net mineralization N:P within and across forest ecosystems, consistent with the relationships for nutrient mineralization in the open ocean (Anderson & Sarmiento, 1994; Gruber & Sarmiento, 1997).

The alternative hypothesis (H2) is that the N:P of mineralization will deviate substantially from that of the substrates, indicating that N and P are mineralized via different pathways or at different rates. Organic N compounds exist in a wide diversity of structures, and decomposers have evolved a suite of enzymes to mineralize N from C substrates. Hence N undergoes 'biological mineralization' in which organisms mineralize N bonded to C during cellular respiration (McGill & Cole, 1981). On the other hand, organic P in the soil is primarily found in ester linkages; thus, a single class of enzymes, the phosphatases, mineralize P via 'biochemical mineralization,' independently of C respiration and N mineralization (Swift *et al.*, 1979; McGill & Cole, 1981). P-cleaving enzymes are much more responsive to soil nutrient conditions than N-cleaving enzymes, probably because organic N compounds exist in a wide diversity of structures and are mineralized by several mechanisms, often coupled to energy acquisition (Sinsabaugh *et al.*, 2008; Marklein & Houlton, 2011). In addition, the tendencies of N- and P-mineralizing enzymes to accumulate in stabilized soil pools are not significantly different (Allison, 2006). Thus, N versus P mineralization could behave independently of one another and litter substrate N:P.

METHODS

We compiled data from the primary literature to calculate the N:P of net mineralization from pools of leaf, wood and root litter across forest ecosystems world-wide (see Appendix S1 in the Supporting Information). All compiled data are shown in Fig. 1 and studies are presented in Table S1 and Appendix 1 (89 separate studies). After preliminary data exploration we found significant differences between temperate and tropical leaf chemistry (defined by a 23.5° latitudinal cut-off, unless the

primary literature specifically called an ecosystem temperate or tropical) using the Wilcoxon signed rank test, so we contrasted these biome classes throughout the analyses.

To estimate terrestrial nutrient mineralization ratios, we used data from tethered-leaf and litterbag (leaf, wood and roots) experiments across an array of global sites. Specifically, we calculated the proportion of mass remaining, the proportion of mass decomposed and the net loss (mineralization) of N and P over the course of *in situ* decomposition (Fig. S1). We define net nutrient mineralization as the period in which neither N nor P was immobilized. We equate net nutrient mineralization to the loss of a given nutrient from the litterbag (see Appendix S1).

We examined the linear associations between the N and P mineralized in tropical and temperate forests using reduced major axis regression (Appendix S1). Owing to data limitations in the case of root and wood litter, we focused primarily on nutrient mineralization ratios from leaf litter, where there are numerous data for a range of sites, including robust comparison of temperate versus tropical forests. Finally, we performed a weighted-average calculation of the N:P of net mineralization of total litter in temperate versus tropical forests based on the biome-specific fractions of root, wood and leaf litter (Appendix S2 and Table S2).

We used ordinary least squares regressions to predict the N:P of net mineralization from the N:P of litter substrates (Appendix S1). As many stoichiometric relationships are non-normal, we log-transformed these data prior to the analysis (Cleveland & Liptzin, 2007).

Because we compare N:P in this study, the time component of the rate of change of N and P is not explicitly considered in our analysis. Instead, we address absolute loss or percentage loss of N and P throughout the course of decomposition. Nevertheless, we also examined net immobilization (Fig. S2) and the temporal dynamics of N and P during decomposition (Figs S3 & S4) to obtain a more complete picture of N and P dynamics during decomposition. Eliminating the time component does not affect the results of the analysis, as the net mineralization data span all phases of decomposition, and neither the N:P of litter, net mineralization nor net immobilization significantly change throughout decomposition (Appendix S1, Figs S3 & S4; $P = 0.034$).

RESULTS

Our quantitative synthesis included data from 89 separate studies (78 leaf litter, 9 stem-wood litter, 7 root litter) in 95 different ecosystem sites (85 leaf, 4 stem-wood, 6 root), 506 decomposition sequences (435 leaf, 34 stem-wood, 37 root) for a total of 2733 individual observations (2239 leaf, 187 stem-wood, 307 root) (Table 1). We observed several distinct phases of decomposition in our analysis, with factorial combinations of net immobilization and mineralization of N and P (Appendix S3, Fig. S4). The data were roughly split between temperate and tropical forest ecosystems, based on total data points (51% tropical, 49% temperate) or litterbag experiments (48% tropical, 52% temperate). However, coverage was relatively sparse in

	Litter		Net mineralization		No. of sites	No. of sequences
	Mean	r	Mean	r		
Leaf (temperate)	19 (15–23)	0.69	9 (7–12)	0.42	54	192
Leaf (tropical)	50 (43–59)	0.90	36 (31–42)	0.92	30	169
Wood	11 (4–30)	0.93	2 (1–5)	0.96	4	9
Root	13 (5–37)	0.74	9 (4–25)	0.81	5	16
Total (temperate)	15		6			
Total (tropical)	28		17			

Table 1 Geometric means of litter and net mineralization N:P determined by reduced major axis regression. Values in parentheses indicate the 2.5–97.5% confidence intervals and *r* is the correlation coefficient.

tropical sites, especially in the Amazon and Congo Basins, where only two litterbag experiments were available in the published literature (Fig. 1).

The N:P of net mineralization was strongly correlated with initial leaf litter N:P ($\rho = 0.751$, slope = 1.44, 95% CI = 1.16–1.72, $R^2 = 0.56$, $P < 0.0001$; Fig. 2a), weakly correlated with initial root litter N:P ($\rho = 0.795$, slope = 0.79, 95% CI = 0.9–1.49, $R^2 = 0.51$, $P = 0.108$; Fig. 2c) and not correlated with initial wood litter N:P ($\rho = 0.023$, slope = 0.02, 95% CI = −1.20 to 1.25, $R^2 = -0.5$, $P = 0.9766$; Fig. 2b). The N:P of net mineralization was not strongly correlated with either the litter N or litter P concentration alone (Fig. S5; $\rho = 0.386$, $P < 0.0001$ for leaves versus [N]; $\rho = -0.088$, $P < 0.0001$ for leaves versus [P]; $\rho = 0.209$, $P = 0.191$ for stem versus [N]; $\rho = -0.474$, $P = 0.002$ for stem versus [P]; $\rho = -0.080$, $P = 0.356$ for root versus [N]; and $\rho = -0.405$, $P < 0.0001$ for root versus [P]). In addition, neither the N:P of net mineralization nor the N:P of net immobilization is strongly correlated with percentage mass loss (Fig. S4; $\rho = -0.066$, $P = 0.0905$ for temperate net mineralization; $\rho = -0.347$, $P < 0.001$ for tropical net mineralization; $\rho = -0.007$, $P = 0.931$ for temperate net immobilization; and $\rho = 0.025$, $P = 0.755$ for tropical net immobilization).

At the biome scale, the N:P of net mineralization of leaf litter was significantly lower in temperate forests (9:1, 95% CI = 7:1–12:1, $R^2 = 0.18$, $P = 0.002$, $\rho = 0.421$, $n = 54$) than in tropical forests (36:1, 95% CI = 31:1–42:1, $R^2 = 0.85$, $P < 0.001$, $\rho = 0.921$, $n = 30$; Table 1, Fig. 3a), roughly tracking the average N:P of leaf-litter substrates (19:1 in temperate forests and 50:1 in tropical forests; Table 1, Fig. 4a). In fact, the relationship between the N:P of net mineralization from decomposing leaves and N:P of initial leaf litter was not significantly different between temperate (slope = 1.29, 95% CI = 0.92–1.66, $R^2 = 0.52$) and tropical forests (slope = 1.77, 95% CI = 1.15–2.38, $R^2 = 0.48$). However, the slopes of N:P of net mineralization versus N:P of leaf litter deviated significantly from a 1:1 relationship in tropical but not temperate forests.

Geometric means of the molar N:P of initial wood litter and its corresponding mineralization N:P were 11:1 (Fig. 4b) and 2:1 (95% CI = 1:1–5:1, $R^2 = 0.93$, $P = 0.036$, $\rho = 0.964$, $n = 4$; Table 1, Fig. 3b), respectively, based on three sequences in temperate forests and one sequence in tropical forests. For roots, geometric means of the N:P of litter and net mineralization were 13:1 (Fig. 4c) and 10:1 (95% CI = 4:1–25:1, $R^2 = 0.66$, $P = 0.093$,

$\rho = 0.814$, $n = 5$; Table 1, Fig. 3c), respectively, based on one sequence in temperate forests and four sequences in tropical forests. Slopes of the relationship between the N:P of net mineralization and the N:P of litter did not deviate significantly from 1:1 for wood and root litter.

While the N:P of net mineralization and litter N:P were correlated among leaves and roots, the N:P of net mineralization was lower than the N:P of the litter substrates in 80% of all data examined (83% of temperate leaf data, 77% of tropical leaf data, 100% of stem data, 80% of root data; Fig. 2). In addition, the bimodal distribution of the N:P of net mineralization versus litter shows that when the N:P of litter is relatively low, net mineralization N:P is lower than predicted by the linear model, while when the N:P of litter is relatively high, net mineralization N:P is higher than predicted by the linear model. While this relationship is strong, the variance of the residuals is much higher at these extremes, weakening the predictive value of the relationship at high and low litter N:P (Fig. S6).

Finally, we estimated bulk forest mineralization ratios by weighting the net N:P of leaf, wood and root mineralization by their relative contributions to the total litter pool (Appendix S2, Table S2). This calculation revealed a marked shift in the N:P of total net mineralization across forest ecosystems globally. The N:P of net mineralization of tropical forests was *c.* 17:1, much higher than estimated for temperate forests (6:1; Table 1).

DISCUSSION

N:P of initial litter substrates

Geometric means of the N:P of leaf, wood and root litter fell within the range of previous compilations. The average N:P of wood in our analysis (11:1) was lower than the N:P used in models to date (i.e. 15:1; Wang *et al.*, 2007) but equal to the N:P of bole material reported previously (11:1; Vitousek *et al.*, 1988). The root litter N:P in our assessment (13:1) was much lower than Gordon & Jackson's (2000) value (40:1) but higher than the N:P of root litter published by Vitousek *et al.* (1988) (7:1). In addition to the small sample size in our compilation, differences between our results and those of Gordon & Jackson (2000) probably reflect root class; our compilation was dominated by fine roots, which have a lower N:P than roots with a larger diameter (Gordon & Jackson, 2000). The N:P of leaf litter was higher in tropical than temperate forests, at 50:1 in tropical forests and 19:1
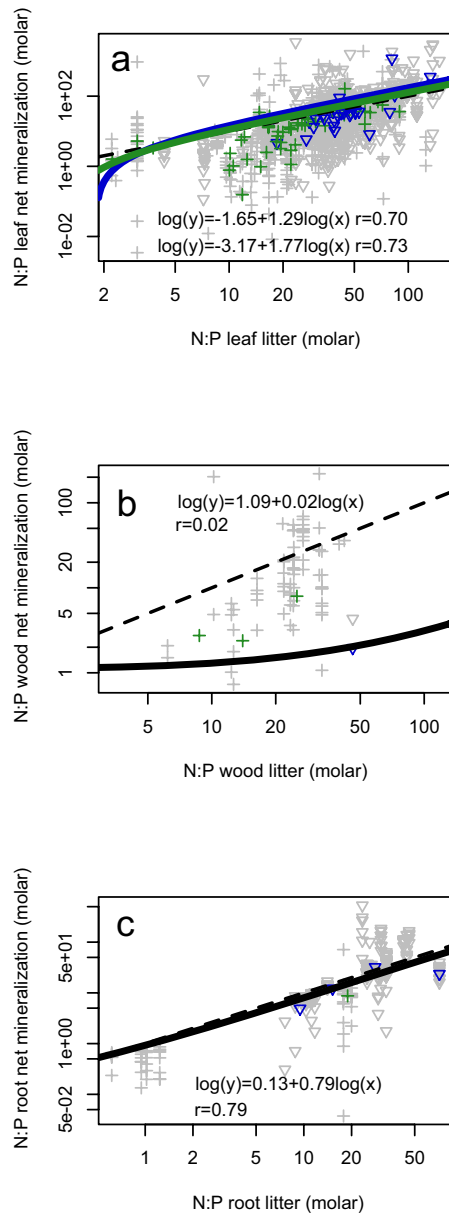
Figure 2 Relationship between N:P of litter and N:P of net mineralization of (a) leaf litter, (b) wood litter, and (c) root litter. The grey symbols represent data for each individual litterbag (temperate leaf, $n = 193$; tropical leaf, $n = 169$; wood, $n = 9$; root, $n = 16$), where the coloured symbols are the site means (temperate leaf, $n = 54$; tropical leaf, $n = 30$; wood, $n = 4$; root, $n = 5$). Blue triangles indicate the site average for tropical forests; green plus signs indicate temperate forests. The dashed line is the 1:1 line and the solid lines are the least squares linear regressions. All units are in mmol. Note that the axes are logarithmic. *P*-values are < 0.001 for temperate forests, < 0.001 for tropical forests, 0.977 for wood and 0.108 for roots.
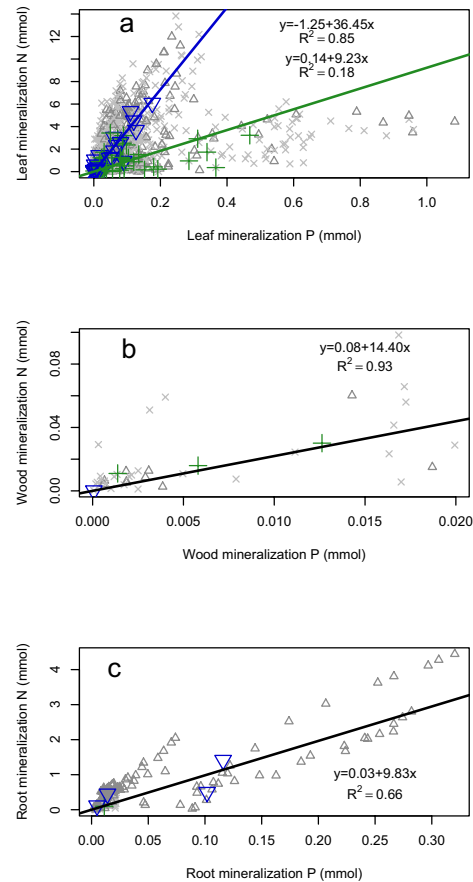
Figure 3 Relationship between N and P during the net mineralization phase of decomposition of (a) leaf litter, (b) wood litter, and (c) root litter. The grey symbols represent an individual litterbag (temperate leaf, $n = 193$; tropical leaf, $n = 169$; wood, $n = 9$; root, $n = 16$). Dark grey triangles indicate tropical forest litterbags and light grey crosses indicate temperate forest litterbags. The coloured symbols represent the site means (temperate leaf, $n = 54$; tropical leaf, $n = 30$; wood, $n = 4$; root, $n = 5$). Blue triangles indicate tropical forests, green plus signs indicate temperate forests, and the solid lines are the reduced major axis regressions for temperate and tropical forests separately (a) or combined (b,c). All units are in mmol.

in temperate forests, a pattern consistent with previous findings (McGroddy *et al.*, 2004). Arithmetic means of all litter N:P values were higher than their corresponding geometric means (as dictated by the inequality of arithmetic and geometric means), except for leaf litter N:P in tropical forests which are equal due to the right-skewedness of the tropical data (Fig. 3).

Dependence of net N:P mineralization on substrate

Consistent with H1, we found evidence for a strong substrate dependences in the net N:P of mineralization of leaf litter and, to a lesser extent, root litter across forest ecosystems world-wide.
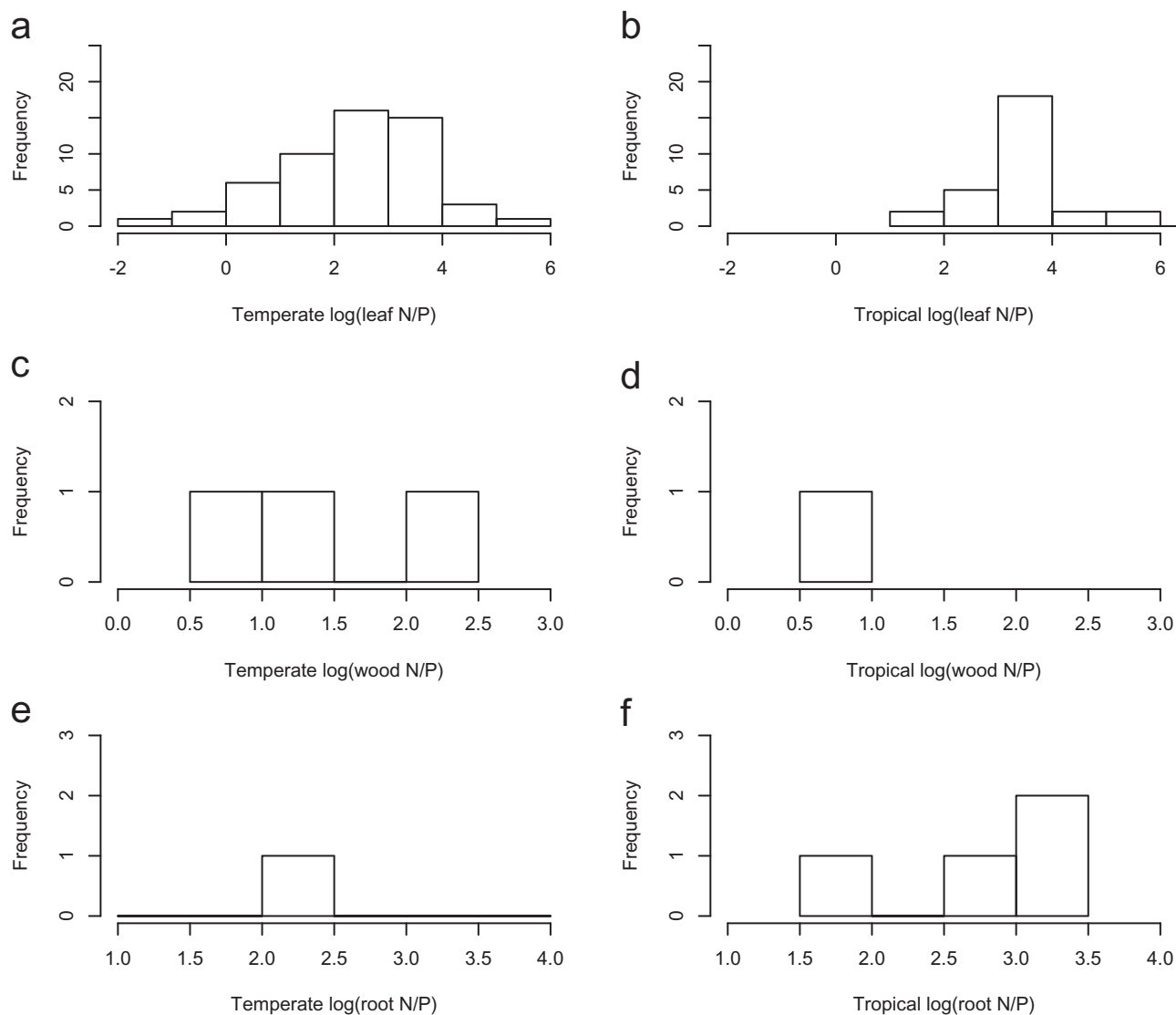
Figure 4 Histograms showing the distribution of site means of N:P of (a,b) leaf litter, (c,d) wood litter, and (e,f) root litter in temperate (a,c,e) and tropical (b,d,f) forests. The *y*-axis, frequency, is the number of studies. Data are log-transformed using the natural logarithm (base e). All units are in mmol.

These results are consistent with previous studies showing that net N mineralization rates strongly correlate with litter N content (Parton *et al.*, 2007). In contrast, we did not find evidence for such a relationship in the case of wood litter, which could be due to its high lignin content, variations in the chemistry of different wood compounds available to decomposers and the long-term nature of wood decay, which could transiently offset relationships between the N:P of substrates and nutrient mineralization. Nitrogen can react with lignin during wood decomposition; this can reduce the biological availability of N in decomposing substrates (Aerts, 1997), and similar relationships could affect rates of P mineralization.

While we found evidence for primary substrate regulation of net mineralization, particularly for leaf litter, the N:P of net mineralization was not always perfectly related to substrate N:P. In root litter, wood litter and temperate forest leaf litter, the confidence intervals of the slope of the N:P of mineralization versus litter overlapped with 1:1, suggesting that the N:P of net mineralization is not significantly different from the N:P of leaf litter (i.e. H1). On the other hand, in tropical forest leaf litter, the slope of the relationship between the N:P of litter and that of mineralization did not conform to a 1:1 relationship, thus pointing to a decomposition-driven alteration of the proportions of nutrients released from forest litter (i.e. H2). In addition, across all leaf and root litter, the N:P of net mineralization had a strong tendency to be lower than the N:P of litter, which indicates that the alteration was systematically skewed toward more rapid rate of release of P than N from leaf and root litter pools. This tendency agrees with results observed for the open ocean, where the N:P of net mineralization corresponds to but is slightly lower than the N:P of organic matter (Clark *et al.*, 1998; Monteiro & Follows, 2012).

Several specific factors could explain the systematic tendency for the N:P of net mineralization to be lower than the N:P of tropical forest leaf litter. Asymbiotic N fixation could change the relationships between the N:P of litter and mineralization by increasing N of decomposing litter compared with P during decomposition; however, a simple calculation shows that asymbiotic N fixation is only 0.7% of the N mineralization rate from forest litter globally, and is thus unlikely to have affected the N:P patterns we found (see Appendix S4). Another possibility involves differences in the physical leaching of N versus P from fresh litter – specifically given the different solubilities of these elements in dissolved organic matter (Neff *et al.*, 2003). Preferential leaching of P from litter has been observed in Panama (Schreeg *et al.*, 2013), for example. P that leaches from a litterbag is likely to become geochemically bound to mineral surfaces in the soil, and doesn't necessarily leave the ecosystem in the short term. However, preferential leaching of P is not likely to exist in all ecosystems, and this mechanism was only important during the initial phases of decomposition (Swift *et al.*, 1979). Finally, preferential immobilization of N into litter (i.e. the microbial recruitment of N from outside the litterbag), more rapid mineralization of P via phosphatase enzymes, or both, probably affected the patterns we observed. In a global meta-analysis of the rates of release of N from decomposing litter, Parton *et al.* found evidence for preferential immobilization of N, especially at low litter [N] (Parton *et al.*, 2007). Phosphatase enzymes can respond more quickly to changes in nutrient availability than N-mineralizing enzymes (McGill & Cole, 1981; Sinsabaugh *et al.*, 2008), pointing to the capacity for P to be rapidly mineralized during litter decay (Marklein & Houlton, 2011). Future experiments could help gain insights on where, when and how these mechanisms interact in causing preferential P (versus N) mineralization of litter pools in forest ecosystems.

In addition, the relationship between the N:P of net mineralization and litter substrates was not perfectly linear (Fig. 2). In sites with very low litter N:P, the N:P of net mineralization is even lower than expected. Thus, at relatively high litter P contents, P is mineralized more than predicted by a linear model. This finding implies that at extremes of nutrient concentration, where the N:P is substantially unbalanced with respect to biological demands, the more abundant nutrient has a tendency to cycle more rapidly than the less abundant nutrient.

Global nutrient mineralization ratios

We found that the N:P of net mineralization of bulk litter was much higher in tropical forests (17:1) than in temperate forests (6:1). This pattern was consistent with the theory and evidence for changes in N and P cycling across forest biomes, where N is thought to behave in excess of P in tropical but not temperate forest sites (Vitousek & Farrington, 1997; Vitousek *et al.*, 2010). This analysis agrees qualitatively with model-based predictions for nutrient mineralization, which suggest a latitudinal decline in the molar N:P of net mineralization from tropical (*c.* 20:1) to temperate (*c.* 10:1) forest ecosystems (Cleveland *et al.*, 2013).

Our results for temperate ecosystems are similar to Manzoni *et al.*'s (2010) mineralization N:P of 9:1 (molar); however, the tropical results were not similar – probably due to the small proportion (19%) of tropical data in the previous estimate (Manzoni *et al.*, 2010). We conclude that there is no single, canonical N:P mineralization ratio for terrestrial ecosystems. Rather, litter N:P exerts primary regulation over the net mineralization of N:P, with distinct differences between the N:P of net mineralization in temperate versus tropical forest biomes that mimic the N:P of leaves, litter and resorption across latitudes (McGroddy *et al.*, 2004; Reich & Oleksyn, 2004; Reed *et al.*, 2012; Sistla & Schimel, 2012; Vergutz *et al.*, 2012).

Limitations of our approach

There are several caveats concerning our estimate of nutrient mineralization ratios. The correlations between N and P were strong but litter N:P accounts for only about 50% of the variation in net N:P mineralization. Litter N and P concentrations did not strongly correlate with the N:P of net mineralization ($r = 0.03$ and -0.07, respectively). Other environmental factors, such as soil decomposer stoichiometry, soil chemistry and hydrology, could account for the other 50% of variation (Swift *et al.*, 1979). As mentioned above, leaf litterbags can exclude larger members of the microbial decomposer community, which could alter the release of nutrients and N:P of net mineralization. However, we note that the offsets in N:P of net mineralization are consistent among litter types, with no evidence for mesh-size effects in our global compilation (mean litterbag mesh size = 1.6 mm, min. = 0.3 mm, max. = 7.5 mm, $R^2 = 0.00$, $P = 0.55$). In addition, abiotic sinks could affect the N:P supplied by litter mineralization, though geochemical fixation by P would be limited to the mineral rather than surface organic soils, which are typically excluded from litterbags. Finally, decomposing microbes can transfer nutrients from the surrounding soil to litter substrates (immobilization). When both N and P are being immobilized, the N:P ratio of net immobilization is 46:1 in tropical leaf litter, 13:1 in temperate leaf litter, 7:1 in wood litter and 68:1 in root litter (Fig. S7). Overall, in both temperate and tropical forests, the N:P of net immobilization (40:1 and 49:1, respectively) is substantially higher than litter N/P (Fig. S7).

Implications of terrestrial nutrient mineralization ratios

Results of our synthesis have several implications. First, widespread evidence for more rapid mineralization of net P than N from decomposing litter pools across forest sites suggests that preferential mineralization of net P compared with N is a general feature of forest nutrient cycling. This result agrees with conceptual models that point to fundamental differences in nutrient cycling between N and P in relation to microbial enzymatic processes during decomposition (McGill & Cole, 1981) and increasing empirical support for preferential uptake of P and conservation by plants and soil decomposers (Vergutz *et al.*, 2012; Mulder *et al.*, 2013; Sardans & Peñuelas, 2015). Neverthe-

less, this analysis is limited in its ability to infer patterns of terrestrial nutrient limitation, as soil organic matter can be an important nutrient reservoir in forest ecosystems – especially in temperate sites where soil organic pools are substantial. In tropical ecosystems, where litter is thought to be the primary path of nutrient cycling, our results could point to less substantial effects of P limitation than previously thought, consistent with recent fertilization experiments pointing to lack of consistent P limitation in lowland tropical forests (Kaspari *et al.*, 2007; Lambers *et al.*, 2008; Wright *et al.*, 2011; Alvarez-Clare *et al.*, 2013).

In addition, our results would suggest that the N:P of litter increases during decomposition through the process of humification. However, a previous global analysis showed that the N:P of forest soils is on average 15:1 (molar) (Cleveland & Liptzin, 2007), lower than the average N:P of litter in both temperate and tropical forests. This suggests that the chemistry of organic matter continues to change after litter decomposition (measured via litterbag experiments) but before the formation of humus is complete – either due to relative enrichment of P in organic matter (by immobilization) or decreases in N (by N mineralization, gaseous losses and/or N leaching).

Our results also have implications for understanding the effects of nutrient constraints on microbial decomposers in temperate and tropical ecosystems. In order to survive, all organisms must meet the proportions of nutrients demanded at equilibrium. For microbial decomposers, these demands are met largely by organic substrates produced by plants. Distinct patterns emerge when we compare the available data on average soil microbial stoichiometry with the stoichiometry of litter mineralization and litter across forest biomes. For instance, in tropical forests, the higher litter (50:1) and net mineralization (36:1) N:P versus decomposer biomass (7:1–15:1) (Cleveland & Liptzin, 2007; Xu *et al.*, 2012) suggests that decomposers must rely on soil P reservoirs, whether organically or mineral bound, in addition to litter. In contrast, decomposers in temperate forests mineralize at a N:P ratio (9:1) that is within the range of their biomass (6:1–15:1). This implies that P is scarce relative to the demands of microbial decomposers in tropical forests, whereas N and P may be more co-limiting when compared with microbial biomass in the temperate zone, similar to hypothetical predictions (Zechmeister-Boltenstern *et al.*, 2015).

The patterns of relative nutrient limitation of decomposing organisms mimic those of global plant communities based on N:P resorption ratios (Drenovsky & Richards, 2004; Reed *et al.*, 2012; Vergutz *et al.*, 2012) and established ecological theory, where plants in the tropics are considered to be P limited and plants in temperate regions N limited (Walker & Syers, 1976; Vitousek *et al.*, 2010). In tropical forests, the N:P of litter is higher than the N:P of leaves, showing that plants resorb relatively more P than N; the opposite is true in temperate forests (Zechmeister-Boltenstern *et al.*, 2015). Similarly, we show that decomposing organisms are mineralizing at a N:P much higher than the average microbial biomass in tropical forests, showing that microbes retain relatively more P than N in the tropics. In temperate forests, microbes mineralize at a N:P within the range

of their stoichiometry, suggesting more co-limitation of N and P. These patterns suggest that plants and microbes are likely to compete more strongly for P in tropical than temperate forests.

Finally, results of this analysis have implications for modelling global nutrient cycling interactions within the context of environmental change, such as elevated CO_2, climate change and rising N deposition. Current models show that C and N are coupled in decomposition (McGill & Cole, 1981; Parton *et al.*, 2007; Wang *et al.*, 2007, 2010; Manzoni *et al.*, 2008; Manzoni & Porporato, 2009), but C and P are not necessarily linked (McGill & Cole, 1981), thus challenging our ability to model these elements together using C-based stoichiometric principles. Biogeochemical models that consider N limitation of decomposition rates reveal constraints on C storage and uptake (Thornton *et al.*, 2007; Wang *et al.*, 2007, 2010; Gerber *et al.*, 2009). The inclusion of P dynamics and its biogeochemical cycling also contributes to more realistic predictive models, particularly in the tropics, as evident by several recent global models (Wang *et al.*, 2007, 2010; Goll *et al.*, 2012). We have demonstrated a stoichiometric link between N and P during mineralization for the forest biome, which can be used to model these global element cycles in these large areas of global C storage (Appendix S5). These improvements have the potential to help predict responses of nutrient-limited forest ecosystems to global climate change and the sustainability of the terrestrial CO_2 sink.

ACKNOWLEDGEMENTS

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Figure S1 Patterns of (a) mass, (b) nitrogen, and (c) phosphorus dynamics of leaf, wood and roots during decomposition.

Figure S2 Net mineralization and net immobilization of N and P of data in (a) temperate and (b) tropical forests.

Figure S3 N:P ratio of leaf, stem and root litter during decomposition in (a) temperate and (b) tropical forests.

Figure S4 Net N:P of (a,b) leaf , (c,d) stem , and (e,f) root mineralization versus (a,c,e) N and P (b,d,f) concentrations.

Figure S5 N:P of net (a,b) mineralization and (c,d) net immobilization in (a,c) temperate and (b,d) tropical forests.

Figure S6 (a,d,g) Residuals versus fitted plots , (b,e,h) QQ-plots and (c,f,i) bar plots showing the distribution of residuals of N:P of mineralization versus N:P of initial litter of (a–c) leaves, (d–f) wood and (g–i) roots (based on Fig. 2).

Figure S7 Net immobilization of (a,b) leaf, (c) wood and (d)roots.

Table S1 Papers included in the study and their biome and plant pool.

Table S2 Proportion of roots, wood and leaves in litter and live plant biomass.

Appendix S1 Supplemental methods.

Appendix S2 Leaf, wood and root partitioning calculation.

Appendix S3 Phases of decomposition.

Appendix S4 Calculation of litter N fixation as a fraction of net N mineralization.

Appendix S5 Equation of P mineralization, given initial substrate N and P and mineralized N, and derivation.

BIOSKETCH

Alison Marklein is a post-doctoral scientist at the University of Montana. Her research works to uncover global patterns and mechanisms found in biogeochemical cycles and biogeochemistry, and to address their feedbacks with the changing climate and nutrient distributions.

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APPENDIX 1 DATA SOURCES

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