

# The $\delta^{15}\text{N}$ signature of the detrital food web tracks a landscape-scale soil phosphorus gradient in a Costa Rican lowland tropical rain forest

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**Abstract:** In this study, we investigated whether landscape-scale variation of soil P accounts for  $^{13}\text{C}$  and  $^{15}\text{N}$  composition of detrital invertebrates in a lowland tropical rain forest in Costa Rica. The top 10-cm soil, leaf-litter samples and plant foliage were collected among 18 plots representing a three-fold soil P gradient during 2007–2009. Body tissue of litter invertebrates (extracted from leaf-litter samples) along with soil, leaf litter and green foliage were analysed for total C, total N,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values. Differences in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  signatures across plots and relative trophic distances of detrital food webs ( $\Delta \delta^{15}\text{N}$ ), and their variation with soil P gradient were evaluated. We found soil P gradient had a significantly positive correlation with  $\delta^{15}\text{N}$  of *Asterogyme martiana* foliage, leaf litter, collembolans and oribatid mites. The  $\delta^{15}\text{N}$  of the collembolans and pseudoscorpions positively correlated to leaf-litter  $\delta^{15}\text{N}$ .  $\Delta \delta^{15}\text{N}$  between the trophic levels remained consistent across the soil P gradient. Higher  $\delta^{15}\text{N}$  in the collembolans and oribatid mites might be derived from their consumption on  $^{15}\text{N}$ -enriched decayed debris or fungal hyphae growing on it. It suggests that fine-scale soil P variation can affect trophic dynamics of detrital arthropods via regulation of microbial community and nutrient dynamics.

**Key Words:**  $\delta^{13}\text{C}$ , collembolan, leaf litter, oribatid mite, stable isotope

## INTRODUCTION

Natural abundance of stable isotopic carbon ( $^{13}\text{C}$ ) in consumer body tissue is widely applied to indicate resource availability and accessibility to the consumers, as well as to reflect their preference for specific resources (Ponsard & Arditì 2000, Scheu & Falca 2000). The measurement of  $^{15}\text{N}$  can be linked to relative trophic position and predator–prey relationships in food webs. In concert,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  can explain food-web structure, reveal food-web dynamics, and track energy flow through food webs across spatial and temporal scales (Albers *et al.* 2006, Hyodo *et al.* 2010, Ponsard & Arditì 2000, Post 2002, Scheu & Falca 2000, Schmidt *et al.* 2004, Tiunov 2007).

Spatial heterogeneity of resource and nutrient availability, which determine baseline  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ,

affect  $^{13}\text{C}$  and  $^{15}\text{N}$  composition of food webs and food-web dynamics. Jennings *et al.* (1997) showed that fine-scale variation in resource availability altered  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of fish communities, which reflects the flexible feeding strategy and trophic position changes in aquatic ecosystems. In terrestrial ecosystems, most soil and litter inhabitants experience restriction to available resources due to their cryptic life cycle and minute size (Ponsard & Arditì 2000, Scheu & Falca 2000). Landscape-scale resource heterogeneity could possibly drive divergent litter arthropod communities and food-web structures. Yet, whether fine-scale nutrient variation has a measurable influence on litter invertebrates in terms of trophic structure of food webs is still unclear.

An existing landscape-scale soil phosphorus (P) gradient has been described during long-term ecological research in a lowland tropical rain forest at La Selva Biological Station of Costa Rica (CARBONO-project plots, Clark & Clark 2000). This fine-scale soil P variation has been shown to affect tree species composition (Clark

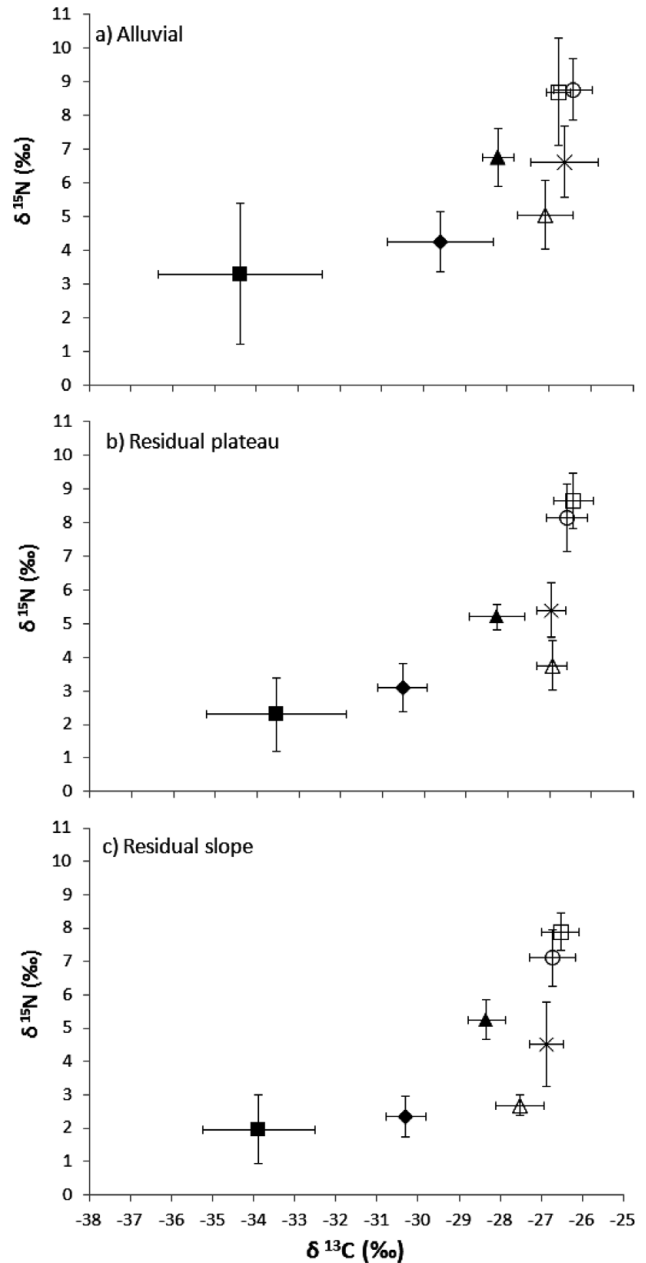
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*et al.* 1999), density of total litter arthropods (McGlynn *et al.* 2007), and  $\delta^{15}\text{N}$  in forest-floor leaf litter and an ant species (body tissue, *Aphaenogaster araneoides*) (McGlynn *et al.* 2009). Soil P in tropical forests has been shown to affect net primary production and below-ground C cycling through regulating soil respiration, decomposition processes and N fixation and turnover rates (Cleveland *et al.* 2011, Kaspari *et al.* 2008, Townsend *et al.* 2011). Decomposition rates could be facilitated via enhancing the interactions between microbes and the microvores by soil P fertilization (Kaspari *et al.* 2008). Soil P variation at temporal and spatial scales could contribute to N limitation and affect N availability in a tropical ecosystem (Townsend *et al.* 2011). These findings raise the question of whether fine-scale soil P variation in La Selva has impacts on  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of detrital food webs through regulating C and N dynamics of soil and litter resources. In this study, we first investigated  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  composition of major litter invertebrate groups in detrital food webs, the variation of C, N,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  in soil organic matter, plant foliage and leaf litter across this soil P gradient. We then evaluated whether the variation in resource (soil and litter) C, N,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  and soil P relates to the changes of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of detrital food webs. We hypothesized that higher  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of detrital food webs in accordance with higher concentration of basal resource nutrients (i.e. soil/leaf litter C, N,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) would be observed in the P-enriched plots.

## MATERIALS AND METHODS

### Study sites

The CARBONO-Project plots are located in a lowland tropical rain forest at the La Selva Biological Station, Costa Rica (10°26'N, 84°00'W; 37–150 m asl; McDade *et al.* 1994). The region receives 4000 mm  $\text{y}^{-1}$  of rainfall, with an average daily temperature of 26 °C (Sanford *et al.* 1994). The soils of all plots are categorized as Oxisols (Haplic Haploperox; Ferralsols in the FAO/WRB system) based on soil mineralogical analyses by Kleber *et al.* (2007). Three major edaphic conditions are the relatively fertile alluvial terraces ('alluvial' plots); less-fertile, older ridge-top sites ('residual plateau' plots); and less-fertile slope ('residual slope' plots; Sollins *et al.* 1994). The deposited soils in the alluvial plots are deeply weathered clay, and are considered similar to the soils of residual plots but younger. Eighteen 0.5-ha CARBONO plots were established in a stratified-block design across soil type and topography (Clark & Clark 2000). The plots span substantial landscape variation in soil P as well as in cation concentrations (e.g. potassium (K), calcium (Ca), manganese (Mn), iron (Fe) and aluminium (Al); Espeleta



**Figure 1.** The  $\delta^{13}\text{C}$  (‰) and  $\delta^{15}\text{N}$  (‰) enrichments ( $\pm$  SD) of the different trophic levels in the detrital food webs from three edaphic site-types: alluvial (a), residual plateau (b) and residual slope (c), in a lowland tropical rain forest at La Selva Biological Station, Costa Rica. Symbols represent the following: ■ = green leaves; ▲ = soil; ◆ = leaf litter; △ = collembolans; × = oribatid mites; □ = pseudoscorpions; ○ = spiders.

& Clark 2007). The alluvial soil (0–100 cm depth) had higher C, P, K, Ca, Mn and Fe than the residual plateau soil (Figure 1 in Espeleta & Clark 2007). The La Selva forest is dominated by a leguminous tree, *Pentaclethra macroloba*, distributed broadly along all edaphic gradients (Clark & Clark 2000). The palm species, *Welfia regia*, *Socratea exorrhiza* and *Iriartea deltoidea*, comprise one quarter of the total density of stems larger than 10 cm

in diameter (Clark & Clark 2000, Clark *et al.* 1999). A map showing the spatial distribution of these 18 plots in different soil gradients can be found in Espeleta & Clark (2007; Appendix A: Ecological Archives M077–012-A1). More description about the background and history of CARBONO plots can be found in Espeleta & Clark (2007).

### $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of detrital food webs

To determine  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  patterns of the detrital food web, forest-floor leaf litter and litter invertebrates were collected from two 50-m bordering transects (10 m apart from one another) in each CARBONO plot during May–August 2008. At each transect, five 0.25-m<sup>2</sup> quadrats of forest-floor leaf litter were collected (a total of ten leaf-litter samples for each plot). The quadrats (subsamples) were 10 m apart from one another to ensure that they share equivalent edaphic properties and the same species pool but are still functionally independent of one another. The multiple subsamples per plot were then aggregated to represent a cumulative assessment of invertebrate community for each plot.

Litter invertebrates were extracted from the collected leaf litter by using mini-Winkler bags (Bestelmeyer *et al.* 2000, Fisher 1999). Extraordinary high alpha diversity of litter invertebrates is observed; however, specific trophic guilds have not been established at La Selva. In this study, taxonomic groups (i.e. collembolans, oribatid mites, spiders and pseudoscorpions) have been adapted to fulfil the sample requirement (a minimum of 1 mg dry animal tissue) for isotopic ratio analysis. The plots in which the invertebrate tissue samples were not sufficient for isotopic ratio analysis were not considered for further correlation analysis (collembolans, oribatid mites and spiders:  $N = 16$ ; pseudoscorpions:  $N = 13$ ). The litter invertebrate samples were maintained in aqueous solution and sorted into taxonomic categories (Collembola, Oribatida, Araneae and Pseudoscorpionida) using a stereomicroscope. The samples were then oven dried inside tin capsules prior to closure in preparation for stable-isotope analyses. Tin capsules were sent to the Stable Isotope Facility at University of California Davis, California, USA, for total C, N and  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  analysis.

The leaf-litter samples were drawn from a 10-L collection of fine leaf litter, from which arthropods were extracted. Leaf litter was oven-dried to a constant mass (at 60 °C) and weighed before and after combustion in a muffle furnace to determine ash-free weight. Subsamples of leaf litter were ground, shifted through No. 20-mesh (diameter = 0.8 mm; Wiley Mill; Thomas Scientific, Inc., Swedesboro, NJ, USA) and packed in tin capsules for stable-isotope analyses (C, N,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ).

Topsoil samples (0–10 cm depth;  $N = 3$  per plot) were collected simultaneously at each CARBONO plot along

the sampling transects described earlier in 2009. Fresh foliar tissue from each of three dominant plant species (*Pentaclethra maculosa*, *Welfia regia* and *Asterogyne martiana*) was collected in August 2009. Foliar samples (mature leaves of large saplings) were collected from three arbitrarily selected individuals per plant species per CARBONO plot. Both soil and foliage samples were oven-dried to a constant mass (at 60 °C), then ground to < 2 mm and packed in tin capsules for stable-isotope analyses (C, N,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ).

### Leaf-litter chemistry

Chemistry of leaf litter other than  $^{13}\text{C}$  and  $^{15}\text{N}$  fractions was adapted from a long-term litterfall-monitoring project that had been conducted in CARBONO plots since 1997. Within each plot, fine litterfall (leaves, reproductive material and twigs < 1 cm in diameter) were collected every other week from nine 0.25-m<sup>2</sup> standing basket traps and nine paired 0.25-m<sup>2</sup> ground traps for the large (> 50 cm long) leaves; (D.A. Clark, pers. comm.). Samples from the litter traps in each plot were combined, sorted by litter category, and oven-dried to constant mass (65 °C). The dried leaf material (combined samples from both trap types) was then run through a Wiley Mill to pass through a No. 20-mesh screen (mesh size = 0.8 mm). Ground litter samples were dry-combusted on an elemental analyser (Carlo Erba, Model NA 2500, Milan, Italy) to determine total C and N. Samples were digested using a modified Kjeldahl protocol on a Tecator 2000 digestion System (Perstorp Analytical, Sweden). The method uses 30% hydrogen peroxide and concentrated sulphuric acid at 320 °C to hydrolyse organic P, Mg, Ca and K into inorganic form. Digestates were analysed on an AlpKem Flow Solution IV Autoanalyzer (OI Analytical, College Station, Texas, USA) in accordance with US EPA method for total P. Total Mg, Ca and K in digestates were analysed on an atomic absorption spectrometer (AAAnalyst 100, PerkinElmer, Connecticut, USA). The data collected during 2005–2007 were adapted in this study. All data are reported on a dry mass basis. Nutrient ratios (e.g. C : N) are reported on a molar basis.

### Statistical analysis

All collected data were first analysed by PROC UNIVARIATE procedure in SAS statistic software (version 9.1, SAS Institute Inc., USA) to pass the normality of data. We used a one-way analysis of variance (ANOVA) method under PROC GLM procedure (SAS) to examine the difference in soil nutrients (C, N, P, C : N and C : P ratios), leaf-litter chemistry (C, N, P, C : N and C : P ratios),  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  composition of soil, leaf litter, plant foliage

**Table 1.** Carbon (C), nitrogen (N), phosphorus (P), C:N and C:P ratios in surface soil (0–10 cm depth) and leaf litter in the alluvial, residual-plateau and residual-slope edaphic site-types within a 500-ha landscape of a lowland tropical rain forest at La Selva Biological Station, Costa Rica. Data (shown as mean  $\pm$  SD) with different letters indicate significant difference between three edaphic site-types (Tukey HSD at  $P < 0.05$ ). Soil P and C:P ratio data were adapted from Espeleta & Clark (2007).

	Edaphic site-type		
	Alluvial	Residual plateau	Residual slope
0–10 cm soil			
C (mg g <sup>-1</sup> )	61.0 $\pm$ 2.4	68.0 $\pm$ 17.8	61.7 $\pm$ 12.3
N (mg g <sup>-1</sup> )	5.4 $\pm$ 0.2	5.7 $\pm$ 1.2	5.2 $\pm$ 0.9
C:N	11.3 $\pm$ 0.3	11.9 $\pm$ 0.8	11.9 $\pm$ 0.4
P (mg g <sup>-1</sup> )	1.3 $\pm$ 0.3 <sup>a</sup>	0.7 $\pm$ 0.1 <sup>b</sup>	0.8 $\pm$ 0.2 <sup>b</sup>
C:P	43.3 $\pm$ 18.3 <sup>a</sup>	90.0 $\pm$ 15.4 <sup>b</sup>	81.3 $\pm$ 23.6 <sup>b</sup>
Leaf litter			
C (%)	49.6 $\pm$ 0.5 <sup>a</sup>	48.6 $\pm$ 0.4 <sup>b</sup>	48.9 $\pm$ 0.4 <sup>b</sup>
N (%)	1.71 $\pm$ 0.08 <sup>a</sup>	1.54 $\pm$ 0.04 <sup>b</sup>	1.61 $\pm$ 0.02 <sup>b</sup>
C:N	31.5 $\pm$ 1.8 <sup>a</sup>	34.1 $\pm$ 0.9 <sup>b</sup>	32.9 $\pm$ 0.6 <sup>ab</sup>
P (mg g <sup>-1</sup> )	0.74 $\pm$ 0.09 <sup>a</sup>	0.56 $\pm$ 0.05 <sup>b</sup>	0.60 $\pm$ 0.05 <sup>b</sup>
C:P	689 $\pm$ 84.3 <sup>a</sup>	884 $\pm$ 67.9 <sup>b</sup>	843 $\pm$ 68.8 <sup>b</sup>

and litter invertebrates among the three edaphic types (alluvial, residual plateau and residual slope; six plots per edaphic type). Post hoc Tukey HSD test (significance level at  $P \leq 0.05$ ) was applied to test the differences among edaphic types. The average values of soil nutrient concentrations, litter chemistry and  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of each invertebrate group from each CARBONO plot were calculated and used to run correlation analyses (soil nutrients and litter chemistry data:  $N = 18$ ; collembolans, oribatid mites, and spiders:  $N = 16$ ; pseudoscorpions:  $N = 13$ ). Pearson correlation analysis (PROC CORR Pearson, SAS) was used to examine the relationships among soil nutrients, litter chemistry and  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of litter invertebrates.

## RESULTS

The alluvial site had the highest leaf-litter C, N and P concentrations, and the lowest C:N and C:P ratios. However, soil C and N did not significantly differ among the three edaphic site-types over the same landscape at La Selva (Table 1).

Plant foliage was the most depleted in  $^{13}\text{C}$  ( $\delta^{13}\text{C}$  ranging from  $-37.8\text{‰}$  to  $-30.4\text{‰}$ ), followed by leaf litter ( $\delta^{13}\text{C}$  ranging from  $-30.6\text{‰}$  to  $-28.0\text{‰}$ ), and then by soil ( $\delta^{13}\text{C}$  ranging from  $-29.2\text{‰}$  to  $-27.4\text{‰}$ ) (Figure 1). Foliar  $\delta^{13}\text{C}$  of the understory palm, *Asterogyne martiana* ( $-35.7\text{‰} \pm 1.1\text{‰}$ ) was significantly lower than the foliage from the canopy-tree species *Pentaclethra macroloba* ( $-33.0\text{‰} \pm 1.0\text{‰}$ ) and the subcanopy palm *Welfia regia* ( $-33.2\text{‰} \pm 1.4\text{‰}$ ) (Tukey HSD,  $P < 0.0001$ ). Litter invertebrates were higher in  $\delta^{13}\text{C}$  than basal resource leaf litter. The  $\delta^{13}\text{C}$  of the detritivores (collembolans and oribatid mites)

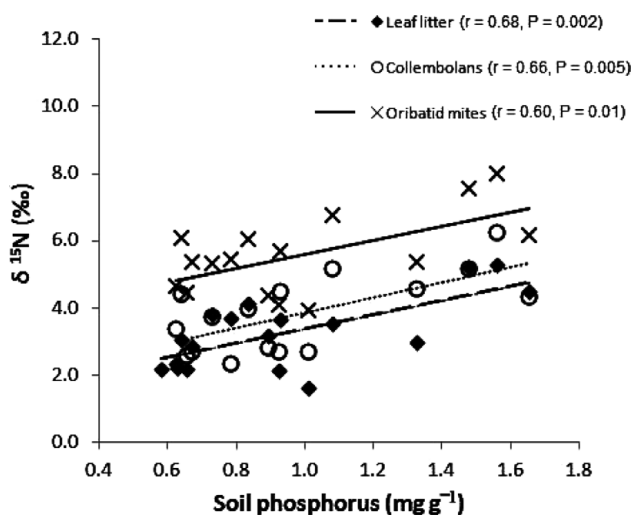
was 2.9‰ and 3.3‰ higher than leaf litter, respectively; while the  $\delta^{13}\text{C}$  of pseudoscorpions and spiders were 3.7‰ and 3.6‰ higher than leaf litter, respectively (Tukey HSD, all  $P < 0.05$ ; Figure 1). Among litter invertebrates, the spiders were significantly more  $^{13}\text{C}$ -enriched ( $\delta^{13}\text{C} = -26.6\text{‰} \pm 0.14\text{‰}$ ) than the collembolans ( $\delta^{13}\text{C} = -27.2\text{‰} \pm 0.1\text{‰}$ , Tukey HSD;  $P < 0.05$ ). The  $\delta^{13}\text{C}$  distribution patterns of topsoil, plant foliage, leaf litter and litter invertebrates were not significantly different among sites (Figure 1).

The  $\delta^{15}\text{N}$  of resources (plant foliage, topsoil, leaf litter) and litter invertebrates (except pseudoscorpions) were significantly higher in the alluvial site than in the other two sites (Figure 1, Table 2). Soil  $\delta^{15}\text{N}$  was significantly higher ( $6.8\text{‰} \pm 0.9\text{‰}$ ) in the alluvial site than in the residual-plateau and residual-slope sites ( $5.2\text{‰} \pm 0.7\text{‰}$  and  $5.3\text{‰} \pm 0.6\text{‰}$ , respectively; PROC GLM,  $F = 26.8$ ,  $df = 2, 51$ ,  $P < 0.0001$ ) (Table 2). Higher  $\delta^{15}\text{N}$  values were also observed in plant foliage (no species-specific difference), leaf litter and litter invertebrates collected from the alluvial site (Figure 1, Table 2). Delta  $^{15}\text{N}$  values ranged from 2.3‰ in plant foliage to the 8.4‰ in the pseudoscorpions (Figure 1). Three distinct guilds in the detrital food web can be identified by their  $\delta^{15}\text{N}$  values. The predators had the highest  $\delta^{15}\text{N}$  value (spiders:  $7.9\text{‰} \pm 0.3\text{‰}$  and pseudoscorpions:  $8.4\text{‰} \pm 0.3\text{‰}$ ), with oribatid mites in the middle ( $5.6\text{‰} \pm 0.3\text{‰}$ ), and collembolans with the lowest  $\delta^{15}\text{N}$  ( $3.8\text{‰} \pm 0.3\text{‰}$ ) (Figure 1). By adopting leaf litter as the  $\delta^{15}\text{N}$  baseline ( $3.3\text{‰} \pm 0.3\text{‰}$ ) of detrital food webs, the  $\delta^{15}\text{N}$  signatures of the collembolans and oribatid mites were 0.4‰ and 2.2‰ higher, respectively, than leaf litter. Spiders and pseudoscorpions were 4.1‰ and 4.7‰ higher than collembolans. The  $\delta^{15}\text{N}$  distribution pattern of the detrital food webs was consistent in all three edaphic-type sites (Figure 1).

Across-plot  $\delta^{15}\text{N}$  variation of detrital food webs was significantly correlated to plot-specific soil P concentration and soil C:P ratio (Table 3). Higher  $\delta^{15}\text{N}$  in leaf litter, collembolans and oribatid mites was correlated with higher soil P concentration (Pearson correlation  $r = 0.68, 0.66, 0.6$ , respectively, all  $P < 0.05$ ; Figure 2, Table 3) and negatively correlated to soil C:P ( $r = -0.59, -0.59, -0.52$ , respectively, all  $P < 0.05$ ; Table 3). Leaf-litter  $\delta^{15}\text{N}$  value was also positively correlated to leaf-litter C and P concentrations, and negatively related to leaf litter C:P (Table 3). The  $\delta^{15}\text{N}$  of the collembolans and the pseudoscorpions were positively correlated to leaf-litter  $\delta^{15}\text{N}$  ( $r = 0.72$  and  $0.75$ , respectively, both  $P < 0.05$ ; Table 3). Spider  $\delta^{15}\text{N}$  had a positive correlation with leaf-litter P concentration ( $r = 0.52$ ,  $P < 0.05$ ), but not soil P concentration. Foliar  $\delta^{15}\text{N}$  of *Asterogyne martiana* was correlated to soil P concentration ( $r = 0.58$ ,  $P = 0.01$ ). However, soil and leaf-litter P concentration and its C:P ratio did not affect the distance of  $\delta^{15}\text{N}$

**Table 2.** Delta  $^{15}\text{N}$  enrichment in soil (0–10 cm depth), leaf litter and litter invertebrate groups from contrasting edaphic site-types within a 500-ha landscape of a lowland tropical rain forest at La Selva Biological Station, Costa Rica. Values (shown as mean  $\pm$  SD) are from six plots sampled per site-type, and F values with degrees of freedom (df) are also shown in the table. Green leaves samples were the average values of three tree species collected in this study. Data with different letters indicate significant difference among three edaphic site-types (Tukey HSD at  $P < 0.05$ ).

	Edaphic site-type			F(df)	P-value
	Alluvial	Residual plateau	Residual slope		
$\delta^{15}\text{N}$ (‰)					
Green leaves	3.3 $\pm$ 2.1 <sup>a</sup>	2.3 $\pm$ 1.1 <sup>ab</sup>	2.0 $\pm$ 1.0 <sup>b</sup>	3.9(2,45)	0.027
Soil	6.8 $\pm$ 0.9 <sup>a</sup>	5.2 $\pm$ 0.7 <sup>b</sup>	5.3 $\pm$ 0.6 <sup>b</sup>	26.8(2,51)	< 0.0001
Leaf litter	4.3 $\pm$ 0.3 <sup>a</sup>	3.1 $\pm$ 0.3 <sup>b</sup>	2.4 $\pm$ 0.3 <sup>b</sup>	9.9(2, 15)	0.0018
Collembolans	4.9 $\pm$ 0.3 <sup>a</sup>	3.7 $\pm$ 0.3 <sup>b</sup>	2.7 $\pm$ 0.3 <sup>b</sup>	13.8(2, 13)	0.0006
Oribatid mites	6.7 $\pm$ 0.3 <sup>a</sup>	5.4 $\pm$ 0.3 <sup>b</sup>	4.4 $\pm$ 0.3 <sup>b</sup>	12.1(2,13)	0.0011
Pseudoscorpions	9.0 $\pm$ 0.5	8.6 $\pm$ 0.4	7.0 $\pm$ 0.3	1.9(2,10)	0.20
Spiders	8.8 $\pm$ 0.3 <sup>a</sup>	8.4 $\pm$ 0.3 <sup>a</sup>	7.0 $\pm$ 0.3 <sup>b</sup>	10.7(2,13)	0.0018



**Figure 2.** Relationships between soil phosphorus (P) concentration and  $\delta^{15}\text{N}$  (‰) in leaf litter, collembolans and oribatid mites in a lowland tropical rain forest at La Selva Biological Station, Costa Rica. Symbols represent the following:  $\blacklozenge$  = leaf litter (dashed line);  $\circ$  = collembolans (dotted line);  $\times$  = oribatid mites (solid line). Each data point indicates the average value of soil P concentration and  $\delta^{15}\text{N}$  of each invertebrate group from each CARBONO plot.

between trophic levels (relative trophic position:  $\Delta \delta^{15}\text{N}$ , Table 3). Interestingly, higher leaf-litter C and  $\delta^{15}\text{N}$  were found to relate to shorter  $\delta^{15}\text{N}$  distance between the pseudoscorpions and leaf litter ( $\Delta \delta^{15}\text{N}_{\text{P-L}}$ :  $r = -0.59$  and  $-0.67$ , respectively, both  $P < 0.05$ ; Table 3). The plot-specific annual litterfall and forest-floor leaf-litter stock during 2007–2009 did not relate the  $\delta^{15}\text{N}$  variation of the leaf litter and any litter invertebrates (data not shown, Pearson correlation analysis, all  $P > 0.05$ ).

**DISCUSSION**

Overall,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  distribution patterns of the detrital food webs were relatively consistent across the landscape-

scale variation of soil P in this lowland tropical rain forest. The  $\delta^{15}\text{N}$  signature spanned over 8‰, which suggests at least three trophic levels in the detrital food webs (assuming 2.3‰–3.4‰ per trophic level; DeNiro & Epstein 1981, McCutchan *et al.* 2003, Minagawa & Wada 1984). The significant enrichment in  $^{15}\text{N}$  of the spiders and the pseudoscorpions (4.1‰ and 4.7‰, respectively, higher than the collembolans) indicated the occurrence of intraguild predation, cannibalism among the spider and pseudoscorpion populations, or a mixed diet of other  $^{15}\text{N}$ -enriched secondary decomposers (i.e. earthworms) (DeNiro & Epstein 1978, McCutchan *et al.* 2003, McNabb *et al.* 2001, Post 2002, Tiunov 2007). However, it could also be a residual effect of a wide range of life stages we analysed (Ponsard & Arditì 2000, Scheu & Falca 2000).

Higher  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  signatures in soil and leaf litter than in the foliage samples can be attributed to the accumulation of heavy isotopic  $^{13}\text{C}$  in the decayed leaf litter during the litter decomposition process. Microbial activities often primarily utilize  $^{12}\text{C}$ -compound carbohydrates and release  $^{13}\text{C}$ -depleted  $\text{CO}_2$  (Hyodo *et al.* 2010, Melillo *et al.* 1989, Nadelhoffer & Fry 1988). Fluxes of relatively  $^{13}\text{C}$ -enriched dissolved organic carbon from leaf litter and/or sorption of humic fraction within soils can result in the heavier  $^{13}\text{C}$  enrichment in the soils (Cleveland *et al.* 2004). The collembolans and oribatid mites (the detritivores) were 2.9‰ and 3.1‰ higher in  $\delta^{13}\text{C}$ , respectively, than their basal resource leaf litter (Figure 1), which falls at the higher end of the 1–3‰ range suggested by DeNiro & Epstein (1978). Higher  $\delta^{13}\text{C}$  in the detritivores could result from their preferential assimilation of  $^{13}\text{C}$ -enriched compounds from decayed/humified debris (such as cellulose and starch; Pollierer *et al.* 2009), and consumption of  $^{13}\text{C}$ -enriched fungal hyphae as a significant portion of their diet (Beare *et al.* 1992, Hobbie *et al.* 1999, Hyodo *et al.* 2010, Pollierer *et al.* 2007, Ruf *et al.* 2006). The preferential utilization of fungal hyphae (often relatively  $^{15}\text{N}$ -enriched) may also account for the

**Table 3.** Relationships (Pearson correlation coefficient,  $r$ ) between soil and leaf-litter carbon (C), nitrogen (N), C:N ratio,  $\delta^{15}\text{N}$ , phosphorus (P) and C:P ratio, with  $\delta^{15}\text{N}$  values of leaf litter and litter invertebrate groups in a lowland tropical rain forest at La Selva Biological Station, Costa Rica. Asterisks indicate statistically significant. \* =  $P < 0.05$ . \*\* =  $P < 0.01$ .  $\Delta \delta^{15}\text{N}$  indicate the distance of  $\delta^{15}\text{N}$  signature between different trophic levels, and the subscript letters indicate the different trophic groups: C = collembolans; L = leaf litter; O = Oribatid mites; P = pseudoscorpions; and S = spiders.

	$\delta^{15}\text{N}$ measurement					$\delta^{15}\text{N}$ difference between different trophic levels ( $\Delta \delta^{15}\text{N}$ )					
	Leaf litter	Collem-bolans	Oribatid mites	Pseudo-scorpions	Spiders	$\Delta \delta^{15}\text{N}_{(\text{C-L})}$	$\Delta \delta^{15}\text{N}_{(\text{O-L})}$	$\Delta \delta^{15}\text{N}_{(\text{P-L})}$	$\Delta \delta^{15}\text{N}_{(\text{S-L})}$	$\Delta \delta^{15}\text{N}_{(\text{P-C})}$	$\Delta \delta^{15}\text{N}_{(\text{S-C})}$
Soil											
C	-0.07	0.02	0.18	-0.28	0.04	0.06	0.44	-0.32	0.19	-0.33	0.10
N	0.04	0.13	0.29	-0.23	0.14	0.06	0.44	-0.40	0.18	-0.39	0.10
C:N	-0.38	-0.35	-0.23	-0.46	-0.28	0.04	0.33	-0.09	0.18	-0.06	0.11
$\delta^{15}\text{N}$	-0.06	0.09	-0.20	-0.01	-0.25	0.33	-0.15	0.23	-0.13	-0.07	-0.33
P	0.68**	0.66**	0.60*	0.47	0.48	0.11	0.06	-0.41	-0.03	-0.50	-0.10
C:P	-0.59**	-0.59*	-0.52*	-0.42	-0.46	-0.15	-0.11	0.25	-0.13	0.31	0.01
Leaf litter											
C	0.48*	0.36	0.44	0.09	0.34	-0.13	-0.02	-0.59*	-0.03	-0.42	0.08
N	0.41	0.37	0.37	0.23	0.40	0.06	0.11	-0.09	0.14	-0.08	0.07
C:N	-0.31	-0.34	-0.28	-0.24	-0.35	-0.18	-0.18	-0.13	-0.25	0.02	-0.07
$\delta^{15}\text{N}$		0.72**	0.89	0.75**	0.85	-0.27	-0.03	-0.67**	-0.003	-0.30	0.19
P	0.53*	0.45	0.47	0.44	0.52*	0.02	-0.10	-0.09	0.09	-0.08	0.06
C:P	-0.48*	-0.41	-0.40	-0.39	-0.45	-0.07	-0.10	< 0.001	-0.08	0.05	-0.01

higher  $\delta^{15}\text{N}$  values in oribatid mites than that in the collembolans and leaf litter (Schneider *et al.* 2004).

To our knowledge, this is the first study to demonstrate a positive correlation between  $\delta^{15}\text{N}$  signature in soil, leaf litter and body tissue of the collembolans and oribatid mites and soil P fertility, an essential nutrient other than C and N. In a review by Cleveland *et al.* (2011), soil P as a limiting nutrient affects net primary production and below-ground C cycling via regulating N fixation and turnover rates, soil respiration and decomposition processes of the tropical forests. Resource C and N (i.e. N concentration and C:N ratio) have been known to affect  $\delta^{15}\text{N}$  values of animal consumers at higher trophic levels via trophic cascade (Adams & Sterner 2000, Haubert *et al.* 2005, Jennings *et al.* 1997, Robbins *et al.* 2005, Thomas & Cahoon 1993, Webb *et al.* 1998). Thus, higher P concentration could possibly cause stronger  $\delta^{15}\text{N}$  signature in the collembolans and the oribatid mites by facilitation of higher N concentration along with enriched  $^{15}\text{N}$  in the leaf litter from the alluvial plots. No correlations of leaf litter (or soil) N to its own  $\delta^{15}\text{N}$  and to detritivore  $\delta^{15}\text{N}$  eliminates the possibility of higher detritivore  $\delta^{15}\text{N}$  driven by N-rich resources. However, we did find collembolan and pseudoscorpion  $\delta^{15}\text{N}$  had a positive correlation with leaf-litter  $\delta^{15}\text{N}$ . The increase of soil P fertility has been shown to relate to higher foliage  $\delta^{15}\text{N}$  signature (and lower plant foliage N:P ratio) in nutrient-limited tropical forest ecosystems (Clarkson *et al.* 2005, Hidaka & Kitayama 2011, McKee *et al.* 2002). Clarkson *et al.* (2005) proposed that soil P enhances plant N demand and diminishes plant discrimination between  $^{15}\text{N}$  and  $^{14}\text{N}$  isotopes to cause the heavier foliar  $^{15}\text{N}$ . In this study, *Asterogyne martiana* foliar  $\delta^{15}\text{N}$  and leaf-litter  $\delta^{15}\text{N}$  were both observed in the P-enriched alluvial plots. Higher  $\delta^{15}\text{N}$  values in the collembolans and oribatid mites might be derived from their consumption on  $^{15}\text{N}$ -enriched leaf litter at the P-enriched plots. Strong  $\delta^{15}\text{N}$  signals in collembolans further cascaded down to the spiders and/or pseudoscorpions. The collembolans and oribatid mites are easily affected by environmental stoichiometry; often seeking resources to meet their minimum N and P requirements (Davidson *et al.* 2003, Sterner & Elser 2002). Such sensitivity to nutrient limitation may explain why collembolans and oribatid mites responded strongly to a smaller magnitude of soil P variability than spider and pseudoscorpions at higher trophic levels. However, stronger detritivore  $\delta^{15}\text{N}$  derived as a result of  $^{15}\text{N}$ -enriched decayed/humified debris or their preferential consumptions of fungal hyphae colonized on leaf litter (or both) need further investigation.

Detrital food webs, in terms of trophic structure and community composition, are a key component in regulating below-ground nutrient dynamics and biogeochemical cycles (e.g. mineralization and decomposition processes), particularly in the tropics (González & Seastedt 2001,

Heneghan *et al.* 1999, Powers *et al.* 2009). Unfortunately there is still limited understanding of relationships between the microbes and detrital invertebrates, and their interactions with soil nutrient dynamics and biogeochemical processes in the tropics (Hättenschwiler & Jørgensen 2010). Ecological roles of detrital invertebrates are often omitted and probably considered negligible while addressing plant–soil nutrient dynamics and cycling at ecosystem scales (Cleveland *et al.* 2011). In addition to the positive soil P–detritivore  $\delta^{15}\text{N}$  correlation found in this study, fine-scale soil P variation over the same landscape also affected below-ground soil  $\text{CO}_2$  efflux (Schwendenmann *et al.* 2003), plant root dynamics (Espeleta & Clark 2007), density of total litter invertebrates (McGlynn *et al.* 2007), and  $\delta^{15}\text{N}$  signature of leaf litter and a gypsy ant, *Aphaenogaster araneoides* (McGlynn *et al.* 2009). This study addresses the relevance of fine-scale soil P variation in regulation of nutrient dynamics through its interrelations with leaf litter and arthropod components of detrital food webs. Interrelationships between soil nutrients, plants and components of detrital food webs (such as the microbes, detritivores and predators) are important for better understanding of soil nutrient dynamics and food-web structures, especially in the tropics. As for many broader-scale comparative studies, interpretation and comparison of results are often complicated due to methodological differences, contrasting soil types, differences in species composition and divergent climate and precipitation regimes between sites (Cleveland *et al.* 2011, Powers *et al.* 2009). Thus, field research at the fine-scale provides an opportunity to test specific hypotheses, to identify mechanisms, as well as to obtain in-depth understandings of interactions between soil, plants and the detrital food web.

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