

# Variations in net litter nutrient input associated with tree species influence on soil nutrient contents in a subtropical evergreen broad-leaved forest

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**Abstract** The influence of tree species on soils has received much attention, but we know little about either the pattern and underlying mechanisms of net nutrient and carbon inputs under canopy for various tree species or the effects of net nutrient input on soil nutrient contents. To address these issues, we selected three tree species with distinct leaf sizes and arranged litter traps around the target individuals to test what affected net nutrient and carbon inputs under canopy of target individuals, and how net nutrient inputs influenced soil nutrient contents. The results showed that net litter manganese (Mn) and lignin inputs were significantly different among these tree species, as well as soil exchangeable potassium (K), available iron (Fe) and available Mn. The results also revealed that the species with the smallest sized leaves may stimulate more net Mn and lignin inputs than the species with the largest sized leaves. At the same time, net nutrient inputs correlated with soil available Fe, while the ratio of lignin to nitrogen of net litter correlated with total phosphorus contents. These results demonstrated that litter production may be the main factor deciding net nutrient and carbon inputs under different tree species' canopy, which significantly differentiated soil iron's availability.

**Keywords** Leaf litter · Net nutrient input · Soil nutrient · Leaf size

## 1 Introduction

Many studies have focused on the role of tree species in forest nutrient cycling [1–5]. Binkley [6] reviewed this research conducted over almost a century and put forward a framework for examining the processes by which species differ in their influence on nutrient flows and soil fertility. Subsequent research [7, 8] has not yet gone beyond Binkley's framework. The previous work demonstrates that variation in tree species resulted in, or at least correlated with, variability of soil nutrient contents, acidity, nutrient release processes, etc. These imply that tree species may exert unique influences on soils. Eisenhauer et al. [9] provided concrete evidence for this concept. Jacob et al. [10] also emphasised the significance of species identity.

Aboveground litter input undoubtedly has strong effects on forest soils [6] among various impacts of tree species on soils. Sayer [11] reviewed observational and manipulative experiments to integrate the forest ecosystem's processing of litter. She found that litter is an inherent part of nutrient and carbon cycling and acts as a protective layer buffering changes in soils, and that litter provides habitats for soil fauna, fungi and microorganisms. The impact of litter on nutrient and carbon cycling, particularly how the litter from different tree species influences dynamics of soil organic matter has been reviewed [12, 13]. How litter decomposition affected N<sub>2</sub> fixation has also been studied [14]. Furthermore, nutrient inputs can differ between hardwood and coniferous species [7]. Many of these studies compared different tree species on different sites, and most experiments were carried out in temperate forests. To the best of

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our knowledge, most studies focus on direct litter input (litter collected directly by litter trap or reserved on the forest ground), but there is little research exploring the effects of net nutrient and carbon inputs under canopy of different tree species (abbreviated as under tree species or mother trees below) on soil nutrients.

Therefore, we need to know the pattern of net nutrient and carbon inputs under different tree species and what factors may decide this pattern. Net nutrient and carbon inputs under a specific mother tree depend on two litter sub-divisions: the litter produced by the mother tree itself dispersing outside of the canopy (export litter), the other litter produced by the surrounding trees distributing under the mother tree (import litter). Any factors affecting export or import litter's production may finally decide net nutrient and carbon inputs.

A probable underlying mechanism is that different tree species can have a range of leaf sizes in the same forest community, which may result in different dispersal patterns. The larger leaves will tend to fall near the mother tree, while smaller leaves have the potential to disperse further away. Under this supposition, soil carbon and nutrients may accumulate under the tree species with larger leaves, and vice versa. Another explanation may be that some species may yield more litter than others. The species yielding more litter may produce more export litter and obtain less net input under mother trees, and vice versa. Every species has a characteristic leaf size scope and may also have a specific litter production. Therefore, soils under distinct tree species in a forest community will obtain different net carbon and nutrient inputs from aboveground litter, which may increase spatial variation in soil nutrients.

The present study wants to test (i) specific leaf size and/or litter production with regards to how they decide the net nutrient and carbon inputs under different tree species; and (ii) differences in net nutrient and carbon inputs and how they can consequently modify soil nutrient contents.

## 2 Materials and methods

### 2.1 Study site

This study was conducted in a subtropical evergreen broad-leaved forest located in Xujiaba Region ( $24^{\circ}32'N$ ,  $101^{\circ}01'E$ , 2450 m above sea level), in the Ailao Mountains in the Yunnan Province of southwest China. The average annual temperature and average annual precipitation were  $11.3^{\circ}C$  and 1931.1 mm from 1991 to 1995 [15]. Dominant tree species are *Lithocarpus xylocarpus*, *Castanopsis wattii*, *Lithocarpus hancei* and *Schima noronhae*, which comprise a closed canopy layer [16]. In this forest, the canopy was quite flat and well closed; there were few

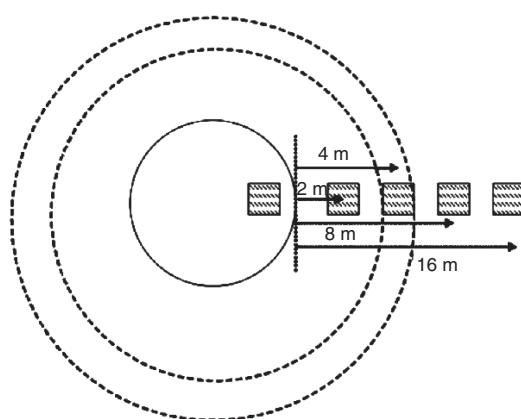
individual trees emerging from the canopy layer. The mineral soil is an Alfisol with an average pH of 4.3, covered by a thick litter layer up to 30 cm deep [15].

### 2.2 Sampling and analysis

We selected *Manglietia insignis* (MI), *Schima noronhae* (SN) and *Ilex corallina* (IC) for this study according to the following criteria: (i) these three tree species (in the aforementioned order) had the largest, intermediate and smallest leaf sizes in this forest; (ii) the nearest conspecifics were at least 45 m apart; (iii) four individuals for each species with adequate spacing were targeted; and (iv) all targeted individuals had similar heights. After determining the target individuals, we estimated the canopy areas, and we found that there were no conspecifics apart from each targeted individual within a 45-m radius. We did not consider litter production when selecting the tree species due to a lack of relevant data at the time.

To measure export and import litter, 20 litter traps were evenly arranged around each individual in four directions: five litter traps were placed in a straight line along each key compass point (N, E, S and W). The closest traps were under the canopy of the target individuals, while the other four traps were placed 2, 4, 8 and 16 m away from the edge of canopy, respectively (Fig. 1).

The traps were square (0.8 m edge length) with the opening 1 m above ground. Fresh aboveground litter was collected at the beginning of each month after the traps were placed, from May, 2008 to April, 2009. The litter was sorted, in the laboratory, into leaf, twig, fruit, flower and other residue. All leaf litter was identified by species: leaves from different species were generally readily



**Fig. 1** Sketch map of sampling design around an individual tree. The circle (black line) indicates the canopy zone; hatched squares indicate litter traps in one direction; arrows with numbers show distances between canopy edge and litter traps. The ring between the dotted line and enclosing litter trap indicates the area used to calculate litter mass at a specific distance

discerned. After sorting, the litter was oven-dried at 80 °C [17, 18] to constant mass, and then weighed. The dried litter from the same species was stored separately in sealed polyethylene bags and was ground into powder for carbon and nutrient analysis.

To quantify net nutrient and carbon inputs under the target individuals (abbreviated as net nutrient and carbon inputs below), we calculated export and import litter separately. Firstly we calculated import litter. We estimated leaf litter input density (per unit area) from the litter traps under canopy, and then we calculated total leaf litter input according to multiplying this density by the projected area of the canopy. For export litter, we first calculated litter input at a specific distance from the target individual. The litter mass falling on the area of the circular rings which enclosed litter traps at specific distance represents the litter input ascribed to that ring (as illustrated in Fig. 1). The width of the rings was 0.8 m, also the side length of the litter traps. The internal and external diameters of the rings were the distances from the centre of the canopy to the internal and external sides of the litter traps. According to the area of the rings and litter mass per square metre (calculated from the litter traps), we calculated the litter input at each specific distance. When regressing the aboveground litter mass at the specific distance with that distance, we fitted logarithmic models for each target individual. After integrating the model, we got the total litter mass outside the canopy.

To evaluate the effects of net nutrient and carbon inputs on soil nutrients, we sampled the top 10 cm of the mineral soils twice, in August, 2008 (wet season) and February, 2009 (dry season). Four samples were collected under each target individual, and in four compass bearing directions from the stem. For each sample, a sub-plot (50 cm × 50 cm) was chosen with four soil cores taken from the corners and one soil core in the centre. These five soil cores were combined into a single sample. Thus for each measurement, there were four samples for each individual tree and 48 samples in total. The samples were air dried in the laboratory. Plant roots, stones and chars were carefully removed from these soil samples, and they were sieved through a 2-mm square aperture mesh. A sub-sample of these soils was ground to pass the 60-mesh.

Leaf litter was analysed for carbon (C), nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), iron (Fe), manganese (Mn) and lignin. Organic C (OC), total N (TN), total P (TP), exchangeable K (EK), exchangeable Ca (ECa), exchangeable Mg (EMg), available Fe (AFe), available Mn (AMn) and pH were assayed for each soil sample. All the litter and soil samples were analysed by the Biogeochemistry Laboratory of Xishuangbanna Tropical Botanical Gardens, Chinese Academy of Sciences.

### 2.3 Statistics

One-way analysis of variance (ANOVA) was used to identify significant differences between samples. At the same time, we invoked an LSD (least significance difference) multiple-comparison test to identify differences between tree species. Pearson correlation analysis was conducted to analyse relationships between litter inputs and soil nutrient contents and step-wise linear regression was invoked to further analyse the data. To obtain the normal distributions, soil EK and AMn contents were log-transformed for ANOVA. All statistical analyses used R 2.10.1 software [19].

## 3 Results

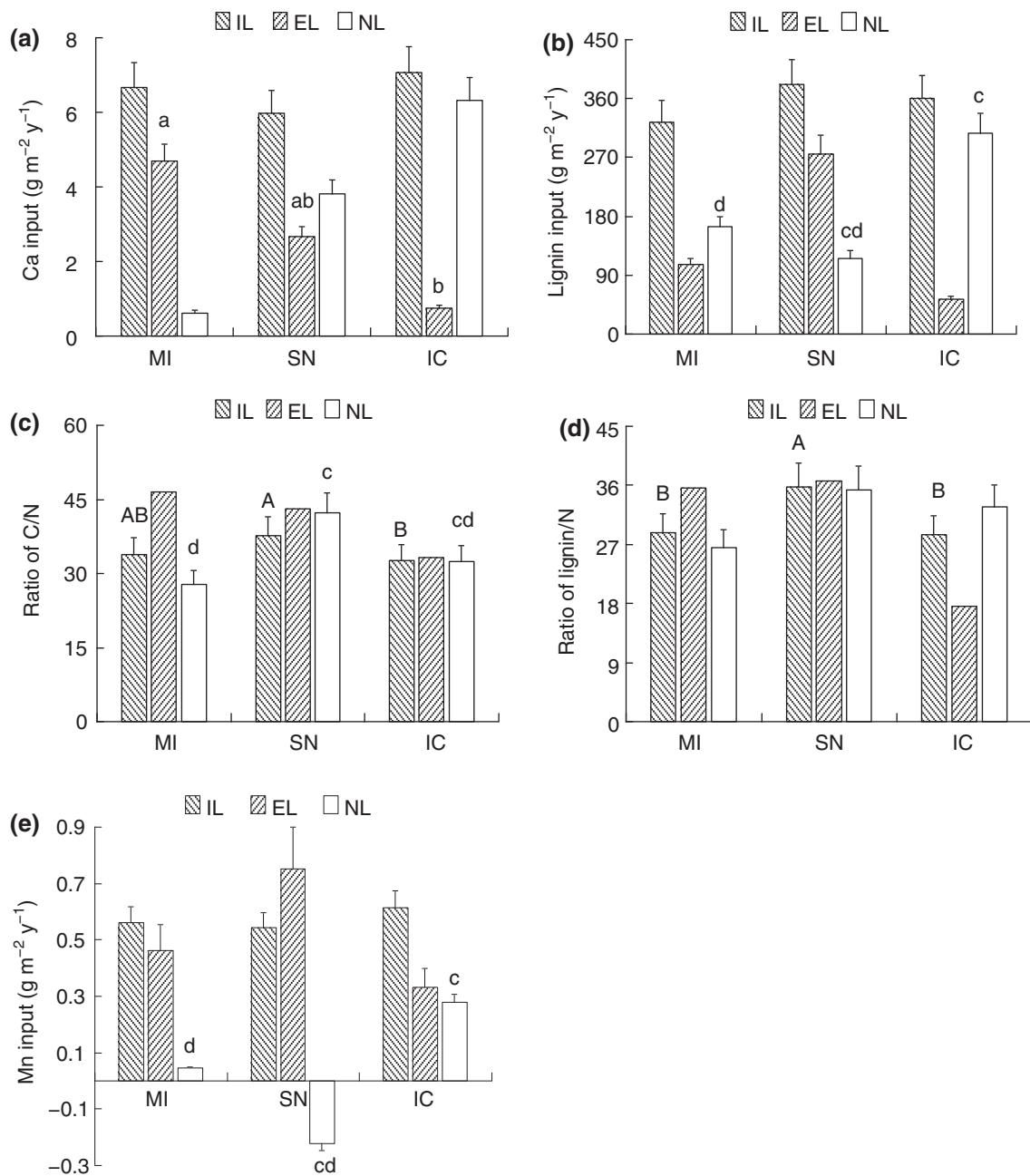
### 3.1 Net litter input under canopy of target individuals

The nutrient inputs of import litter were not significantly different among the target tree species except the two ratios of C/N and lignin/N. We found that export litter constituted more than 60 % of the total leaf litter production of target trees. Only the Ca input of export litter exhibited significant difference between MI and IC, the former being higher (Fig. 2).

We have mentioned in the introduction that net nutrient and carbon inputs were decided by the difference between import litter and export litter. All elements showed positive net inputs under the canopy of these target species except for Mn, which exhibited positive net input for IC and MI, but net output for SN. Net inputs of Mn and lignin of IC were significantly higher than those of MI, while C/N of SN was higher than that of MI (Fig. 2).

### 3.2 Nutrient and carbon contents in the soil under canopies and correlation with net litter inputs

The nutrient and carbon contents in the topmost 10 cm of mineral soil under the canopy of the target individuals are shown in Table 1. The AFe content in the soil was higher under SN and MI than that under IC. For EK content in the soil, SN was higher than MI and IC, while the AMn content exhibited the inverse pattern that soil AMn content under MI and IC were higher than under SN. C/N in the soil presented significant differences, with the ratio under IC higher than those under MI and SN. Soil AFe content was negatively correlated with net carbon and nutrient inputs, together with C/N (Table 2). Soil TP content was negatively correlated with lignin/N. Further, step-wise linear regression showed that net nitrogen input alone could explain 56.2 % of the variation of soil AFe content and lignin/N could explain 63.4 % of the variation of soil TP content.



**Fig. 2** Inputs of litter nutrients. *IL* import litter from surrounding individuals dispersed under canopies, *EL* leaf litter of target individuals dispersing outside canopies, *NL* net input from litter. Abbreviations for tree species refer to the text. Capital letters indicate significant difference in *IL* among target tree species. Lower case *a* and *b* indicate significant differences in *EL* among target tree species; *c*, *d* indicate significant differences in *NL* among target tree species. There are no one-way ANOVA and standard deviation bars of C/N and lignin/N for *EL* as the two ratios were the same for four individuals of the same species

## 4 Discussion

### 4.1 Net nutrient and carbon input under canopy of target individuals

The results revealed that net nutrient input exhibited significant differences among various tree species. According to general knowledge and reasonable presumption, tree

species with the largest leaves may obtain positive net nutrient and carbon inputs under their canopy, species with intermediate leaf sizes would have smaller net inputs, and species with the smallest leaves may experience net losses. However, for the tree species (with extreme local leaf sizes) we selected, most elements showed positive net inputs for all three species. Furthermore, the reverse pattern was seen for those tree species with the smallest leaves which had

**Table 1** Soil pH, soil OC content, soil nutrient contents, the ratio of C/N under canopy of target individuals

Target tree species	pH	OC (g kg <sup>-1</sup> )	TN (g kg <sup>-1</sup> )	TP (g kg <sup>-1</sup> )	EK (cmol kg <sup>-1</sup> )	ECa (cmol kg <sup>-1</sup> )	EMg (cmol kg <sup>-1</sup> )	AFe (mg kg <sup>-1</sup> )	AMn (mg kg <sup>-1</sup> )	C/N
IC	4.72 (0.31)	81.70 (21.71)	5.83 (1.46)	1.26 (0.34)	0.57 (0.19)b	6.38 (5.95)	2.01 (1.38)	160.22 (78.18)b	31.75 (13.51)a	14.96 (0.74)a
SN	4.67 (0.38)	87.85 (17.42)	6.17 (1.39)	1.25 (0.26)	0.79 (0.31)a	5.62 (7.95)	2.37 (2.40)	247.44 (124.90)a	19.01 (19.24)b	14.34 (1.13)b
MI	4.75 (0.53)	87.40 (25.27)	6.10 (1.49)	1.30 (0.32)	0.64 (0.31)b	9.11 (10.41)	2.55 (1.64)	261.16 (89.47)a	30.69 (21.80)a	14.19 (1.10)b

Abbreviations for tree species and soil variables refer to the text. Standard deviations are in brackets. Lower case a and b indicate significant differences in soil variables among target tree species:  $n = 16$ , significance level  $P = 0.05$

higher net inputs of Mn and lignin than the largest-leaved species. These results seemed anomalous because the smaller-sized leaves may disperse further away and the corresponding tree species should have lost more leaf litter. Even if the species with the smallest-sized leaves obtained net nutrient input, it should have been less than that obtained by species with the largest-sized leaves. It may imply in our study that net nutrient input was not mainly controlled by leaf size, but litter mass production. Some other studies also try to identify differences in litter production among different species [20–23], however, few studies have estimated total litter production of specific individuals before. From the perspective of life history, strategy, or evolution, we might deduce that less litter production results in less litter loss outside of canopy, which may result in more net nutrient input under canopy. This means more biomass accumulation or faster growth. In our study, total individual litter production varied among chosen tree species and the tree with the smallest leaves, IC, produced least litter. Consequently, IC lost less leaf litter outside its canopy, and the net nutrient and carbon inputs under the canopy of IC individuals were also positive, even larger than those of MI and IC. It seems that these selected species are all importer species, that is, net positive inputs make them accumulate nutrients under their canopies. On stand or community scales, there should be some exporter species to balance litter inputs, which disperse a high proportion of leaf litter mass under target individuals' canopies, like *Castanopsis wittii*, *Machilus yunnanensis*. Unfortunately, we did not find exporter species in this present study.

There are some other studies that have discussed net litter input. Welbourn et al. [24] defined net litter input as final litter input after relocation by autumnal wind. Boerner and Kooser [25] also used the concept of net litter input when investigating leaf litter redistribution. Though Song et al. [26] mentioned net litter input in their research, it seemed to indicate the monthly aboveground litter input on the ground, which is similar with general litter collection and is distinct from our *net litter inputs*. It was firstly quantified in our study, the extent to which net litter inputs to soils under different tree species' canopies existed.

Actually fruits of different tree species can also have distinct sizes, but leaf litter tends to be the dominant proportion of aboveground fine litter ([27, 28]; in this study; except for e.g. Barnes et al. [29]) and as fruits are animal-rewarding and animal dispersed [30, 31], we did not consider fruit litter in this study.

#### 4.2 Effects of net litter nutrient inputs on soil nutrient contents

Owing to the influence of various tree species, the soil carbon, nitrogen, phosphorus, exchangeable cations and

**Table 2** Correlation between nutrient input of leaf litter and soil nutrient contents and ratio of carbon to nitrogen

Soil variables	Net litter C	Net litter N	Net litter P	Net litter Ca	Net litter Mn	Net litter C/N	Net litter lignin/N
EK	0.032	0.058	0.074	0.141	-0.001	-0.115	-0.272
AMn	0.540	0.568	0.465	0.556	0.568	-0.627	-0.454
C/N	-0.270	-0.243	-0.218	-0.166	-0.267	0.330	0.309
TP	0.017	0.283	0.117	0.150	0.033	0.407	<b>-0.796</b>
AFe	<b>-0.672</b>	<b>-0.750</b>	<b>-0.709</b>	<b>-0.720</b>	<b>-0.668</b>	<b>0.729</b>	0.521

Abbreviations for soil variables and litter variables refer to the text. Correlation coefficients, derived from Pearson correlation analysis, shown in bold were significant;  $n = 12$ , significance level  $P = 0.05$

micro-nutrient contents are probably different under these species [6, 32–35]. Similarly, in our study, soil EK, AFe and AMn contents under the canopy did exhibit significant differences between the target tree species. Particularly, we stressed differences among tree species under their canopies, which was similar to significant influences of crowns of different tree species, a conifer (*Dacrydium gracilis*) and a broad-leaved tree (*Lithocarpus clementianus*) on condensed tannins and pH [36]. Although we have known that litter input obviously affects soil nutrient and carbon contents, we had little knowledge about how net nutrient input functions, which might have an effect on long-term soil nutrient status.

Our results discovered significant correlation between soil nutrient content and net nutrient input. Moreover, we also found the determinants of soil AFe and TP contents from net nutrient input. When the nitrogen of plant litter went into soils, nitrogen was mainly reserved with organic forms [37, 38], then, soil organic nitrogen tended to bind to iron when absorbed on clay surfaces [39], which decreased soil AFe content. This knowledge chain may be the reason why net nitrogen input could explain 56.2 % of the variation of soil AFe content negatively. The ratio of lignin to nitrogen of net litter was negatively correlated with soil TP. It may be that higher ratios slowed litter decomposition [40, 41] and litter nutrients returned more slowly to mineral soil, which lowered soil TP.

We did not examine soil organic matter (SOM) directly, but we can estimate it from OC since there is a known ratio between SOM and OC [42], so we can know that there is no significant difference in SOM under target individuals. There was no correlation between net nutrient input and OC, so variation in net nutrient input, i.e. various tree species had little effect on SOM content in the present study. This differed from some previous research [5, 12, 13], e.g. Vancampenhout et al. [13] demonstrated that variation in litter quality aroused by different tree species influenced soil SOM content significantly.

Although net C, N, P, Ca and Mn inputs were not the determinants of soil AFe content, significant correlations implied that these element inputs were probably influencing

the soil's AFe content to some extent. For example, net litter Mn input may increase soil Mn and soil Mn<sup>4+</sup> is more readily reduced to AMn than reduction of Fe<sup>3+</sup> [43], which explained the negative correlation between soil AFe content and net Mn input. The litter Ca input tends to increase soil ECa content [44], and the higher the soil ECa content, the higher the soil pH [35]. Lower soil pH values correspond to higher soil AFe content because the high acidity increases the availability of Fe [45–47]. By extension, this may explain why the net litter Ca input was negatively correlated with soil AFe content.

It has generally been observed that soil nutrients differ substantially among tree species, both in forests [48] and arid environments [49]. However, our study identified determinants from net nutrient input. Integrating the two strands of data, we can find that variation of plant specific traits, indicating litter production here, determined net nutrient input under mother trees, which in turn affected relevant soil nutrient contents. This might imply that more tree species give rise to more variation in plant traits, in turn, causing more variability in soil nutrient contents.

## 5 Conclusions

Variation of litter production resulted in differences in net nutrient inputs under canopy of mother trees among different tree species, which in turn, partly decided soil available iron and total phosphorus contents. It seems that variation in plant traits contributed to differentiation of soil nutrient contents through net nutrient input, thereby promoting soil variability.

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## References

1. Binkley D, Sollins P, Bell R et al (1992) Biogeochemistry of adjacent conifer and alder-conifer stands. *Ecology* 73:2022–2033
2. Bormann BT, Bormann FH, Bowden WB et al (1993) Rapid N2 fixation in pines, alder, and locust: evidence from the sandbox ecosystems study. *Ecology* 74:583–598
3. Giardina CP, Huffman S, Binkley D et al (1995) Alders increase soil phosphorus availability in a Douglas-fir plantation. *Can J For Res* 25:1652–1657
4. Davidson EA, Hart SC, Firestone MK (1992) Internal cycling of nitrate in soils of a mature coniferous forest. *Ecology* 73:1148–1156
5. Lu S, Chen C, Zhou X et al (2012) Responses of soil dissolved organic matter to long-term plantations of three coniferous tree species. *Geoderma* 170:136–143
6. Binkley D (1995) The influence of tree species on forest soils: processes and patterns. In: Mead DJ, Cornforth IS (eds) Proceedings of the trees and soils workshop, Lincoln University, 28 February–2 March 1994, Agronomy Society of New Zealand Special Publication No. 10, Lincoln University Press, Canterbury, pp 1–34
7. Augusto L, Ranger J, Binkley D et al (2002) Impact of several common tree species of European temperate forests on soil fertility. *Ann For Sci* 59:233–253
8. Ayres E, Steltzer H, Berg S et al (2009) Tree species traits influence soil physical, chemical, and biological properties in high elevation forests. *PLoS ONE* 4:e5964
9. Eisenhauer N, Beßler H, Engels C et al (2010) Plant diversity effects on soil microorganisms support the singular hypothesis. *Ecology* 91:485–496
10. Jacob M, Weland N, Platner C et al (2009) Nutrient release from decomposing leaf litter of temperate deciduous forest trees along a gradient of increasing tree species diversity. *Soil Biol Biochem* 49:2122–2130
11. Sayer EJ (2006) Using experimental manipulation to assess the roles of leaf litter in the functioning of forest ecosystems. *Biol Rev* 81:1–31
12. Hobbie SE, Ogdahl M, Chorover J et al (2007) Tree species effects on soil organic matter dynamics: the role of soil cation composition. *Ecosystem* 10:999–1018
13. Vancampenhout K, De Vos B, Wouters K et al (2010) Determinants of soil organic matter chemistry in maritime temperate forest ecosystems. *Soil Biol Biochem* 42:220–233
14. Dommergues YR (1995) Nitrogen fixation by trees in relation to soil nitrogen economy. *Fertil Res* 42:215–230
15. Qiu XZ, Xie SC (1998) Studies on the forest ecosystem in Ailao Mountains, Yunnan, China (in Chinese). Yunnan Sciences and Technology Press, Kunming
16. Liu WY, Xie SC, Xie KJ et al (1995) Preliminary studies on the litterfall and coarse woody debris in mid-mountain humid evergreen broad-leaved forest in Ailao Mountains. *Chin J Plant Ecol* 37:807–814
17. Angelina Martínez-Yrízar A, Sarukhán J (1990) Litterfall patterns in a tropical deciduous forest in Mexico over a five-year period. *J Trop Ecol* 6:433–444
18. Escudero A, del Arco JM, Sanz IC et al (1992) Effects of leaf longevity and retranslocation efficiency on the retention time of nutrients in the leaf biomass of different woody species. *Oecologia* 90:80–87
19. R Development Core Team (2009) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. <http://www.R-project.org>
20. Celentano D, Zahawi RA, Finegan B et al (2011) Litterfall dynamics under different tropical forest restoration strategies in Costa Rica. *Biotropica* 43:279–287
21. Hansen K, Veterdal L, Schmidt IK et al (2009) Litterfall and nutrient return in five tree species in a common garden experiment. *For Ecol Manag* 257:2133–2144
22. Jha P, Mohapatra KP (2010) Leaf litterfall, fine root production and turnover in four major tree species of the semi-arid region of India. *Plant Soil* 326:481–491
23. Murovhi NR, Materechera SA, Mulugeta SD (2012) Seasonal changes in litter fall and its quality from three sub-tropical fruit tree species at Nelspruit, South Africa. *Agrofor Syst* 86:61–71
24. Welbourn ML, Stone EL, Lassoie JP (1981) Distribution of net litter inputs with respect to slope position and wind direction. *For Sci* 27:651–659
25. Boerner REL, Kooser JG (1989) Leaf litter redistribution among forest patches within an Allegheny Plateau watershed. *Landscape Ecol* 2:81–92
26. Song M, Yates DJ, Doley D (2012) Rain forest understorey ferns facilitate tree seedling survival under animal non-trophic stress. *J Veg Sci* 23:847–857
27. Adu-bredou S, Haghjara A (2003) Long-term carbon budget of the above-ground parts of a young Hinoki cypress (*Chamaecyparis obtusa*) stand. *Ecol Res* 18:165–175
28. Glaser B, Benesch M, Dippold M et al (2012) In situ <sup>15</sup>N and <sup>13</sup>C labelling of indigenous and plantation tree species in a tropical mountain forest (Munessa, Ethiopia) for subsequent litter and soil organic matter turnover studies. *Organ Geochem* 42:1461–1469
29. Barnes P, Wilson BR, Reid N et al (2011) Litterfall and associated nutrient pools extend beyond the canopy of scattered eucalypt trees in temperate pastures. *Plant Soil* 345:339–352
30. Gautier-Hion A, Duplantier JM, Quris R et al (1985) Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia* 65:324–337
31. Janzen DH (1984) Dispersal of small seeds by big herbivores: foliage is the fruit. *Am Nat* 123:338–353
32. Binkley D (1997) Bioassays of the influence of *Eucalyptus saligna* and *Albizia falcataria* on soil nutrient supply and limitation. *For Ecol Manag* 91:229–234
33. Cross A, Perakis SS (2011) Complementary models of tree species–soil relationships in old-growth temperate forests. *Ecosystem* 14:248–260
34. Finzi AC, Van Breemen N, Canham CD (1998) Canopy tree–soil interactions within temperate forests: species effects on soil carbon and nitrogen. *Ecol Appl* 8:440–446
35. Finzi AC, Canham CD, Van Breemen N (1998) Canopy tree–soil interactions within temperate forests: species effects on pH and cations. *Ecol Appl* 8:447–454
36. Ushio M, Kitayama K, Balser TC (2010) Tree species-mediated spatial patchiness of the composition of microbial community and physicochemical properties in the topsoils of a tropical montane forest. *Soil Biol Biochem* 42:1588–1595
37. Fahey TJ, Yavitt JB, Sherman RE et al (2011) Transport of carbon and nitrogen between litter and soil organic matter in a northern hardwood forest. *Ecosystem* 14:326–340
38. Bimüller C, Naumann PS, Buegger F et al (2013) Rapid transfer of <sup>15</sup>N from labeled beech leaf litter to functional soil organic matter fractions in a Rendzic Leptosol. *Soil Biol Biochem* 58:323–331
39. Matsumoto S, Ae N (2004) Characteristics of extractable soil organic nitrogen determined by using various chemical solutions and its significance for nitrogen uptake by crops. *Soil Sci Plant Nutr* 50:1–9
40. Aerts R (1997) Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. *Oikos* 79:439–449
41. Melillo JM, Aber JD, Muratore JF (1982) Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology* 63:621–626

42. Pribyl DW (2010) A critical review of the conventional SOC to SOM conversion factor. *Geoderma* 156:75–83
43. McBride MB (1994) Environmental chemistry of soils. Oxford University Press, New York
44. Reich PB, Oleksyn J, Modrzynski J et al (2005) Linking litter calcium, earthworms and soil properties: a common garden test with 14 tree species. *Ecol Lett* 8:811–818
45. Straub KL, Benz M, Schink B (2001) Iron metabolism in anoxic environments at near neutral pH. *FEMS Microbiol Ecol* 34:181–186
46. Tagliavini M, Rombola AD (2001) Iron deficiency and chlorosis in orchard and vineyard ecosystems. *Eur J Agron* 15:71–92
47. Wei X, Shao M, Zhuang J et al (2010) Soil iron fractionation and availability at selected landscape positions in a loessial gully region of northwestern China. *Soil Sci Plant Nutr* 56:617–626
48. Koch AS, Matzner E (1993) Heterogeneity of soil and soil solution chemistry under Norway spruce (*Picea abies* Karst.) and European beech (*Fagus sylvatica* L.) as influenced by distance from the stem basis. *Plant Soil* 151:227–237
49. Zuo XA, Zhao XY, Zhao HL et al (2009) Spatial heterogeneity of soil properties and vegetation–soil relationships following vegetation restoration of mobile dunes in Horqin Sandy Land, Northern China. *Plant Soil* 318:153–167