

The structure of a food web in a tropical rain forest in Malaysia based on carbon and nitrogen stable isotope ratios

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Abstract: Carbon and nitrogen stable isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) have been used to study the structure of food webs. However, few studies have examined how a terrestrial food web can be depicted by this technique. We measured $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in various consumers of four trophic groups (detritivores, herbivores, omnivores and predators), including vertebrates and invertebrates (14 orders, ≥ 24 families), as well as canopy and understorey leaves in a tropical rain forest in Malaysia. We found that $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of the consumers differed significantly among the trophic groups. The predators had significantly higher $\delta^{13}\text{C}$ than the herbivores, and were similar in $\delta^{13}\text{C}$ to the detritivores, suggesting that most predators examined depend largely on below-ground food webs. $\delta^{15}\text{N}$ was higher in predators than detritivores by about 3‰. The comparison of $\delta^{13}\text{C}$ in plant materials and herbivores suggests that most herbivores are dependent on C fixed in the canopy layers. The vertebrates had significantly higher $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ than the invertebrates of the same trophic group, likely reflecting differences in the physiological processes and/or feeding habits. This study indicates that stable isotope techniques can help better understanding of the terrestrial food webs in terms of both trophic level and the linkage of above- and below-ground systems.

Key Words: above-ground, below-ground, Lambir National Park, stable isotopes, terrestrial food web, trophic group

INTRODUCTION

Understanding how communities are structured in an ecosystem is a major theme in ecology (Hairston *et al.* 1960, Odum 1969). Determining the trophic position of consumers is essential in understanding community structure and in predicting the effect of the loss of species on an ecosystem's properties (Duffy *et al.* 2007, Thebault & Loreau 2003). Over the decades, carbon (C) and nitrogen (N) stable isotope techniques have been used to examine the flow of energy and materials in communities and the trophic positions of consumers in food webs, because they have advantages that enable time-integrated estimation of trophic positions of a consumer (Fry 2006, Post 2002).

The approach is dependent on the assumption that the stable C isotope ratio ($\delta^{13}\text{C}$) of a consumer is almost identical to that of its diet, while the stable N isotope ratio ($\delta^{15}\text{N}$) is increased, about 3‰, compared with the diet (DeNiro & Epstein 1978, Minagawa & Wada 1984).

Because trophic enrichment ($\Delta\delta^{13}\text{C}$ and $\Delta\delta^{15}\text{N}$), that is, the differences in the isotopic ratios between a consumer and its diet, is key for estimating trophic position (Post 2002), an increasing number of studies have explored factors influencing trophic enrichment using laboratory feeding experiments. These studies have revealed that trophic enrichment is influenced by various factors, such as the tissues and organs used for analyses (Tieszen *et al.* 1983), quality of the diet (Oelbermann & Scheu 2002), developmental stages (Doi *et al.* 2007), and biochemical form of N excretion and feeding habits (McCutchan *et al.* 2003, Vanderklift & Ponsard 2003). The stable isotope technique has been applied successfully

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to studies of food webs primarily in aquatic ecosystems, such as marine and lacustrine systems (Grey & Jones 2001, Yoshii *et al.* 1999).

In terrestrial ecosystems, the technique has been used to examine the feeding habits of a single taxon of organisms, such as earthworms (Briones *et al.* 1999), bats (Herrera *et al.* 2002), and ants (Davidson *et al.* 2003), trophic interactions in some groups of invertebrates in experimental plots (Ostrom *et al.* 1997, Wise *et al.* 2006), and food webs among soil invertebrates (Illig *et al.* 2005, Ponsard & Ardit 2000, Scheu & Falca 2000, Schmidt *et al.* 2004) and vertebrates (Ambrose & Deniro 1986, Bocherens & Drucker 2003). Meanwhile, it is well recognized that terrestrial ecosystems have characteristics distinct from aquatic ecosystems, such as the dominance of the detrital (below-ground) food webs over the grazing (above-ground) food webs, in terms of energy and material flows (Swift *et al.* 1979, Wardle 2002). Additionally, earlier studies revealed some mechanisms associated with the below-ground system that can influence the isotopic signatures of soil organisms, such as ^{13}C enrichment in basidiomycetes (Hobbie *et al.* 1999, Kohzu *et al.* 2005). In fact, it is known that detritivores tend to have higher $\delta^{13}\text{C}$ than plant substrates (Ponsard & Ardit 2000), probably because they selectively feed on the fungal tissues and the ^{13}C -enriched components of the plant materials, such as cellulose (Pollierer *et al.* 2009). In the above-ground system in tropical and temperate forests, it has been reported that $\delta^{13}\text{C}$ in tree leaves shows a vertically increasing trend, from the forest floor to the canopy (Garten & Taylor 1992, Hanba *et al.* 1997), which could influence $\delta^{13}\text{C}$ in consumers. Despite these characteristics of terrestrial ecosystems, few studies have examined how terrestrial food webs, including various organisms above and below ground, can be depicted using C and N isotopic signatures.

We measured $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of diverse organisms (14 orders, ≥ 24 families), classified into four trophic groups (detritivores, herbivores, omnivores, and general predators), in a tropical rain forest in Sarawak, Malaysia. We hypothesize that (1) the general predators are similar in $\delta^{13}\text{C}$ signatures to the detritivores, because of the significance of the below-ground system; (2) the herbivores are more similar in $\delta^{13}\text{C}$ signatures to the canopy leaves than the understorey leaves, because the most primary production occurs in the canopy layers (Osada *et al.* 2001).

MATERIALS AND METHODS

Study site and sample collection

Sampling was conducted in Lambir National Park ($4^{\circ}2'N$, $113^{\circ}5'E$, 20–150 m asl), Sarawak, Malaysia, mostly in June 2005. Additional samples were collected between

November 2004 and January 2006. Mean annual rainfall is about 2700 mm, with no distinct dry season (Nakagawa *et al.* 2000). The consumers used in this study included various taxa (14 orders, ≥ 24 families) and were classified into taxonomic groups at various levels (Appendix 1). The taxonomic groups were assigned a priori into four trophic groups, i.e. detritivores, herbivores, omnivores and predators, according to generally known feeding habits (Davies 1988, Nakagawa *et al.* 2007, Payne *et al.* 1985, Price 1997, Smythies 1999). They were further classified into vertebrates and invertebrates. The invertebrates were collected haphazardly from the forest floor. Some invertebrates were also collected from canopy layers using a walkway and a crane tower system (Yumoto & Nakashizuka 2005). The vertebrates were collected using traps: wire-mesh traps ($15 \times 12 \times 30$ cm) with bait for small mammals, such as rats, mice, squirrels and tree shrews (Nakagawa *et al.* 2007), and mist nets for bats and birds (Fukuda *et al.* 2009, Kanoi 2007). The clipped toes of rats, mice, squirrels and tree shrews, the hairs of bats, and the feathers of birds were used for stable isotope analyses. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for small mammals have already been reported (Nakagawa *et al.* 2007). Plant materials and soils were also collected for comparison. Fresh leaves were randomly sampled from trees at a height of less than 2 m (understorey leaves) and from the canopy layers (canopy leaves). Litter, dead wood and soil (0–10 cm depth) were also sampled randomly from the forest floor.

The samples were dried at 60°C for 24 h. Collected invertebrates were kept in a freezer for 24 h to terminate their activity, before they were dried in a drying oven. The whole bodies or legs of invertebrates and toes of the small mammals were ground into powder using a mortar and pestle prior to the analyses. The leaves, litter and dead wood materials were ground using a ball mill. The soil samples were sieved with a 2-mm mesh and then treated with 0.5 M HCl overnight to remove inorganic carbon.

Stable C and N isotope analyses

For stable C and N isotope analyses, the samples were placed in tin capsules. Stable C and N isotope ratios were measured using a mass spectrometer (Delta^{plus} XP, Germany), coupled with an elemental analyser. The precision of the on-line procedure was better than $\pm 0.2\%$ for both isotope ratios. The natural abundances of ^{13}C and ^{15}N are expressed in per mil (‰) deviation from international standards: $\delta^{13}\text{C}$ or $\delta^{15}\text{N} = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000$, where R in $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ is $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$, respectively. Pee Dee belemnite and atmospheric nitrogen were used as the international standards for carbon and nitrogen, respectively.

Statistical analyses

To examine differences in each isotope ratio among the plant and soil samples (canopy and understorey leaves, litter, soils), we used analysis of variance (ANOVA), with the isotope ratio as the dependent variable and the sample type as the independent variable. The relationship between average $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the consumers in each taxonomic group was examined using a simple linear regression. To test if the isotopic compositions of consumers differ between the canopy and the understorey layers, we used t-test for the taxonomic groups that could be collected in both layers (i.e. leaf beetles, homopterans and spiders). In addition, to examine differences in isotopic signatures among the trophic groups, we used a linear mixed model (Grafen & Hails 2002). Each isotope ratio was used as the dependent variable, and the trophic group, the taxon at the level of vertebrates vs. invertebrates (taxon (VR vs. IN)) (as fixed effects) and the taxonomic group (as a random effect) were used as the independent variables. Taxon (VR vs. IN) was nested within trophic group, and taxonomic group was nested within both trophic group and taxon (VR vs. IN). In the model, the least-squares means, which are within-group means appropriately adjusted for the other effects, were calculated. We used the Tukey–Kramer HSD test to examine differences among trophic groups. The statistical analyses were performed using JMP statistical software (version. 5.1.2 for Macintosh, SAS Institute, Cary, NC, USA).

RESULTS

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in plant materials and soil organic matter

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ differed among plant materials and soil organic matter ($F_{4,66} = 22.9$, $P < 0.0001$ for $\delta^{13}\text{C}$; $F_{4,66} = 32.4$, $P < 0.0001$ for $\delta^{15}\text{N}$; Figure 1a, b). Soil organic matter and dead wood had significantly higher $\delta^{13}\text{C}$ than litter. The $\delta^{13}\text{C}$ of canopy leaves was intermediate between them. Understorey leaves had significantly lower $\delta^{13}\text{C}$ than the rest. Soil organic matter had significantly higher $\delta^{15}\text{N}$ signatures than canopy and understorey leaves or the litter, which were also more enriched than dead wood.

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of consumers and the difference between canopy and understorey layers

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of consumers varied from -32.3‰ (average value of scale insect) to -23.0‰ (white-rumped shama), and from -1.6‰ (average value of fungus-growing termite) to 7.2‰ (white-rumped shama), respectively (Figure 2, Appendix 1). There was a significant relationship between average values of $\delta^{13}\text{C}$

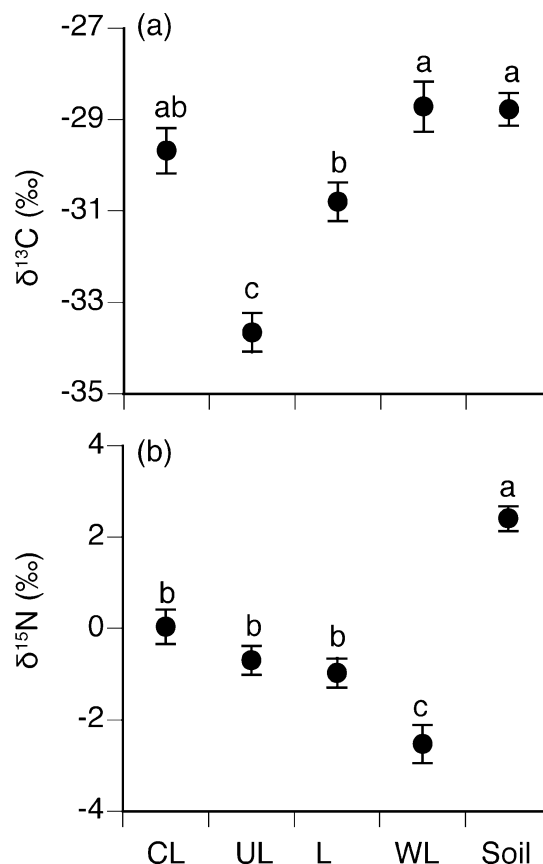


Figure 1. $\delta^{13}\text{C}$ (a) and $\delta^{15}\text{N}$ (b) (mean \pm SE) of canopy and understorey leaves, litter, and woody litter in Lambir National Park, Sarawak, Malaysia. Means marked with the same letter do not differ, according to the Tukey–Kramer HSD test at $P = 0.05$ following ANOVA. CL, canopy leaves; UL, understorey leaves; L, litter; WL, woody litter; Soil, soil (0–10 cm).

and $\delta^{15}\text{N}$ in each taxonomic group ($r^2 = 0.445$, $n = 39$, $P < 0.001$).

$\delta^{13}\text{C}$ did not differ significantly between the two layers for the leaf beetles (canopy, $-26.5\text{‰} \pm 0.3\text{‰}$, $n = 3$; understorey, $-27.5\text{‰} \pm 1.7\text{‰}$, $n = 6$), and spiders (canopy, $-26.8\text{‰} \pm 0.9\text{‰}$, $n = 13$; understorey, $-27.2\text{‰} \pm 1.4\text{‰}$, $n = 15$). However, there was a significant difference in $\delta^{13}\text{C}$ of homopterans between the two layers (canopy, $-26.7\text{‰} \pm 1.3\text{‰}$, $n = 10$; understorey, $-29.0\text{‰} \pm 2.6\text{‰}$, $n = 7$, $P < 0.05$). $\delta^{15}\text{N}$ did not differ for leaf beetles (canopy, $1.7\text{‰} \pm 0.6\text{‰}$, $n = 3$; understorey, $1.2\text{‰} \pm 1.4\text{‰}$, $n = 6$), homopterans (canopy, $1.7\text{‰} \pm 2.5\text{‰}$, $n = 10$; understorey, $1.9\text{‰} \pm 2.3\text{‰}$, $n = 7$) and spiders (canopy, $3.0\text{‰} \pm 1.8\text{‰}$, $n = 13$; understorey, $3.9\text{‰} \pm 1.7\text{‰}$, $n = 15$).

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of consumers of four trophic groups

$\delta^{13}\text{C}$ of consumers differed between trophic groups ($F_{3,34} = 3.83$, $P < 0.05$, Figure 3a). Predators had

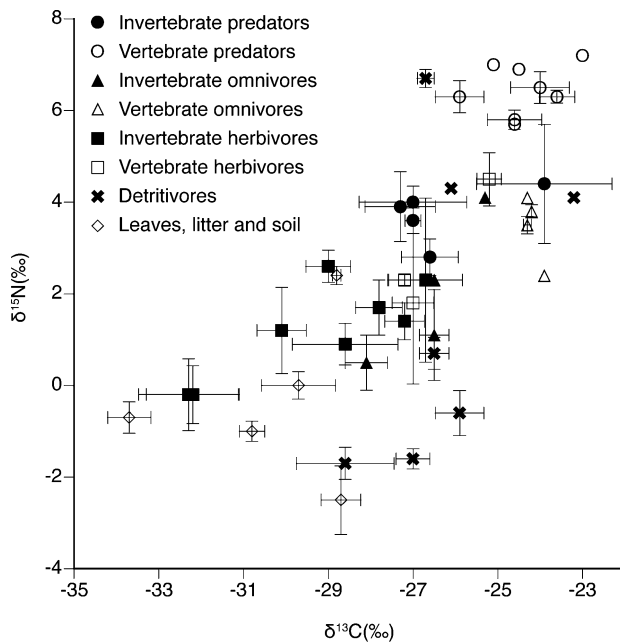


Figure 2. Scatter plot of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of the taxonomic groups, leaves, litter, and soil (mean \pm SE) in Lambir National Park, Sarawak, Malaysia. The taxonomic groups examined are listed in Appendix 1. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of canopy and understorey leaves, litter, woody litter and soil are also presented for comparison.

higher $\delta^{13}\text{C}$ ($-25.4\text{‰} \pm 0.5\text{‰}$; least-squares mean \pm SE) than herbivores ($-27.8\text{‰} \pm 0.6\text{‰}$). Omnivores ($-25.7\text{‰} \pm 0.7\text{‰}$) and detritivores ($-26.6\text{‰} \pm 0.7\text{‰}$) had intermediate levels. Taxon (VR vs. IN) had significant effects on $\delta^{13}\text{C}$ ($F_{3,34} = 5.36$, $P < 0.01$), and vertebrates had higher $\delta^{13}\text{C}$ than invertebrates in the same trophic group.

$\delta^{15}\text{N}$ of consumers differed between trophic groups ($F_{3,34} = 9.38$, $P < 0.001$; Figure 3b). Predators ($5.1\text{‰} \pm 0.5\text{‰}$) had significantly higher $\delta^{15}\text{N}$ than omnivores ($2.5\text{‰} \pm 0.7\text{‰}$), herbivores ($2.1\text{‰} \pm 0.6\text{‰}$), and detritivores ($1.4\text{‰} \pm 0.7\text{‰}$). Taxon (VR vs. IN) also influenced $\delta^{15}\text{N}$ ($F_{3,34} = 4.47$, $P < 0.001$), and vertebrates had higher $\delta^{15}\text{N}$ than invertebrates in the same trophic group. Consequently, predators showed elevated $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Figure 2, 3a, b). Comparison of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in consumers and plant materials showed that the consumers had higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ than canopy leaves and the herbivores showed $\delta^{13}\text{C}$ similar to the canopy leaves rather than the understorey leaves.

DISCUSSION

We demonstrated that there is a significant correlation between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of consumers for each taxonomic group. The values differed significantly among the trophic groups and the values in vertebrates were significantly

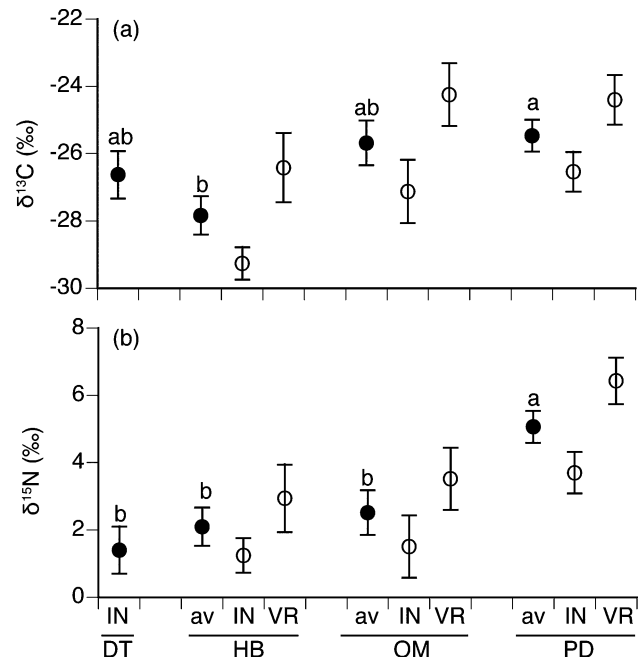


Figure 3. $\delta^{13}\text{C}$ (a) and $\delta^{15}\text{N}$ (b) (least-squares mean \pm SE) of trophic groups in Lambir National Park, Sarawak, Malaysia. DT, detritivores; HB, herbivores; OM, omnivores; PD, predators; VR, vertebrates; IN, invertebrates. The least square means of the trophic groups (av) are indicated by closed circles, and those of the invertebrates and vertebrates of each trophic group by open circles. Note that the least-squares mean of the detritivores is identical to that of the invertebrates, because there were no detritivorous vertebrates. The least-squares means of each trophic group with the same letter do not differ, according to the Tukey–Kramer HSD test at $P = 0.05$, following analysis of a linear mixed model.

higher than those in invertebrates. Predators had $\delta^{13}\text{C}$ closer to those of detritivores and omnivores, rather than that of herbivores. It is well recognized that $\delta^{13}\text{C}$ can be used to trace energy and material flows in food webs, because the C isotopic signature does not change through trophic interactions (DeNiro & Epstein 1978, McCutchan *et al.* 2003). In addition, most primary production enters the below-ground system without being consumed by herbivores in the above-ground system (Swift *et al.* 1979, Wardle 2002). In this light, the present results suggest that most of the predators examined in this study are more dependent on detritivores than on herbivores. The omnivores may also depend to some extent on detritivores as a food source. In temperate regions, it is known that predators can switch temporally from detritivores to herbivores as prey according to their relative abundance and availability (Birkhofer *et al.* 2008). This is unlikely the case in this study, because central South-East Asia, including the study site, is one of the wettest and most aseasonal climates of any tropical region (Whitmore 1984).

Although the significance of detritivores in supporting predators in terrestrial ecosystems has been discussed (Polis & Strong 1996), few studies have actually examined

it: field observations in a tropical paddy-field (Settle *et al.* 1996), in tundra ecosystems (Oksanen 1997), and experimental manipulations in agroecosystems (Halaj & Wise 2002) and forest ecosystems (Miyashita *et al.* 2003). Our results support the fundamental importance of the linkage of below- and above-ground food webs in terrestrial ecosystems (Scheu 2001). Based on $\delta^{13}\text{C}$ values, an earlier study suggested that detritivores played an important role in supporting predators in a temperate rice field during the rice growing season (Park & Lee 2006). Thus, we propose that $\delta^{13}\text{C}$ of predators can be used as an indicator of the dependency of predators on below-ground food webs.

The enrichment of ^{13}C in detritivores relative to plant substrates has been reported in a single taxon, as well as in entire soil food webs (Hishi *et al.* 2007, Ponsard & Arditi 2000, Spain & Reddell 1996, Tayasu *et al.* 1997). Although the underlying mechanisms remain unclear, this may reflect the increase in $\delta^{13}\text{C}$ in soil organic matter through microbial activity, as found for $\delta^{15}\text{N}$ (Nadelhoffer & Fry 1988) and the detritivores' selective feeding on the organic matter enriched in ^{13}C (Pollierer *et al.* 2009). In particular, it has been reported that basidiomycetous fungi, which play an important role in decomposition processes (Swift *et al.* 1979), are about 3‰ more enriched in ^{13}C than their substrates (Hobbie *et al.* 1999, Kohzu *et al.* 2005). Indeed, high $\delta^{13}\text{C}$ was observed in a fungus-growing termite (*Macrotermes malaccensis*), which depends on symbiotic basidiomycetes as a food source to some extent (Hyodo *et al.* 2003), as well as a fungus beetle (Appendix 1).

Canopy leaves had higher $\delta^{13}\text{C}$ than understorey leaves, and herbivores had $\delta^{13}\text{C}$ similar to those of canopy leaves, rather than understorey leaves (Figure 3), suggesting that most herbivores examined were sustained by production in the canopy layers. This is likely consistent with most of the litter being yielded by the canopy layers in tropical forests (Osada *et al.* 2001). The increasing trend in $\delta^{13}\text{C}$ in leaves with height in the forest is caused by various factors, such as the source of CO_2 , coming either from the atmosphere (about -8‰) or from the forest floor by soil respiration (about -26‰), and differences in stomatal conductance, due to water and light conditions (Dawson *et al.* 2002).

Note that homopterans were more enriched in ^{13}C in the canopy layers than in the understorey, which likely corresponds to the higher $\delta^{13}\text{C}$ of the canopy leaves, although the difference in $\delta^{13}\text{C}$ between canopy and understorey layers was not observed in the leaf beetles and spiders. In addition, the leaf beetles, weevils and homopterans were relatively enriched in ^{13}C compared to the other invertebrate herbivores. The high $\delta^{13}\text{C}$ of the predators might be explained by their use of these ^{13}C -enriched herbivores. The use of radiocarbon (^{14}C) should allow the quantification of the dependency of predators on

detritivores through the measurement of the ^{14}C contents of detritivores and herbivores; detritivores should have older carbon than herbivores (Hyodo *et al.* 2006). Also, it should enable us to estimate the dependency of herbivores on canopy leaves instead of understorey leaves, because canopy leaves should have the same ^{14}C concentration as that of atmospheric CO_2 in the year of sampling (i.e. 0 y), whereas the ^{14}C concentration of understorey leaves should indicate a mix of CO_2 from the atmosphere and that respired from soil organic matter (>0 y).

As for the $\delta^{15}\text{N}$ in consumers, the value increased as trophic level increased: predators had higher $\delta^{15}\text{N}$ than detritivores, as well as herbivores and omnivores. The $\delta^{15}\text{N}$ of the vertebrate predator, tree shrews (*Tupaia* spp.), which have previously been reported in this site (Nakagawa *et al.* 2007), were comparable to the other predatory mammals, such as bats. The average $\Delta\delta^{15}\text{N}$ observed between predators and detritivores was consistent with a value reported previously, $3.4\text{‰} \pm 1.1\text{‰}$ (Minagawa & Wada 1984). Meanwhile, earlier studies revealed that $\delta^{15}\text{N}$ in soil invertebrates also increased along with humification of diets (i.e. more humified and decomposed organic matter) (Hishi *et al.* 2007, Hyodo *et al.* 2008, Tayasu *et al.* 1997). Indeed, the detritivores that feed on humified organic matter, such as soil-feeding termites (*D. nemorosus*) and a rhinoceros beetle, had high $\delta^{15}\text{N}$ (6.7‰ and 4.7‰, respectively; Appendix 1), which are comparable to the ratios in the predators. Thus, predation on detritivores feeding on humified diets can increase the $\delta^{15}\text{N}$ in such predators (and omnivores). This might explain the high $\delta^{15}\text{N}$ in vertebrate predators and omnivores. On the other hand, invertebrate predators might depend not on such detritivores, but on those feeding on less humified organic matter, like surface litter layers. These possibilities could be tested by measuring the diet ages of the consumers based on the radiocarbon analysis.

In addition to trophic group, taxon (VR vs. IN) had a significant influence on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. The enrichment in ^{13}C in vertebrates should reflect the fact that the tissues used for the isotopic measurements tended to be more enriched in ^{13}C , by $\sim 2\text{‰}$, than the muscles (DeNiro & Epstein 1978, Hobson *et al.* 1996, Tieszen & Boutton 1989). Vertebrates also had higher $\delta^{15}\text{N}$ than invertebrates of the same trophic group. The likely explanation is that vertebrates used food sources with higher $\delta^{15}\text{N}$ than did invertebrates of the same trophic group. For example, vertebrate omnivores may have consumed a higher proportion of prey to plant materials, compared with invertebrates. Vertebrate predators may have preyed on invertebrate predators, as well as herbivores and omnivores. In particular, vertebrates may have used detritivores that feed on humified organic material to a higher extent than the invertebrates, as discussed above. Another explanation may be differences in tissues used for the $\delta^{15}\text{N}$ measurements between the

vertebrates (feathers for birds, hairs for bats, and toe-tips for small mammals) and the invertebrates (whole bodies or body parts), as well as in physiological processes between vertebrates and invertebrates, because several factors influencing $\Delta\delta^{15}\text{N}$ are known to be related to taxonomic identity (Vanderklift & Ponsard 2003).

Overall, based on the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in consumers, we suggest that the predators examined in this study depended largely on detritivores for their energy and materials. Thus, general predators may interconnect the above- and below-ground food webs. The predation on the detritivores and the further ^{13}C enrichment in the hair and feather tissues of vertebrate predators likely account for the observed correlation between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in each taxonomic group. We also suggest that herbivores derive most of their C from forest canopy layers. In this study, we could not examine important consumers in tropical food webs, such as amphibians, reptiles and large invertebrates (e.g. scorpions), the latter of which may feed on vertebrates (Kupfer *et al.* 2006, Reagan *et al.* 1996). In addition, it is well known that the isotopic signatures of consumers within a trophic group and even within a taxonomic group can vary (Ponsard & Arditì 2000, Scheu & Falca 2000). For example, it has recently been reported that $\delta^{15}\text{N}$ ranges between 7.5‰ to 16.5‰ for termite species of the genus *Anoplotermes* in a French Guianan forest reserve (Bourguignon *et al.* 2009). Regarding the invertebrate herbivores, vascular and non-vascular feeders might have different N isotopic signatures due to the different $\Delta\delta^{15}\text{N}$ (McCutchan *et al.* 2003, Spence & Rosentheim 2005), although they did not clearly differ in this study. These factors might affect the present conclusion. As such, further studies are necessary to examine more taxa with higher taxonomic resolution to confirm the isotopic pattern found in this study.

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Appendix 1. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of various organisms in Lambir National Park, Sarawak, Malaysia. n = number of replicates examined for isotopic compositions.

Taxon (common name)	n	$\delta^{13}\text{C}$ (‰) (mean \pm SE)	$\delta^{15}\text{N}$ (‰) (mean \pm SE)
Detritivore			
Invertebrate			
Coleoptera			
Erotylidae (Pleasing fungus beetle)	1	-23.2	4.1
Cerambycidae (Longicorn beetle)	2	-26.5 \pm 0.4	0.7 \pm 0.4
Scarabaeidae (Rhinoceros beetle)	1	-26.1	4.3
Blattaria (Cockroach)	3	-28.6 \pm 1.2	-1.7 \pm 0.3
Orthoptera			
Tetrigidae (Pygmy grasshopper)	2	-25.9 \pm 0.6	-0.6 \pm 0.5
Isoptera			
Termitidae			
<i>Macrotermes malaccensis</i> (Haviland) (Fungus-growing termite)	5	-27.0 \pm 0.4	-1.6 \pm 0.2
<i>Dicuspiditermes nemorosus</i> (Haviland) (Soil-feeding termite)	4	-26.7 \pm 0.2	6.7 \pm 0.2
Herbivore			
Invertebrate			
Coleoptera			
Chrysomelidae (Leaf beetle)	9	-27.2 \pm 0.5	1.4 \pm 0.4
Curculionidae (Weevil)	3	-26.7 \pm 0.9	2.3 \pm 1.8
Lepidoptera (Lepidopteran (adult))	47	-29.0 \pm 0.5	2.6 \pm 0.4
Lepidoptera (Lepidopteran (larvae))	9	-32.2 \pm 1.1	-0.2 \pm 0.6
Phasmida (Stick insect)	5	-30.1 \pm 0.6	1.2 \pm 0.9
Hemiptera (Sucking bug)	5	-28.6 \pm 1.3	0.9 \pm 0.4
Hemiptera (Homopteran)	16	-27.8 \pm 0.6	1.7 \pm 0.6
Hemiptera (Scale Insect)	6	-32.3 \pm 1.2	-0.2 \pm 0.8
Vertebrate			
Chiroptera			
Pteropodidae			
<i>Balionycteris maculata</i> Thomas (Spotted-winged fruit bat)	2	-27.0 \pm 0.5	1.8 \pm 1.8
<i>Cynopterus brachyotis</i> (Muller) (Lesser short-nosed fruit bat)	3	-27.2 \pm 0.4	2.3 \pm 0.1
Columbiformes			
Columbidae			
<i>Chalcophaps indica</i> (Linnaeus) (Emerald dove)	3	-25.2 \pm 0.3	4.5 \pm 0.6
Omnivore			
Invertebrate			
Orthoptera			
Tettigoniidae (Katydid)	1	-26.5	2.3
Mecopodidae (Katydid)	2	-26.5 \pm 0.4	1.1 \pm 1.0
Gryllacrididae (Camel cricket)	9	-28.1 \pm 0.5	0.5 \pm 0.6
Coleoptera			
Tenebrionidae (Darkling beetle)	1	-25.3	4.1
Vertebrate			
Rodentia			
Sciuridae			
<i>Callosciurus prevostii</i> (Desmarest) (Prevost's squirrel)	1	-23.9	2.4
<i>Sundasciurus lowii</i> (Thomas) (Low's squirrel)	1	-24.3	4.1
Muridae			
<i>Niviventer cremoriventer</i> (Miller) (Dark-tailed tree rat)	2	-24.2 \pm 0.0	3.8 \pm 0.1
<i>Maxomys rajah</i> Thomas (Brown spiny rat)	10	-24.3 \pm 0.1	3.5 \pm 0.2

Appendix 1. Continued.

Taxon (common name)	n	$\delta^{13}\text{C}$ (‰) (mean \pm SE)	$\delta^{15}\text{N}$ (‰) (mean \pm SE)
Predator			
Invertebrate			
Coleoptera			
Carabidae (Ground beetle)	2	-27.0 ± 1.3	4.0 ± 0.4
Cicindelidae (Tiger beetle)	4	-23.9 ± 1.6	4.4 ± 1.3
Mantodea			
Mantidae (Praying mantis)	5	-26.6 ± 0.7	2.8 ± 0.4
Araneae (Spider)	38	-27.0 ± 0.2	3.6 ± 0.3
Hemiptera			
Reduviidae (Assassin bug)	7	-27.3 ± 0.8	3.9 ± 0.8
Vertebrate			
Chiroptera			
Megadermatidae			
<i>Megaderma spasma</i> (Linnaeus) (Lesser pulse vampire bat)	2	-24.6 ± 0.6	5.8 ± 0.2
Rhinolophidae			
<i>Hipposideros diadema</i> (Geoffroy) (Diadem roundleaf bat)	2	-23.6 ± 0.4	6.3 ± 0.1
<i>Rhinolophus borneensis</i> Peters (Bornean horseshoe bat)	1	-25.1	7.0
<i>Rhinolophus trifolius</i> Temminck (Trefoil horseshoe bat)	1	-24.6	5.7
Scandentia			
Tupaiaidae			
<i>Tupaia</i> spp. (Tree shrew)	3	-24.0 ± 0.7	6.5 ± 0.3
Passeriformes			
Muscicapidae			
<i>Copsychus malabaricus</i> (Scopoli) (White-rumped shama)	1	-23.0	7.2
Sylviidae			
<i>Stachyris nigricollis</i> (Temminck) (Black-throated babbler)	1	-24.5	6.9
<i>Stachyris erythroptera</i> (Blyth) (Chestnut-winged babbler)	2	-25.9 ± 0.6	6.3 ± 0.4