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REGULAR ARTICLE

Scale-dependent soil macronutrient heterogeneity reveals effects of litterfall in a tropical rainforest

Shang-Wen Xia · Jin Chen · Doug Schaefer · Matteo Detto

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Abstract
Aims Soil spatial heterogeneity is an important factor partitioning environmental niches and facilitating species coexistence, especially in tropical rainforests. However, fine-scale spatial variability of soil macronutrients and its causative factors are not well understood. We investigate this fine-scale variability and how it relates to environmental factors.
Methods We conducted intensive soil sampling (361 samples) in a 1 ha plot in a tropical rainforest in Southwest China to investigate patterns of spatial heterogeneity in soil acidity and macronutrients and explored how the soil properties were influenced by topography and litterfall using a scale-wise wavelet analysis.
Results Topography showed great variability at larger scales (>25 m) compared to litterfall properties, which peaked at about 25 m. Soil pH showed variation at large scales and was significantly correlated with topography, whereas soil total nitrogen, ammonium nitrogen, available phosphorus, and potassium showed variation at finer scales and were significantly correlated with litterfall chemical fluxes. A dominant species of canopy tree was non-randomly distributed in high litterfall input sites.
Conclusions This study shows that fine-scale spatial variability of soil macronutrients is strongly influenced by litterfall chemical fluxes, highlighting the importance of biotic factors for understanding fine-scale patterns of soil heterogeneity in tropical rainforests.

Keywords Litterfall properties · Plant-soil feedback · Soil spatial heterogeneity · Topography · Wavelet analysis · Xishuangbanna

Introduction

Soil spatial heterogeneity has been recognized as an important dimension of plants' ecological niches, which may facilitate species coexistence in forests (Ettema and Wardle 2002; Silvertown 2004). Spatial partitioning of tree species in response to soil type and topography has been frequently observed in forests (Debski et al. 2002; Potts et al. 2002; Paoli et al. 2006; Slik et al. 2011). For example, a study conducted in three large plots of the Center for Tropical Forest Science (CTFS) showed that

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36–51 % of tree species distributions were associated with soil nutrient patterns (John et al. 2007). A subsequent study of eight tropical plots showed that, after taking topography into account, local soil properties still accounted for substantial variation in tree community composition (Baldeck et al. 2013).

Despite the significant role of soil in partitioning forest niches, a mechanistic understanding of soil spatial heterogeneity is still incomplete, especially for fine-scale (defined here as smaller than 1 ha) variations in tropical rainforests (Dent et al. 2006). Most previous studies focused on spatial heterogeneity at scales that are dominated by topographic and hydrological processes, such as erosion, transport, and sedimentation (John et al. 2007; Yavitt et al. 2009; Baldeck et al. 2013). However, soil spatial heterogeneity may vary on a wide range of scales that may be associated with different ecological processes (Wiens 1989). Detecting fine-scale soil spatial heterogeneity and its driving forces may enhance our understanding of the forest ecosystem processes associated with soil nutrients. Unfortunately, studies on soil nutrient heterogeneity at fine scales in forests remain rare, and the results of the few existing studies were controversial. For example, clear fine-scale spatial patterns have been found in both tropical and subtropical forests (Powers 2006; Wang et al. 2007), but no significant tree species effects were founded in a tropical forest in Costa Rica (Powers et al. 2004). This suggests that fine-scale soil heterogeneity in tropical rainforests may exist, but its causes need further investigation.

Soil chemical properties, such as soil pH, moisture, organic carbon content, total nitrogen (N), available N, and other nutrients, have been shown to decrease upslope within 60–200 m distance (Enoki et al. 1996; Chen et al. 1997; Tateno and Takeda 2003; Poulsen et al. 2006; Wang et al. 2007). The contribution of topography to soil nutrient heterogeneity is also affected by scale and may be less at fine scales (<1 ha) than local scales (20–50 ha) for two reasons. First, topographic gradients at fine scales are small, since topographic variability decreases with decreasing scale (Gagnon et al. 2006). Second, biotic factors may create significant soil nutrient heterogeneity at fine scales, which may dilute the effects of abiotic factors.

Soil properties are not only affected by topography but also by fine-scale biotic factors, such as individual plants, which can modify soil properties and thus generate heterogeneity (Schwinning and Weiner 1998; Ehrenfeld et al. 2005; Townsend et al. 2008). The ability of plants to modify soil nutrients varies among species. For example, nitrogen-fixing plants increase nitrogen in soil (Rodríguez et al. 2009b; Inagaki et al. 2010), lianas return nutrients under their host trees far from their root uptake zone because of their distinctive growth form (Putz 1984; Tang et al. 2011), and leaf size variation among species can influence whether nutrients are returned under or outside tree crowns (Qiao et al. 2013). Furthermore, the root-crown asymmetry of plants (Hruska et al. 1999) suggests that trees with root/crown ratios larger than one may capture nutrients from trees with smaller root/crown ratios. Because a great variety of species and life forms can be found in close proximity in tropical rainforests, we expect spatial heterogeneity of soil nutrients to persist at fine scales.

Among all soil properties, plants may affect soil macronutrients stronger than soil pH in tropical rainforest. Soil macronutrients are strongly recycled by plants in tropical rainforest (Vitousek 1984), so the heterogeneous distribution of plants can easily cause heterogeneity in soil macronutrients. However, plant effects on soil pH are indirect and mainly transmitted by cations such as Ca, Mg, Al, Fe, etc. (Finzi et al. 1998). While these elements are strongly correlated to topography as a result of leaching processes, heavy leaching in rainforest will dilute the effect of plants on soil pH.

One mechanism by which plants influence soil macronutrients may litter input. Most nutrients absorbed by plants return to soil as leaf litter (Vitousek and Sanford 1986; Attiwill and Adams 1993; Wieder et al. 2012). Individuals assimilating more nutrients should return more nutrients to the soil because of lower resorption efficiency under nutrient-rich physiological conditions (Aerts 1996; Kobe et al. 2005). While litterfall amounts affect soil nutrients (Sayer et al. 2012; Leff et al. 2012), heterogeneity of litterfall may also generate soil nutrient spatial variability (Facelli and Pickett 1991). Unfortunately, to our knowledge, few studies have examined how heterogeneity of soil properties is affected by litterfall at fine spatial scales.

We performed high-density soil and litterfall sampling throughout a 1 ha tropical rainforest in Southwestern China and measured soil properties (pH, N, P, and K) and corresponding litterfall properties (mass, N, P, and K). We then mapped the spatial distributions of these variables and calculated topographic position indexes using geostatistical analysis. Finally, we detected scale-dependent variation of all variables and tested effects of litterfall and topography on soil chemical heterogeneity along scale gradients using wavelet analysis (Detto et al. 2013). We aimed to provide a mechanism that explained fine-scale soil heterogeneity. We hypothesized that at the low level of topographic variation found in a 1 ha plot, the levels of soil macronutrients will be driven by leaf litter and vary at very small spatial distances, while pH, more influenced by topography, will vary over a larger scale.

Methods

Study site

This study was conducted within a 20-ha forest dynamics plot (21° 37′ 08″ N, 101° 35′ 07″ E), in a tropical seasonal rainforest in Xishuangbanna Prefecture, Yunnan Province in Southwest China (Hu et al. 2012) (Fig. 1a). This area is at the northern limit of Asian tropical rainforest, with a mean annual rainfall (recorded from the weather station located 14 km south of the study site in Mengla County) of 1532 mm and annual mean temperature of 21.0 °C (Zhu 2006). The area is dominated by warm, wet air masses from the Indian Ocean in the summer and by continental air masses in the winter, resulting in an alternation between rainy (May to October) and dry (November to April) seasons. The soil is lateritic and developed from siliceous rocks (Cao et al. 2006). The entire 20-ha plot is covered by tropical seasonal rainforest with 468 species of trees, including dominant canopy species *Parashorea chinensis* (Cao et al. 2008).

At the southeast corner of the 20-ha plot, we established a 100 × 100 m subplot, with elevation ranging from 711.3 to 736.6 m (Table 1). There were 76 trees with diameter at breast height (DBH) larger than 40 cm. The four most common canopy species were (in order of frequency) *Sloanea tomentosa*, *P. chinensis*, *Pometia tomentosa*, and *Nephelium chryseum*, and these accounted for 46 trees (Table 2).

Data collection

Soil samples were collected from 1 m^2 areas located at 5 m intervals across the plot. Obstructions including

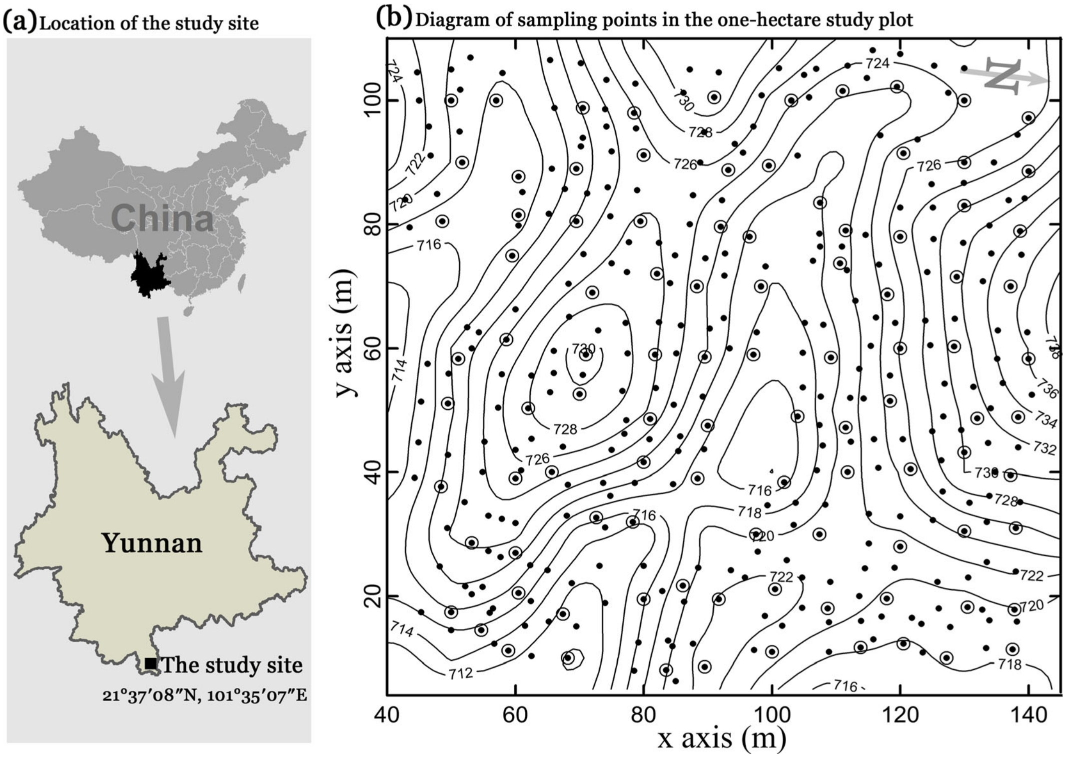

Fig. 1 Location of the study plot (**a**) and diagram of sampling points in the 1 ha study plot (**b**). *Solid points* represent soil samples; *hollow circles* represent litterfall traps

Table 1 Descriptive statistics of the soil properties, topographic position index (TPI), and litterfall properties

Variables	Units	*N*	Values	Ranges	Coefficient of variation (%)
pH		361	5.0	4.3–7.2	
Hydrogen ion		361	8.5×10^{-6} (7.9×10^{-6})	6.9×10^{-8}–4.8×10^{-5}	93
NO_3-N	mg/kg	361	12.5 (12.7)	0.1–104.8	102
Total N	g/kg	361	2.1 (0.4)	1.2–3.7	19
NH_4-N	mg/kg	361	12.4 (4.3)	5.8–55.5	34
Inorganic N	mg/kg	361	24.9 (15.5)	6.1–160.4	62
Available P	mg/kg	361	9.9 (6.3)	1.7–59.2	63
Available K	mg/kg	361	242 (116)	78–941	47
Elevation	m	361	722.6 (4.9)	711.3–736.6	0.7
TPI		361	0.002 (0.015)	−0.030–+0.046	
Litterfall	g/m^2/year	99	662 (153)	343–1185	23
Litter total N	g/m^2/year	99	11.4 (2.9)	5.8–21.2	26
Litter total P	g/m^2/year	99	0.7 (0.2)	0.3–1.6	29
Litter total K	g/m^2/year	99	3.7 (1.2)	1.5–8.8	31

Values are means and standard deviation. Because TPI was an index designed with expected mean value of zero, its coefficient of variation was not calculated

large or dead trees or very steep slopes were avoided by 1 to 3 m shifts in a random compass direction, and points located in streams were discarded, resulting in 361 samples (Fig. 1b). The exact location of each sample point was measured with a laser distance meter (DLE70, Bosch, Robert Bosch GmbH, Germany).

All soil samples were collected from August 23–24, 2011. At each 1 × 1 m sampling point, the litter layer was removed and five cores of topsoil were taken with a 4 cm diameter corer from a depth of 0–10 cm. These were mixed and stored in plastic bags for transport to the Biogeochemistry Laboratory of the Xishuangbanna Tropical Botanical Garden on the same day. Soil clods were broken by hand into smaller pieces, then air-dried with a fan under shade for 30 days, and lastly ground and sieved. Half of each bag's contents was sieved through 2-mm mesh (for available P and K) and the other half through 0.25-mm mesh (for soil pH, total N,

Table 2 The size and number of the four most common canopy species on the plot and their association with nutrient rich sites

	Sloanea tomentosa	*Parashorea chinensis*	*Pometia tomentosa*	*Nephelium chryseum*
Mean diameter at breast height (cm)	65	101	58	60
Total number in study plot	19	18	6	3
Litterfall mass	9	13	4	2
Litterfall N	8	13	3	3
Litterfall P	8	16	3	0
Litterfall K	12	16	3	3
Soil total N	13	13	4	3
Soil NH_4-N	9	14	1	3
Soil NO_3-N	11	18	2	3
Soil available P	12	16	4	3
Soil available K	11	12	2	3
Mean	10.3 (54 %)	14.6 (81 %)	2.9 (48 %)	2.6 (85 %)

For each soil or litterfall property, we show the number of trees found in sites that were above the median level. All selected trees were larger than 40 cm DBH

NH_4-N and NO_3-N), and these samples were stored in separate plastic bags for analyses.

Soil pH was measured in water (soil:deionized water=1:2.5) with a pH meter (PHS-3C, Shanghai Precision Scientific Instrument Co., Ltd, China). Total N was measured with a Carbon-Nitrogen analyzer (Vario MAX CN, Elementar Analysensysteme, Germany). NH_4-N and NO_3-N were extracted by 2 mol/L KCl solution and then measured using a continuous flow analyzer (Auto Analyzer 3, SEAL Analytical, Germany). Available P and K were extracted with the Mehlich III solution (John et al. 2007; Tran and Ziadi 2007). The available P concentration was measured using a spectrophotometer (T723, Shanghai Spectrum Instruments Co., Ltd, China), and available K was measured using an inductively coupled plasma atomic-emission spectrometer (IRIS Advantage-ER, Thermo Jarrell Ash Corporation, USA).

Ninety-nine litterfall traps of 1 m^2 were placed directly to one side of a soil sample site, 1 m above ground, and at intervals of 10 m (Fig. 1b). Each trap was collected every 2 weeks during 2011. Twigs, which constituted 13 % of overall mass, were excluded because of low nutrient contents (Ferrari 1999; Tang et al. 2010). Fruits and seeds were excluded because they may be naturally moved by rodents and other seed-dispersing or predatory animals and thus may not represent local nutrient inputs at the trap location. Leaves, flowers and pieces of insect bodies or feces, and unidentified residues were collected from each trap and dried at 70 °C for 72 h and then weighed and stored separately. The 26 stored litter collections from each trap were mixed together, and representative 50-g subsamples were ground, sieved though 0.25-mm mesh, and then stored in separate plastic bags for chemical analyses.

Three litterfall nutrients were measured. Total N was measured with a Carbon-Nitrogen analyzer (Vario MAX CN, Elementar Analysensysteme, Germany). Total P and Total K were digested using HNO_3-$HClO_4$ solution and measured with an inductively coupled plasma atomic-emission spectrometer (IRIS Advantage-ER, Thermo Jarrell Ash Corporation, USA).

Data analysis

All data analyses were performed in R (R Development Core Term 2012). The spatial distribution maps of all tested variables in the study plot were interpolated with a geostatistical method, using the ***geoR*** package (Rossi et al. 1992; Ribeiro and Diggle 2001). First, data normality was checked and variables were Box-Cox transformed if the normality tests failed. Second, the spatial trends of variables were removed by trend-surface regressions to meet the intrinsic stationary assumption of empirical semi-variograms. Third, semi-variogram models were fitted. Models were chosen based on three criteria: close-to-zero residual sum of squares, minimal extrapolation of semi-variance at scales less than the smallest lag distance (3 m in this study), and fitted model shape. Then, nugget, partial-sill, and range of semi-variogram models were fitted for each variable. Finally, values for each 1×1 m block were predicted for all variables using best fitted semi-variogram models with trends added back and inverse Box-Cox transformed to the original scales.

The topography position index (TPI) is an index of topographic slope positions, with positive values associated with upslopes, negative values with downslopes, and zero with midslopes (Jenness 2006). TPI values for each 1×1 m block of soil sampling points were calculated from interpolated elevations using the ***raster*** package (Hijmans 2014). The interpolation maps of litterfall properties were finally obtained using the inverse distance weight method in the ***gstat*** package (Pebesma 2004) because semi-variogram models are determined by few distance pairs and were thus less robust.

Spatial variability and bi-variate correlation of all tested variables was quantified and tested using wavelet analysis. Wavelets decompose the variability of a spatial process on a scale-based function. A plot of wavelet variance versus scale indicates which scales are important contributors to the total process variance (Percival 1995). Considering the geometrical constraints of the experiment, wavelet analyses were performed at spatial scales from 2 to 33 m using Morlet wavelet functions (Electronic supplementary material 1). While different ecological processes may have effects on target variables at different spatial scales, wavelet analysis can separate contributions of these processes to observed spatial patterns (Detto and Muller-Landau 2013).

Tree site should be relatively nutrient rich if one tree returned more nutrients in litterfall. To explore this, we checked the litterfall chemical fluxes and soil nutrient conditions of each tree's site and determined how many trees had sites that were above the median (i.e., were "rich in") levels of the macronutrients. We use chi-squared goodness-of-fit tests to investigate whether the most numerous species were found in sites richer in soil macronutrients than expected by chance.

Results

Variations in soil properties, topography, and litterfall

Among the six soil properties, hydrogen ions and NO$_3$-N had relatively larger variation, with coefficient of variations (CVs) of 93 and 102 %, respectively, while total N, NH$_4$-N, available P and K had lower variation, with CVs ranging from 19 to 63 % (Table 1). None of the soil properties were normally distributed, with all showing some degree of skew, with the overrepresentation of high values (Supporting information (SI) Fig. 1). Litterfall also showed a substantial amount of variation, both in mass and chemical fluxes, with CVs ranging from 23 to 32 % (see Table 1).

The wavelet variance of TPI increased monotonically, with a steeper slope at scales larger than 25 m (Fig. 2a). A similar pattern was observed for soil pH (hydrogen ion, see Fig. 2a), except for a small peak at 20 m. In contrast, litterfall mass had a prominent peak at about 25 m, and its variance decreased at larger scales (Fig. 2a). Total soil N, soil NH$_4$-N, and litter N also showed a peak at 25 m and low variability at larger scales (Fig. 2b), whereas NO$_3$-N had a small peak at 23 m, but its variance increased at larger scales, similar to TPI (Fig. 2b). Soil and litter P and K also showed an intermediate peak around 25 m (Fig. 2c, d).

Relations of soil properties to topography and litterfall

Soil pH was significantly correlated with topography on a broad range of scales as revealed by wavelet coherence analysis (Fig. 3a) but not significantly correlated with litter mass (Fig. 3a). In contrast, all other nutrients, except for NO$_3$-N, showed significant correlations with corresponding litterfall properties (Fig. 3b, c, e, f). These correlations were particularly strong at the 25 m scale. NO$_3$-N showed a marginally significant correlation to litter N only at the scale of 25 m (Fig. 3d).

Effect of trees on litterfall properties and soil nutrients

Of the four most numerous species in the plot, a majority of *P. chinensis* tree were located in sites rich in soil macronutrients (Table 2, Fig. 4, see also SI Fig. 2 and SI Fig. 3). All 18 trees of this species were found at sites with high NO$_3$-N levels ($X^2_1=16.06$, $P<0.0001$); 16 of 18 trees were found in sites with high levels of litterfall P

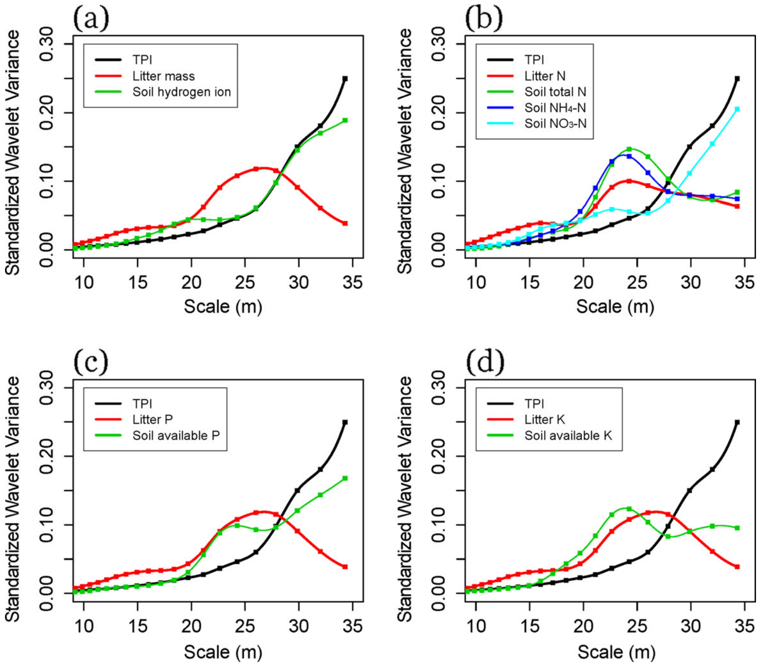

Fig. 2 Wavelet variance of soil properties compared to topography (TPI) and litterfall properties at different spatial scales. *Y-axis values* indicate the proportion of the total variance that is explained at specific scales

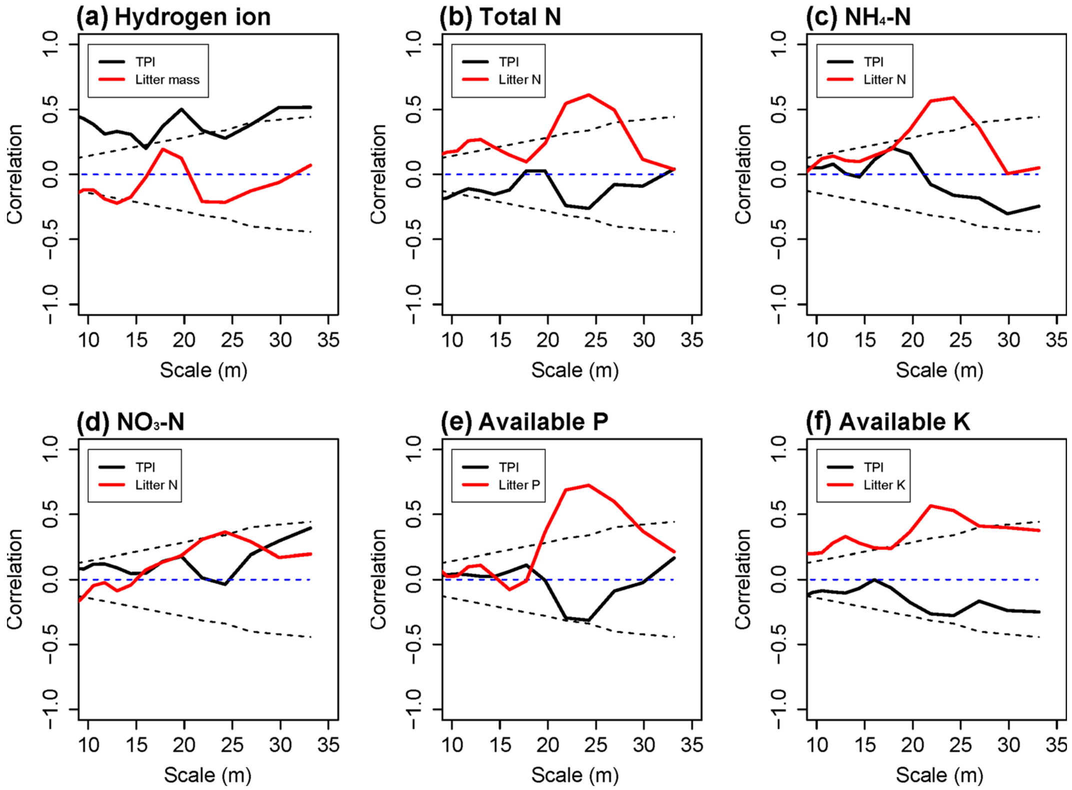

Fig. 3 Wavelet correlation of topography (TPI) and litterfall properties to six soil nutrients at different spatial scales. *Dashed black lines* indicate the significance threshold (α=0.05); *black solid lines* indicate the correlation of the soil property and topography, and *red solid lines* indicate the correlation of the soil and litter property (litter mass for the hydrogen ion)

(X^2_1=9.38, P=0.0022), and the same numbers of trees were found at sites with high levels of litterfall K and soil available P. No significant patterns were founded for the other three species.

Discussion

We found that soil properties had large and distinct spatial variability within our 1 ha plot. The wavelet

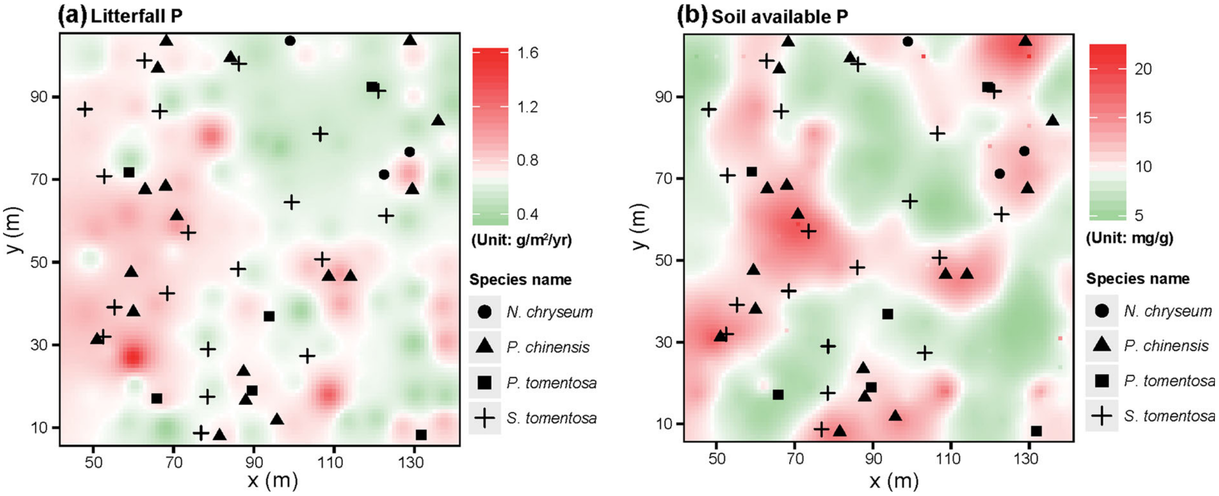

Fig. 4 Spatial pattern of litterfall P (**a**) and soil available P (**b**) related to the location of canopy trees larger than 40 cm DBH. *Red color* represents values larger than the median, and *green color* represents values less than the median

variance indicated two main recurrent features: a peak of variation at intermediate scales (~25 m) and a rapid increase in variation at larger scales (>25 m). This suggests that two different processes influence soil heterogeneity. The low level of topographic variation within this small area was strongly associated with soil pH but poorly associated with all soil nutrients. Soil nutrients were significantly correlated to litterfall chemical fluxes. This finding supports the hypothesis that spatial heterogeneity of soil macronutrients in tropical rainforests can be strongly affected by biotic factors, while soil pH is strongly influenced by geochemical processes and that biotic factors act at smaller scales than geochemical processes.

All soil nutrients in our study plot all had high spatial heterogeneity. Such variations also occur in other forests at similar or larger scales. For example, the range of pH was 2.9 (from 4.3 to 7.2, although only one point was >6.2) here, similar to a range of 2.4 in a tropical dry forest in the West Indies (Gonzalez and Zak 1994). The CVs of soil NH_4-N and NO_3-N were 34 and 102 % here, compared to 41 and 77 % in a subtropical forest in Southwest China (Wang et al. 2007). The soil available P had a CV of 63 % here, compared to 95 % in the dry forest in the West Indies (Gonzalez and Zak 1994). In studies with larger sites, like that of John et al. (2007), CVs may be calculated as means of larger plots (10× 10 m in the study of Johns and colleagues) and hence hide some variability. For example, the CV of inorganic N ($NH_4^+ + NO_3^-$), available P, and available K were 62, 63, and 48 %, respectively here. Those CVs were 31, 56, and 44 % on Barro Colorado Island (50 ha), 31, 2, and 12 % in La Planada (25 ha), and 38, 9, and 65 % in Yasuni (25 ha) (John et al. 2007). Since soil nutrient heterogeneity explained distributions of 36–51 % of tree species in these CTFS plots (John et al. 2007), the higher variability we found may also have substantial ecological impacts.

Litterfall nutrients had significant effects on fine-scale heterogeneity of total N, NH_4-N, available P, and available K and had marginal effects on NO_3-N in our study plot. Litterfall mass fluxes were highly variable within this 1 ha (from 343 to 1185 g/m^2/year). Such a range has rarely been reported in the same region (Tang et al. 2010). This may be because a high density of traps (99 here) is needed to capture spatial heterogeneity. Other studies use fewer traps for the purpose of determining mean values but may miss the variation in litterfall. Here, we found that litterfall variation significantly affected variation in soil total N, NH_4-N, available P, and available K, and it occurred at 25 m scales (Fig. 3b, c, d; see also Fig. 4, SI Fig. 2, and SI Fig. 3). Marginal effects of litterfall on NO_3-N indicate that spatial patterns in this nutrient were affected by other factors. NO_3-N wavelet variances were close to topography at scales larger than 25 m, suggesting a possible link to topography. Previous manipulative studies have shown that litterfall affects soil nutrients (Sayer 2006; Sayer and Tanner 2010; Sayer et al. 2012; Leff et al. 2012). Although litter input was doubled artificially, these studies illustrated the potential effects on soil heterogeneity. However, these effects varied among nutrients and locations, possibly because other factors, including topography, soil type and climate, can also affect soil nutrient status (Townsend et al. 2008; Prescott and Vesterdal 2013). Therefore, we suggest that while litterfall affects soil nutrients, the strength can be further modified by abiotic factors.

Previous studies suggest that single plants can modify soil nutrients, with this ability varying among species (Zinke 1962; Putz 1984; Rodríguez et al. 2009a; Qiao et al. 2013). This study provided new evidence of causality based on scale-dependent variation and correlations among spatial distributions (Detto et al. 2012, 2013). This was possible because litterfall had distinct spatial patterns compared to topography (Fig. 2, see also SI Fig. 4 and SI Fig. 5). Litterfall mass and chemical fluxes had peaks at scales of about 25 m (Fig. 2), roughly corresponding to variability created by crowns and the gap distributions created by big trees (Fig. 4, see also SI Fig. 2 and SI Fig. 3). Indeed, the giant (mean DBH= 101 cm) *P. chinensis* trees on the plot were almost all on nutrient-rich sites, suggesting the importance of their large input of litter to the soil surface. The peaks of litterfall under these trees and the low litterfall where they are absent helped create the spatial heterogeneity in soil nutrient concentrations (Fig. 4, see also SI Fig. 2 and SI Fig. 3). In contrast, no tree species effects were founded in another study in Costa Rican rainforest (Powers et al. 2004). This may reflect the large individual sizes of the canopy-emergent *P. chinensis* trees in our study, compared with the more even tree sizes in the Costa Rican plot. However, we cannot exclude the possibility that the variation in soil nutrients reflects differences that existed prior to the recruitment of the current cohort of trees. Tree roots may also contribute to soil heterogeneity but were not investigated here.

Although topography has important effects on soil heterogeneity (Tateno and Takeda 2003; Tsui et al. 2004; Wang et al. 2007), in our study plot, it affected only soil pH significantly (see Fig. 3). The negative relationship between the topographic gradient and pH here is consistent with earlier studies (Chen et al. 1997; Tsui et al. 2004), even though there was only a 25 m elevation gradient in our plot. Topography had insignificant effects on soil nutrients, possibly because of the small elevational range. In a 1 ha subtropical forest in Southwest China with a 50 m elevation gradient, both NH_4-N and NO_3-N were significantly affected by topography (Wang et al. 2007). Another reason may be that the strong effects of litterfall on soil nutrients at intermediate scales (i.e., ~25 m) dilute the effect of topography.

A limitation of our study is that the air-drying method may bias the available N value (Turner and Romero 2009). To minimize that, we placed the soil in a thin layer on paper and used a fan to accelerate soil drying. Since long-term room temperature storage is known to increase NH_4-N and NO_3-N (Turner and Romero 2009), the very low values we found (5.8 for NH_4-N and 0.1 for NO_3-N, see Table 1) suggests only small biases occurred. Finally, even a systemic bias should not significantly affect the spatial heterogeneity patterns we detected.

A caveat of our study is that the litterfall traps had lower spatial resolution than the soil samples. The geostatistical interpolation cannot reproduce variability between sampling points, with a consequence of excessive smoothing and hence the attenuation of wavelet variance at small scales. But because the pattern we detected was strong at 25 m, which is more than double the distance between litterfall observations, by the Nyquist–Shannon sampling theorem, we consider this bias negligible at these scales.

A potentially important factor, not considered here, relates to the stability of soil nutrient patch structures through time. If these patterns are randomized through time by environmental variation and plant absorption, then the heterogeneity we detected may not provide pressure on plants for directional selection or for coexistence. If the patterns are stable through time, then species, especially in seedling or sapling stages, could develop patchy distributions because of selection pressure. Nutrient-patch structures may be stable for 2 months (Wang et al. 2007). However, soil nutrient concentrations also fluctuate seasonally (McGrath et al. 2000), and it is uncertain whether nutrient-rich patches can persist in the face of such fluctuations.

This study was conducted only at one site, so establishing the generality of these patterns requires studies elsewhere in tropical rainforests. We believe that macronutrient heterogeneity patterns generated by plants should be widespread in highly diverse tropical rainforests, although the strength of this effect may vary, depending on abiotic factors such as climate, soil-type distributions, and topography. We suggest two directions for establishing general patterns of fine-scale soil heterogeneity: First, investigate the extent and stability of fine-scale heterogeneity and determine how it varies with abiotic environmental gradients at other sites; second, investigate how this heterogeneity is formed and maintained by litterfall or other biotic mechanisms.

Conclusions

Mechanisms maintaining biodiversity are a key issue in ecology, and this study provides new insights from a soil-plant interaction perspective. Our study extends the finding of plant feedback on soil nutrients from studies that look at individuals or species grown in monoculture, to patterns of fine-scale soil heterogeneity under a natural rainforest community. We find that in an area with little topographic variation, litterfall likely drives the spatial structure of soil macronutrients, with a high proportion of the variance explained at the 25 m scale. This biotic-driven soil heterogeneity may, in turn, be important in influencing the distributions of rainforest organisms, such as providing additional niches for tree seedlings and juveniles.

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