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REGULAR ARTICLE

Effect of topography and litterfall input on fine-scale patch consistency of soil chemical properties in a tropical rainforest

Shang-Wen Xia · Jin Chen · Doug Schaefer · Uromi Manage Goodale

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Abstract
Aims Spatial aggregation of soil chemical properties, or nutrient patches, may be generated by topography and plants and can seasonally fluctuate because of climate. Whether nutrient patches maintain consistency (no change in ranking through sequential sampling), through temporal scales, and whether topography and litterfall contribute to the persistence of such ranking is rarely tested.
Methods In a 1-ha tropical rainforest plot in Southwest China, we measured soil pH, total N, NH_4–N, NO_3–N, and available P and K for four times and assessed the patch structure (patterns of patch distribution) and their temporal consistency. We then tested how structure and consistency of chemical soil properties were affected by topography and chemical inputs from litterfall.
Results All soil chemical properties showed significant seasonal fluctuations, but patch consistency was higher for soil pH, total N, and available P and K compared to NH_4–N or NO_3–N. Topography influenced pH patch consistency while annual litterfall input was important for maintaining patch consistency in total N and available P and K.
Conclusions Fine-scale consistency of patches in soil pH, total N, and available P and K suggest they may exert stable selection pressures on species for niche differentiation, while consistency of soil NH_4–N and NO_3–N require further study.

Keywords Litterfall properties · Seasonal fluctuation · Soil spatial heterogeneity · Topography · Xishuangbanna

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Introduction

Soils are formed by geochemical and biological processes that act upon the parent material. Climate and topography interact with biotic factors, such as canopy-dominant trees and their litterfall, and cause heterogeneity of soil properties across space and time. While topography and hydrological and climatic processes can operate at large scales, biotic factors act at fine-scales (defined here as less than 1 ha; Wiens 1989; Ettema and Wardle 2002; Ehrenfeld et al. 2005; Townsend et al. 2008; Xia et al. 2015). Many studies demonstrate that soil patches, describing spatially aggregated soil variability (Ettema and Wardle 2002), exist at a range of scales (Cambardella et al. 1994; Webster 2000;

Heuvelink and Webster 2001) and are important to species coexistence (John et al. 2007; Baldeck et al. 2013).

Effects of soil patches on species distribution, or niche differentiation, depend on patch consistency, with points in patches keeping their ranking through sequential sampling, although values may vary overall. Various lines of evidence show the importance of spatial heterogeneity (John et al. 2007; Baldeck et al. 2013), but there have been few attempts to quantify nutrient patch consistency though time, especially at fine-scales (Guo et al. 2004; Wang et al. 2007). Even when nutrient spatial patches clearly exist at different times, this is not evidence for patch consistency, unless, nutrient rankings persist. Therefore, studies specifically designed to assess changes in ranks are needed to test the patch consistency hypothesis.

While many factors affect soil chemistry (McBratney et al. 2003), at local scales, variation in these properties may be mainly driven by two distinct forces. First, the climate fluctuation force. Climate factors cause seasonal and annual fluctuations in soil chemical properties (Holmgren et al. 2001; Comita and Engelbrecht 2009). The second, spatial stationary force, includes topography and biotic factors such as tree species and their litterfall, are important forces maintaining fine-scale soil patches (Zinke 1962; Chen et al. 1997; Prescott and Vesterdal 2013; Xia et al. 2015). Because topography and distributions of large trees are stationary over long periods of time, they stabilize patchy distributions of soil chemical properties (Waring et al. 2015), excluding disturbance effects, such as tree falls. However, topography and biotic factors may have different effects on soil chemical properties (Xia et al. 2015). Whether different soil nutrients maintain their patch consistency across seasonal fluctuations is rarely investigated.

Litterfall can be a useful indicator of plant effects on soil nutrient conditions (Sayer et al. 2012; Leff et al. 2012). Litterfall input, as one key process of plant feedback on soil (Dent et al. 2006), may generate soil nutrient spatial variability (Facelli and Pickett 1991), due to asymmetry to root absorption (Vitousek and Sanford 1986; Attiwill and Adams 1993; Wieder et al. 2012). This may arise from root/crown asymmetry, growth habit, or functional differentiation (Hruska et al. 1999; Reed et al. 2008; Rodríguez et al. 2009; Inagaki et al. 2010; Tang et al. 2011). In addition, asymmetry also exists in litterfall quality (Cuevas and Lugo 1998). Plants growing with high nutrient availability are less efficient in nutrient reabsorption and may return more nutrients to the soil via litterfall (Aerts 1996; Vergutz et al. 2012). To our knowledge, few studies have examined whether litterfall maintains soil nutrient patch consistency at fine spatial scales (Zaady et al. 1996).

In this study, we assessed topography, annual litterfall chemical fluxes, and the dynamics of fine-scale soil chemical properties in a 1-ha tropical seasonal rainforest in Southwestern China. Our objective was to assess patch consistency of soil chemical properties and factors that contribute to it. We tested the hypothesis that soil pH, N, and available P and K may have fine-scale patch structure (patterns of patch distribution) and due to the stable effect of topography and litterfall on these chemical properties, these patch structures will keep consistent under seasonal fluctuation.

Methods

Study site

This study was conducted within the 20-ha forest dynamics plot (21° 37′ 08″ N, 101° 35′ 07″ E), belonging to the Center for Tropical Forest Science – Forest Global Earth Observatory network, located in the tropical seasonal rainforest in Southwest China (Xia et al. 2015) (Fig. 1a). We selected this study site because it has already been assessed for topographic variation and tree size and distribution. The soil here is laterite and is developed from siliceous rocks (Cao et al. 2006). This area has a mean annual rainfall of 1532 mm and annual mean temperature of 21.0 °C (Zhu 2006). The rainy season is from May to October followed by dry weather from November to April, with precipitation of 282 mm (Zhu 2006). Litterfall maxima and minima are observed at the ends of the dry and rainy seasons, respectively (Tang et al. 2010). The entire 20-ha plot is covered by tropical seasonal rainforest, which includes 468 species of trees including the canopy-dominant *Parashorea chinensis* (Cao et al. 2008). This study was conducted in a 100 × 100 m subplot established in the southeast corner of the 20-ha plot, with elevation ranging from 711.3 to 736.6 m.

Experimental design and sampling

During four soil sampling times, in December 2010, April 2011, August 2011, and March 2012, a total of 99 soil samples were collected at each time from the 1-ha plot located on a 10-m grid with each sample representing 1 m^2 (Fig. 1). During collection, we

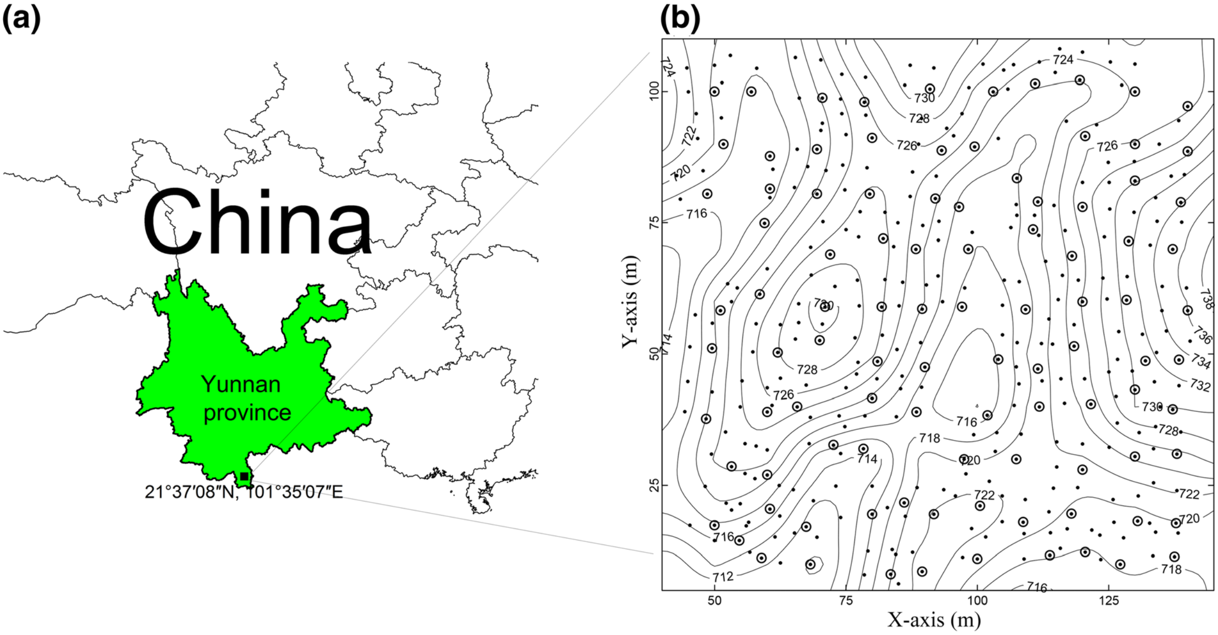


Fig. 1 Diagram of sampling points at the 1-ha study plot. *Solid points* represent high-density soil sampling points (361/ha), *open circles* represent points that include other three times of low-density soil sampling and also 3 years of litterfall input monitoring. The study site is located in the southeast corner of a 20-ha forest dynamics plot (21° 37′ 08″ N, 101° 35′ 07″ E) in Xishuangbanna, Yunnan, China. The coordinates match those of the 20-ha plot

avoided obstructions including large or dead trees or very steep slopes by shifting 1 to 3 m in a random compass direction, and we discarded points located in stream channels. In August 2011, 361 soil samples were collected at 5-m intervals across the 1-ha plot to obtain an explicit map of soil chemical properties.

At each 1 × 1 m sampling point, we removed the litter layer and collected five cores of soil from a depth of 0 to 10 cm using a 4-cm diameter corer. The soil was then mixed and stored for transport to the Biogeochemistry Laboratory of the Xishuangbanna Tropical Botanical Garden on the same day using ground transport. Soil clods were broken by hand into smaller pieces, air-dried using fans under shade for 30 days, and ground and sieved (Wang et al. 2007). Half of each soil sample was sieved through 2-mm mesh for soil pH, NH_4–N, NO_3–N, and available P and K analysis and the rest through 0.25-mm mesh for Total N analysis (Wang et al. 2007; Ziadi and Tran 2007).

Litter was collected from January 2011 to December 2013, every 2 weeks, using 1-m^2 litterfall traps placed to one side of each of the 99 soil sampling sites at 1 m above ground (Fig. 1b). Twigs, which are known to have low nutrient content and constitute a low proportion of total litter (Ferrari 1999; Tang et al. 2010), were removed from the collections. Fruits and seeds were also excluded because they may be naturally moved by rodents and other seed-dispersal or predator animals, and thus may not represent local nutrient inputs at the trap location. Pieces of insect bodies or feces, leaves, flowers, and unidentified residue were collected from each trap and dried at 70 °C for 72 h, and then weighed and stored separately. The stored litter collections of 2011 from each trap were mixed together and representative 50-g subsamples were ground, sieved though 0.25-mm mesh, and then stored at ambient temperature for chemical analyses.

To detect biases of air-drying on soil NH_4–N and NO_3–N assessment, 20 samples were randomly sampled from the study plot in November 2015, and NH_4–N and NO_3–N in fresh and dried soil were compared using methods described in the following section.

Chemical measurement

We measured soil pH in water (soil/deionized water = 1:2.5) using a pH meter (PHS-3C, Shanghai Precision Scientific Instrument Co., Ltd., China) and N using 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; Ziadi and Tran 2007) and measured using a spectrophotometer (T723, Shanghai Spectrum Instruments Co., Ltd., China) and an inductively coupled plasma atomic-emission spectrometer (IRIS Advantage-ER, Thermo Jarrell Ash Corporation, USA), respectively.

We measured total N in litterfall using a carbon-nitrogen analyzer (Vario MAX CN, Elementar Analysensysteme, Germany) and total P and total K after digesting with HNO_3–$HClO_4$ solution and using an inductively coupled plasma atomic-emission spectrometer (IRIS Advantage-ER, Thermo Jarrell Ash Corporation, USA).

Spatial structure analyses

All analyses were conducted with R software (R Development Core Term 2012). Geostatistical analysis of soil chemical properties from August 2011 high-density sampling was conducted to determine the patch structure of the soil chemical properties with the *geoR* package (Ribeiro Jr. and Diggle 2001). First, we used Box-Cox transformations to normalize data where needed. If second- or third-order spatial trends existed in variables, they were removed using trend-surface regressions to meet the intrinsic stationary assumption of empirical semivariograms (Bivand et al. 2013).

Semivariograms depict the spatial auto-correlation of the measured sample points through a series of semi-variance values against corresponding lag distances (Rossi et al. 1992). The semivariogram models were compared with leave-one-out cross validation method and the best models were chosen based on four criteria: mean error, root mean square error, mean squared deviation ratio, and Lin's concordance correlation coefficient (Karunaratne et al. 2014). Gaussian models were always found to fit the data well (ESM 1: Supplementary Table S1) and were applied to all variables to facilitate comparisons of parameters among variables. Anisotropic semi-variances were compared at 0, 45, 90, and 135 °, and if no significant directional patterns were found, then isotropic (omnidirectional) semivariograms were used (Ribeiro Jr. and Diggle 2001). Four parameters were derived from semi-variance models: nugget, partial-sill (Psill), range and SH%. Nugget reflects variability at finer scale or random error. Partial-sill reflects spatial auto-correlation structure. Range reflects spatial auto-correlation distances. The SH% was calculated as Psill/(Psill + Nugget), which reflects the proportion of variation due to spatial auto-correlation and high SH% indicates strong spatial patterns.

Permutation tests were carried out to compare the modeled spatial auto-correlations to null assumptions of complete spatial randomness (Ribeiro Jr. and Diggle 2001). Finally, ordinary kriged maps were produced for all variables following a block kriging approach with a block size of 1 × 1 m with trends added back and data reverted to the original scales (Bivand et al. 2013).

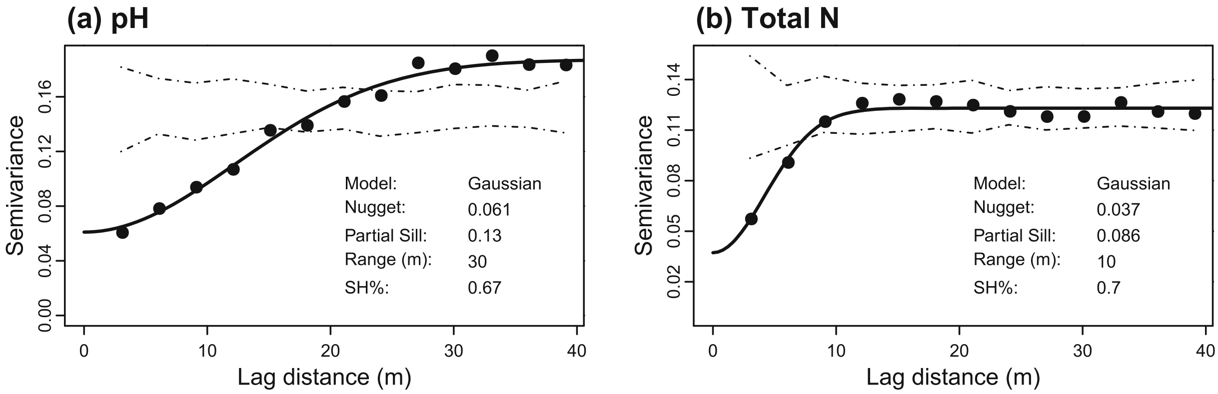
Fluctuation and consistency analyses of soil chemical properties

We used correlation values as proxy for patch consistency of soil chemical properties. We tested the significance of correlation between the four sampling times using the modified-correlation analysis from the *SpatialPack* package (Osorio and Vallejos 2014). First, to ensure data normality, variables were square-root transformed, if needed. Modified-correlation corrected the degrees of freedom based on spatial auto-correlation in the data. The final significance values were Bonferroni adjusted. Using the estimated freedom values obtained from modified-correlation analysis, the significance of multiple comparisons between four sampling times was manually calculated and Bonferroni adjusted. Any soil chemical property that had a mean correlation coefficient value greater than 75 % was considered to be consistent or inconsistent if they had lower correlation values. To visualize how many and which points were less consistent, we classified each soil chemical property, at each time, to low and high conditions based on median values for each soil chemical property for the entire 1-ha plot. Points that shifted from high to low or vice versa, one or more times, were classified as shifted. Then, we mapped locations of all shifted points on to the August 2011 soil chemical property maps.

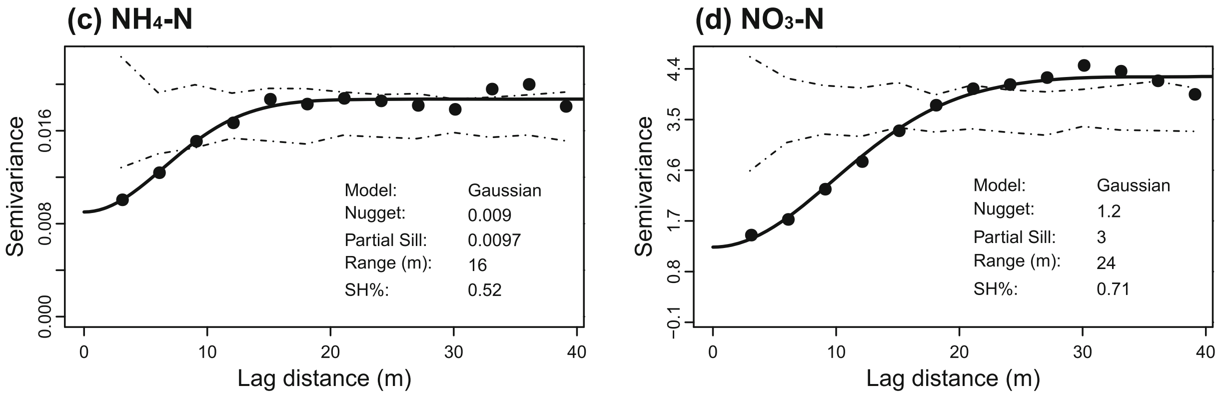
The seasonal fluctuation was tested after patch consistency analysis. Using the estimated freedom value obtains from modified-correlation analysis, the significance of multiple comparisons between four sampling times were manually calculated and Bonferroni adjusted.

Modeling the driving forces of soil chemical property patches for the four sampling times

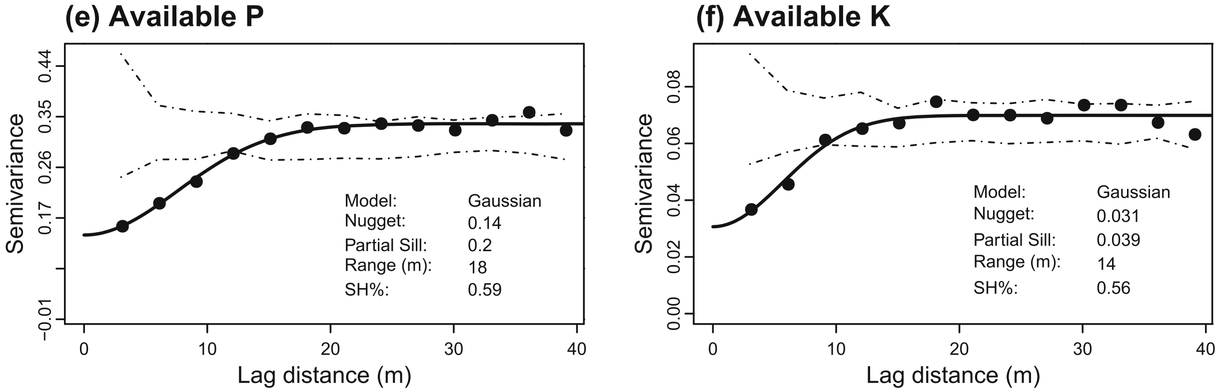
To understand how variation in topographic position, annual litterfall nutrients, and any unidentified/unmeasured spatial variables drive soil nutrient properties for each soil sampling time, we conducted a variation partitioning analysis using varpart function in *vegan* package (Oksanen et al. 2013) for each sampling time. Topographic position index (TPI) was used as a proxy for topographic position by standardizing topographic positions; positive values for up-slope, negative values for down-slope, and zero for mid-position (Jenness 2006). The TPI values for each 1 × 1 m block of soil sampling points were calculated from ordinary kriging interpolated value of elevation using the *raster* package (Hijmans 2014) and then 99 points showing soil seasonal fluctuations were chosen for the next analysis. Principal coordinates analysis of neighbor matrices (PCNM) variables was used as the proxy for unidentified spatial properties using methods described by Borcard and Legendre (2002). To test the consistency in annual litterfall input, we conducted a modified-correlation analysis among 3 years of annual litter mass also using the *Spatial Pack* package.


(a) pH

(b) Total N


(c) NH4-N

(d) NO3-N


(e) Available P

(f) Available K

Fig. 2 Semivariograms of six soil chemical properties in the 1-ha study plot. The *solid points* are mean semi-variance values at each separation distance. The *solid line* is the fitted Gaussian model curve. The *dashed lines* show the maximum and minimum values found in 99 complete spatial randomness permutations

Results

Spatial structure of soil chemical properties

All tested soil chemical properties were spatially autocorrelated and fit well to Gaussian models with semi-variances ranging from 10 to 30 m, where pH and NO_3–N had higher range values than the other four soil chemical properties (Fig. 2). Permutation tests showed that all measured soil chemical properties had significant patch structures (Fig. 2, ESM 1: Supplementary Fig. S1). The SH% values of all soil chemical properties varied from 52 to 71 % indicating strong patch structures.

Fluctuation and consistency of soil nutrient patches

All soil chemical properties fluctuated seasonally (Fig. 3) with relatively high values during rainy seasons (April 2011 and August 2011) and lower values during dry seasons (Dec 2010 and March

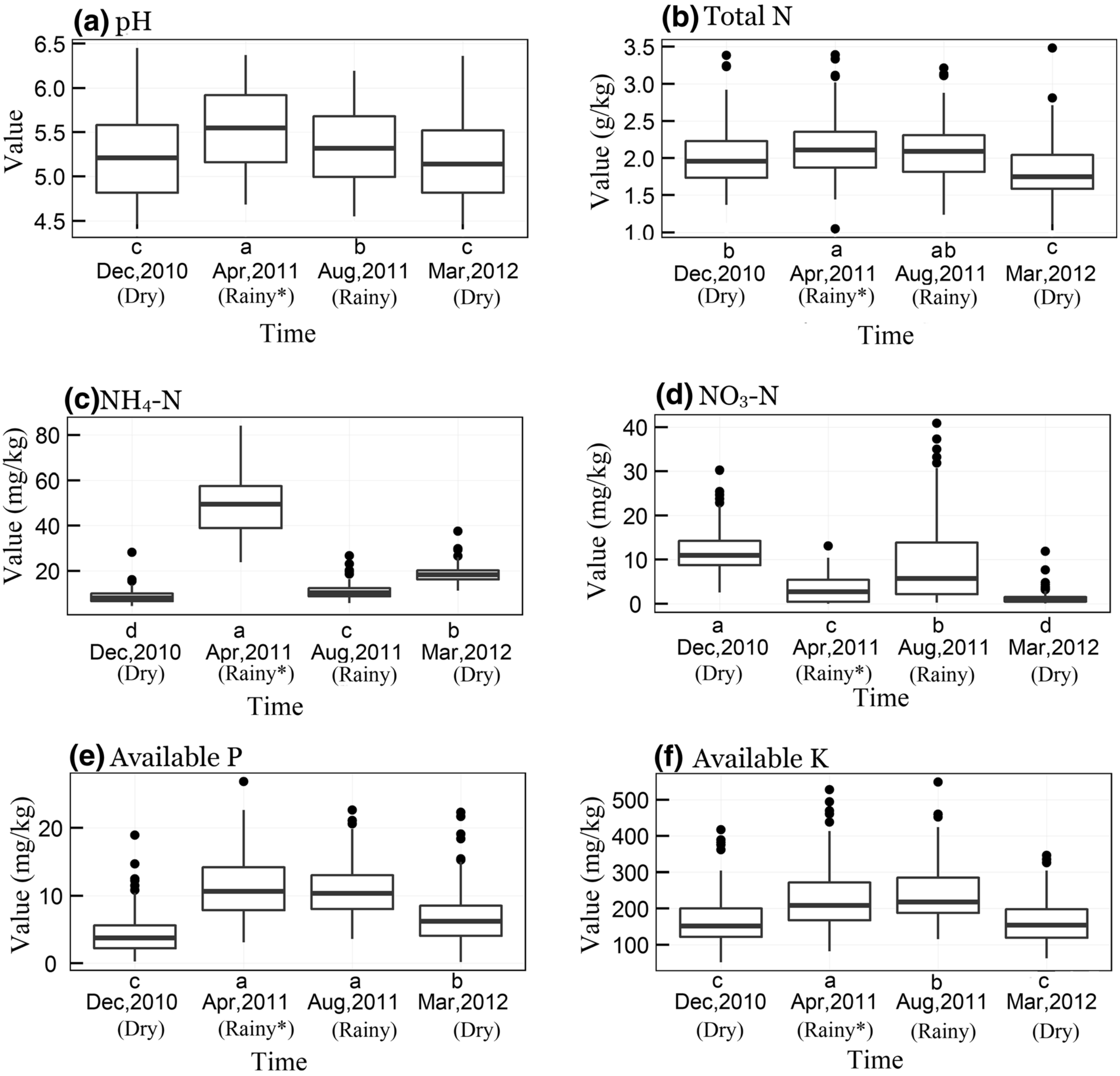


Fig. 3 Seasonal fluctuations of six soil chemical properties. *Asterisk* indicate the beginning of rainy season. Different *letters* indicate significant differences between sampling times. $P < 0.05$. $n = 99$. Degrees of freedom were corrected by modified-correlation based on spatial auto-correlation in the data. The final significance was Bonferroni adjusted

2012) for pH, total N, and available P and K. However, this seasonal trend was not seen for NH_4–N and NO_3–N. Concentrations of NO_3–N were notably high at August and December but were lower at other sampling times. Patterns of NH_4–N concentrations were opposite to those found for NO_3–N.

For each soil property, correlation between the four sampling times was significant (Table 1). However, the correlations were higher for soil pH, total N, and available P and K (each with mean of correlation values >0.80), but lower for NO_3–N and NH_4–N (each with mean of correlation values <0.54). For pH, total N, and available P and K, about one third of (20 to 35 of 99) points shifted conditions (from above to below median values or vice versa at least once). For NH_4–N and NO_3–N, about half of (49 to 55 of 99) points shifted conditions from high to low, or the opposite, through time (Fig. 4).

Air-dried soils had higher values for both NO_3–N and NH_4–N compared to fresh soils (increased 40 and 97 %, respectively; Table 2). The correlation values between air-dried and fresh samples were high for NO_3–N (Spearman r value = 0.90, $P < 0.001$) but we did not find a correlation for before and after dried samples for NH_4–N (Spearman r value = 0.08, $P > 0.05$).

Driving forces of soil chemical properties

Variance contributed by each factor (TPI, litterfall, and PCNM) depended on tested soil chemical properties and sampling times (Fig. 5). During all four sampling times, TPI mainly affected soil pH, NO_3–N (except March 2012) and also affected available K. Litterfall mainly affected total N and available P and K. The PCNM variable, which is a proxy for any unidentified spatial trends, was also important for explaining variations in distributions of soil pH, total N, NO_3–N, and available P, except in March 2012 for total N and NO_3–N.

Annual litterfall mass measured during the 3 years in which soil sampling was conducted showed significant and strong correlations among the three sampling years ($r > 0.83$ for all correlations; Table 3; ESM 1: Supplementary Table S2).

Discussion

Our hypothetical mechanisms that topography and litterfall would maintain patch consistency was supported with varying degrees for different soil chemical properties. Significant spatial structures, a premise for patch consistency, were found in all soil chemical properties in

Table 1 Correlations among four sampling times for six soil chemical properties

(a) pH

	Dec. 2010	Apr. 2011	Aug. 2011
Apr. 2011	0.88		
Aug. 2011	0.92	0.91	
Mar. 2012	0.9	0.81	0.85

(b) Total N

	Dec. 2010	Apr. 2011	Aug. 2011
Apr. 2011	0.84		
Aug. 2011	0.86	0.87	
Mar. 2012	0.80	0.82	0.79

(c) NH_4–N

	Dec. 2010	Apr. 2011	Aug. 2011
Apr. 2011	0.53		
Aug. 2011	0.57	0.44	
Mar. 2012	0.62	0.66	0.49

(d) NO_3–N

	Dec. 2010	Apr. 2011	Aug. 2011
Apr. 2011	0.56		
Aug. 2011	0.41	0.68	
Mar. 2012	0.48	0.42	0.4 *

(e) Available P

	Dec. 2010	Apr. 2011	Aug. 2011
Apr. 2011	0.77		
Aug. 2011	0.82	0.85	
Mar. 2012	0.86	0.74	0.82

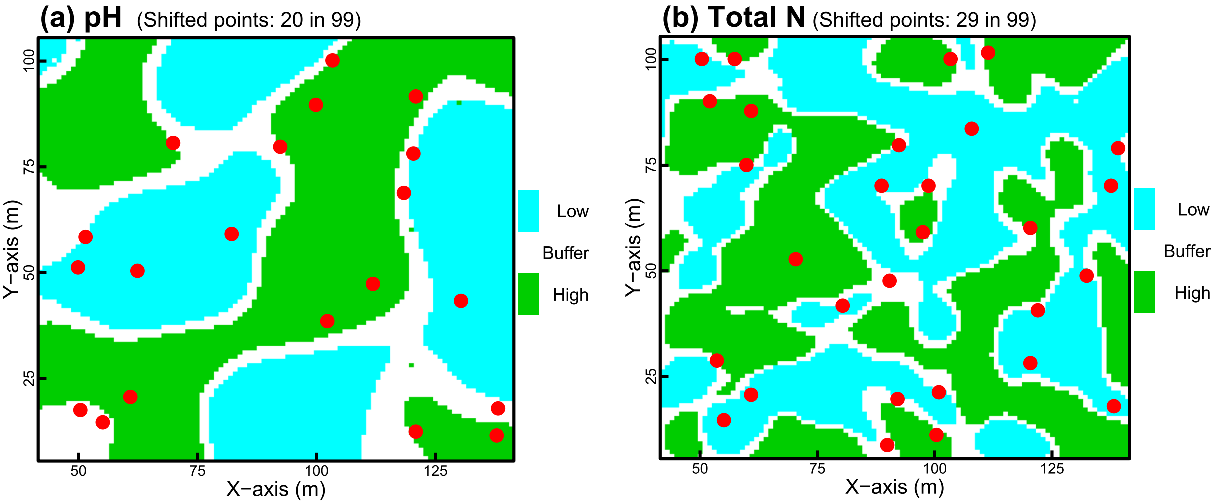
(f) Available K

	Dec. 2010	Apr. 2011	Aug. 2011
Apr. 2011	0.85		
Aug. 2011	0.76	0.78	
Mar. 2012	0.82	0.89	0.81

Dec. 2010 and Mar. 2012 sampling was conducted during the dry seasons and Aug. 2011 sampling was done during the rainy season. The sampling date at Apr. 2011 was at the beginning of rainy season

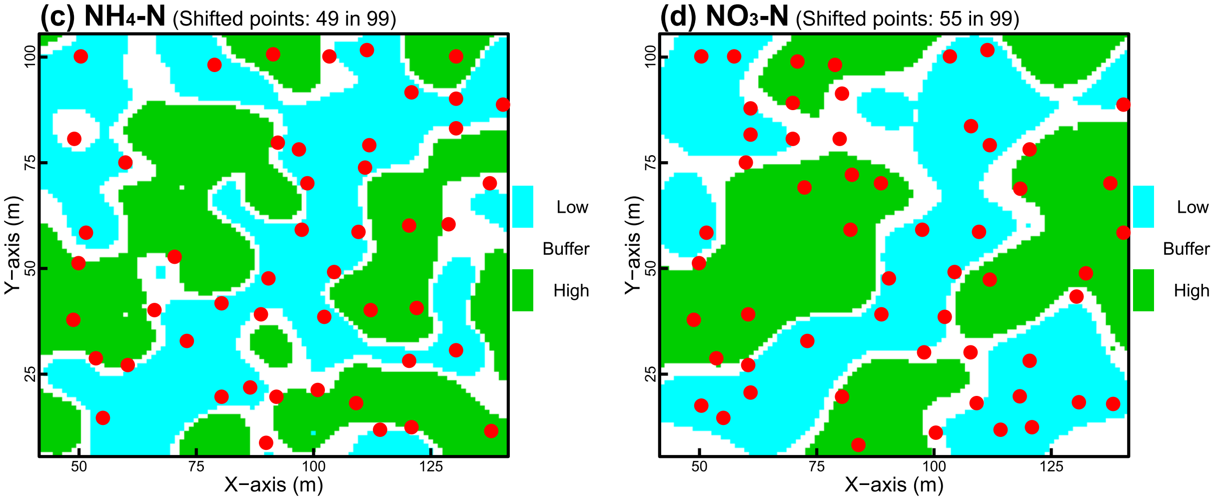
The default significance of all r values is 0.001 and the marks are ignored. Degrees of freedom were corrected by modified-correlation based on spatial auto-correlation in the data. The final significance was Bonferroni adjusted

$^{**}P < 0.01$; $n = 99$



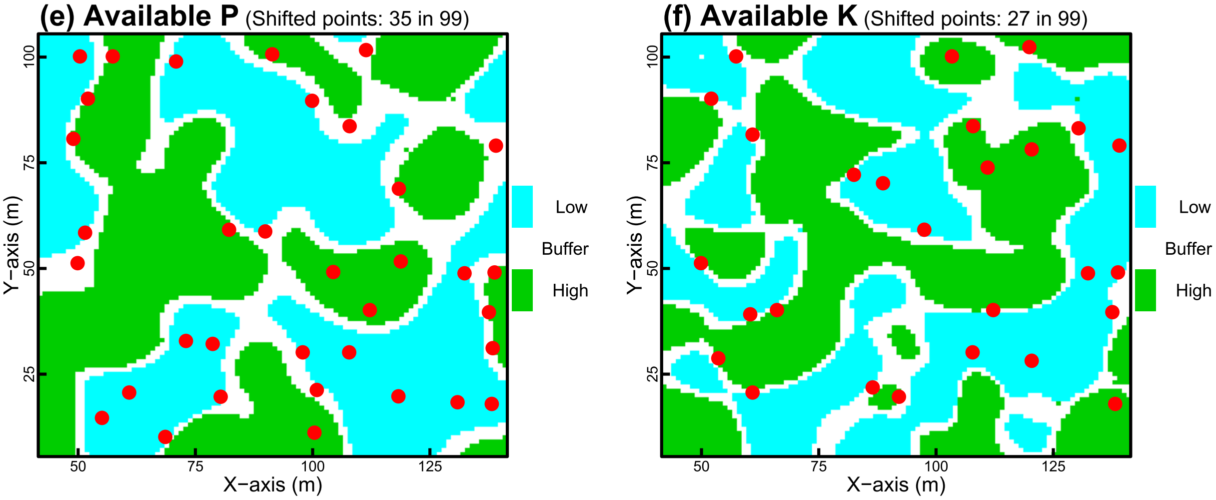
(a) pH (Shifted points: 20 in 99)

(b) Total N (Shifted points: 29 in 99)



(c) NH4-N (Shifted points: 49 in 99)

(d) NO3-N (Shifted points: 55 in 99)



(e) Available P (Shifted points: 35 in 99)

(f) Available K (Shifted points: 27 in 99)

◀**Fig. 4** Shifted points of soil chemical properties following seasonal fluctuation. Patch maps based on August 2011 data, for each soil chemical properties were classified to two classes: High, i.e., values that were above median values, and low otherwise. *Red points* represent points that shifted their conditions (from high to low or inverse) within four sampling times. Buffer represents buffering area between high and low content patches (quintiles of 40 to 60 %)

our study area. Soil pH, total N, and available P and K showed patch consistency indicated by high inter-seasonal correlations. Their patch consistency was significantly related to TPI, litterfall chemical fluxes, and PCNM variables. In contrast, the patches of NO_3–N and NH_4–N showed greater seasonal fluctuations, and were less related to TPI and litterfall. Thus, with causality discussed later, we suggest that litterfall and topography maintain patch consistency of soil nutrients, but patch consistency for N forms may be diluted by complex ways in N conversions.

These results should be assessed cautiously for NH_4–N and NO_3–N, especially for NH_4–N, because our subsequent experiment to assess the differences before and after air-drying showed that both nutrients were higher in air-dried samples, but with greater correlation for NO_3–N and no correlation for NH_4–N. Over estimation of inorganic N in air-dried samples were probably because of increased microbial activity and/or change in microbial community composition during soil drying (Sparling and Ross 1988). High correlation of NO_3–N between fresh and dried soils reveals that spatial structure of NO_3–N was less affected by soil drying. However, drying caused the spatial structure of NH_4–N in dry soils to be different from fresh soils. Another important factor to consider here is that the ratio of NH_4–N/NO_3–N in our study plot is high compared to other tropical forests (the highest was found in March 2012, which was 14.7). While this may be due to soil accumulating more NH_4–N compared to NO_3–N (increased 97 vs. 40 %, respectively) during air-drying, a similar value (13.84) has been reported for a rubber forest in Xishuangbanna tropical area, which used fresh samples for analysis (Li et al. 2012).

Table 2 Concentrations of NH_4–N or NO_3–N and correlations between fresh and air-dried soil

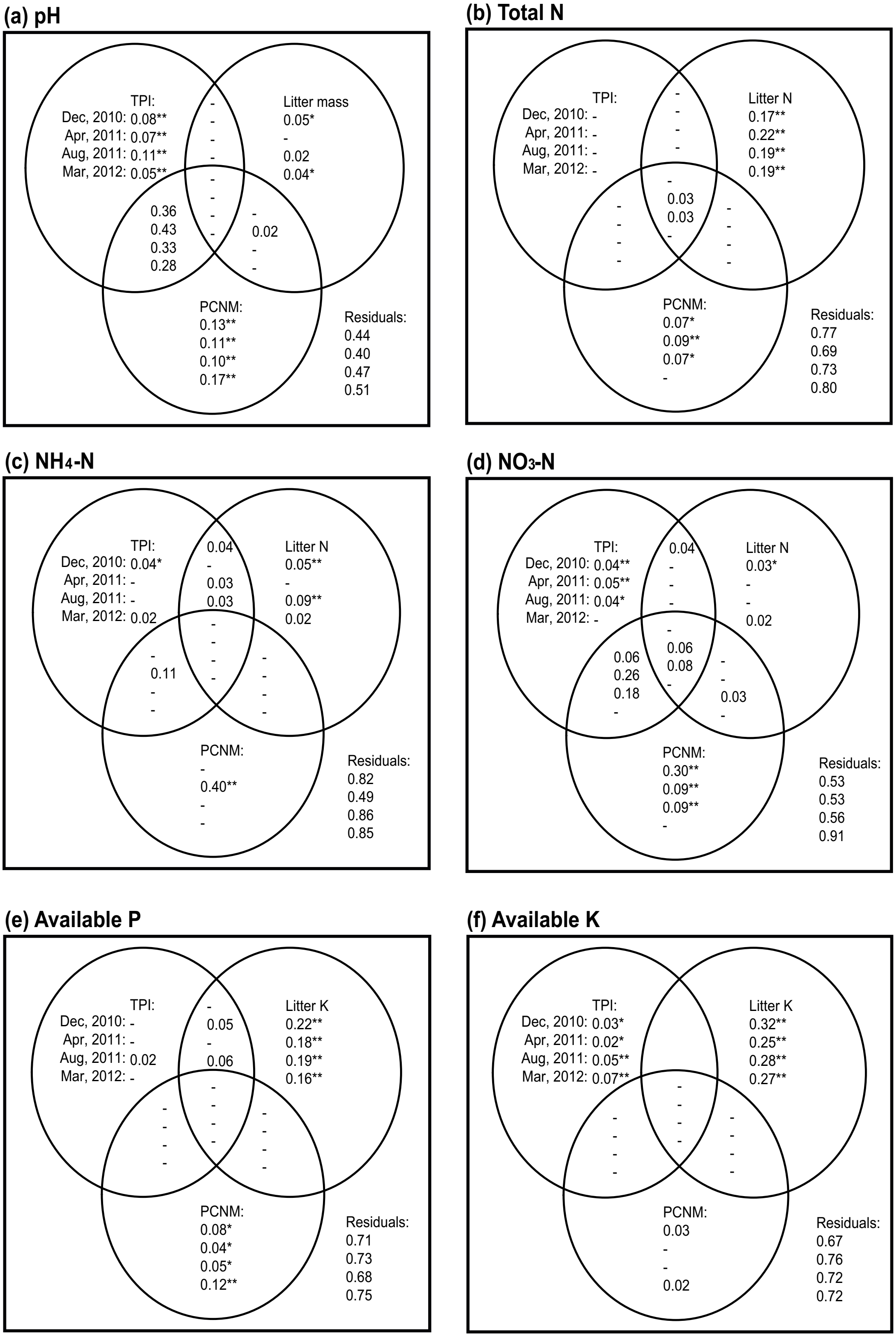
Soil chemical properties	Value in fresh soil (mean ± SD)	Value in air-dried soil (mean ± SD)	Spearman correlation between fresh and air-dried soil samples
NH_4–N	3.85 ± 2.99	7.59 ± 1.45	0.09 NS
NO_3–N	2.50 ± 1.09	3.50 ± 1.55	0.90***

NS non-significance

***$P < 0.001$

Fine-scale patch structures observed for all measured soil chemical properties in our study may be widespread in other forests. For example, we found that the pattern strength for pH (SH% of 55 %) found in our study was comparable to that observed in a tropical dry forest in St. Lucia (SH% of 58 %; Gonzalez and Zak 1994). Total N had an SH% value of 60 %, compared to 56 % in a floodplain forest (Gallardo 2003). NO_3–N had an SH% value of 63 %, compared to 44 and 85 %; NH_4–N had SH% value of 55 %, compared to 43 and 50 % in a floodplain forest and a subtropical forest, respectively (Gallardo 2003; Wang et al. 2007). Further, available P had SH% value of 38 %, similar to 44 and 48 % in a floodplain forest and a tropical dry forest (Gonzalez and Zak 1994; Gallardo 2003), available K had SH% value of 49 %, compared to 96 % in a floodplain forest (Gallardo 2003). Moderate patch strength was also recorded for total C, organic matter, other micro-nutrients, and mineralization and nitrification process in forests (Gonzalez and Zak 1994; Gallardo 2003; Gallardo et al. 2005; Powers 2006; Chang et al. 2007; Gallardo and Paramá 2007).

In our study site, soil pH, total N, and available P and K demonstrated highly consistent patch structures, while NO_3–N and NH_4–N were less consistent. We found no studies focused on consistency among soil nutrient patches, while a few showed dynamic patterns. One such short-term study was conducted in a subtropical forest in Central China and found total N had higher patch consistency compared to NO_3–N or NH_4–N, with r values of 0.7, 0.56, and 0.56, respectively (Wang et al. 2007). However, such correlations were not found among years in a pine forest (Guo et al. 2004). Another study in a sagebrush-wheatgrass steppe found that within 1 year, soil available P and K were highly correlated, but NO_3–N and NH_4–N were not (Ryel et al. 1996). Note that higher values of soil pH, total N, and available P and K in the rainy season compared to the dry season could be mainly attributed to the rain. Although there is abundant litterfall input during the dry season here (Tang et al. 2010), nutrients can only leach or decompose with adequate water. Also, note that one reason for the inverse seasonal fluctuation patterns of NO_3–N and NH_4–N may be high moisture (and low



(a) pH

(b) Total N

(c) NH_4-N

(d) NO_3-N

(e) Available P

(f) Available K

Fig. 5 Variation contribution of TPI, PCNM variables, and litterfall properties to six soil chemical properties' spatial variation at each sampling time. *Dashes* represent values that are less or equal to 0.01

Table 3 Correlation of litterfall mass among 2011–2013

	2011	2012	2013
2011	–		
2012	0.89***	–	
2013	0.83***	0.87***	–

$n = 99$. Degrees of freedom were corrected by modified-correlation based on spatial auto-correlation in the data. The final significance was Bonferroni adjusted

***$P < 0.001$

O_2) in rainy season promoting mineralization but not nitrification, with the inverse during dry seasons (Chapin et al. 2012); another reason should be initial moisture (O_2) differences in air-drying processes. As few studies have yet been published and because soil nutrient concentrations fluctuate seasonally to different degrees in different places (Ryel et al. 1996; McGrath et al. 2000), general patterns of patch consistency are not yet known.

Patch consistency for all tested soil chemical properties, except NO_3–N and NH_4–N, were affected by litterfall and/or topography. Topography consistently had significant effects on soil pH, agreeing with earlier single-time studies (Chen et al. 1997; Tsui et al. 2004; Xia et al. 2015). However, topography did not affect soil total N and available P, unlike studies in other rainforests (Mage and Porder 2013; Weintraub et al. 2015). This may be because topographic variation occurred at small scales in our study plot (Fig. 1), allowing litterfall of dominant trees to mask topographic effects (Xia et al. 2015). While litterfall heterogeneity affected all tested soil nutrients except NO_3–N in our earlier study (Xia et al. 2015), here, we confirmed persistent effects of litterfall on total N and available P and K. Similar litterfall amounts among rainforests (Chave et al. 2010) suggests it may have similar effects on soil. However, litterfall effects were not found for NH_4–N. This may because of different N mineralization in air-dried soils. Another cause of inconsistent associations of NO_3–N or NH_4–N to litterfall or topography may be complex N processing (Schimel and Bennett 2004; Chapin et al. 2012). Dissolved organic nitrogen (DON) in soil will undergo mineralization, nitrification, and denitrification. These processes involve different bacterial groups with different optima for soil moisture, oxygen, and carbon supply, which vary with topography (Silver et al. 1999; Schimel and Bennett 2004; Chapin et al. 2012). All these may weaken effects of litterfall and topography, thus causing complex patterns for NO_3–N and NH_4–N. Mobility of chemicals may also contribute to patch inconsistency. However, in our study plot, strongly mobile NO_3–N did not present much less consistent patterns compared to less-mobile NH_4–N. This may be because our data was collapsed in to mean values of 1 m^2 blocks, and thus they covered fluctuation differences between chemicals within block. Undefined spatial variables' significant effects on soil pH, total N, NO_3–N, and available P suggest important factors were not included in our variation partitioning model, which may include effects of plant roots, microorganisms, or soil bulk density, etc.

Consistency of soil pH, total N, and available P and K patches confirmed the value of one-time soil sampling to investigate plant-soil relationships. However, temporal niches, and spatio-temporal variation, can also promote species coexistence (Wright 2002; Kelly 2008). Large fluctuations found here reveal that temporal aspects of heterogeneity should be examined in future studies. Consistency of patterns for NO_3–N and NH_4–N remain unclear, but high correlations of NO_3–N in fresh and dried soil suggest that spatial patterns of NO_3–N may actually be less consistent.

Soil chemical properties were only assessed over about 1.5 years. However, strong correlations of annual litterfall mass among 3 years (2011 to 2013) can be used as a proxy to indirectly support spatial consistency among years. Few studies have tested multi-year persistence of soil patches. One study tested soil nutrient variations after disturbance, and found that after 4 years of disturbance, soil nutrients returned to previous conditions (Guo et al. 2004). This supports the idea that plants aid in maintaining soil nutrient patch persistence. However, since multi-year phenomena like El Nino can modify forest processes (Holmgren et al. 2001), future studies that span across longer term durations are needed.

Conclusion

Exploring the role of spatial niche in maintaining biodiversity is a key issue in ecology and this study provides new insights into the nutrient consistency perspective. While topography and litterfall contributed to the fine-scale consistency of nutrient patches in soil pH, total N, and available P and K, their effect on soil NO_3–N and NH_4–N were weakened. Patterns of NO_3–N and NH_4–

N require further study. Fine-scale nutrient patch consistency can enhance our understanding of plant niches.

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