

SHORT COMMUNICATION

The role of clumped defecation in the spatial distribution of soil nutrients and the availability of nutrients for plant uptake

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Many types of primate, particularly species of the genus *Alouatta* (howler monkey) defecate as a social group and tend to defecate repeatedly in specific locations (sometimes referred to as latrines; Andresen 2001, 2002; Gilbert 1997). The importance of these clumped defecations in the dispersal of seeds has been well investigated (Andresen 2001, 2002; Estrada & Coates-Estrada 1984, 1991; Julliot 1996). In contrast, no study has yet looked at the role of clumped defecation in the spatial distribution of soil nutrients and the availability of nutrients for plant uptake.

Howler monkeys have poor nutrient assimilation rates and hence their waste excretions tend to be very nutrient-rich (Milton *et al.* 1980, Nagy & Milton 1979). In studies of wild howler monkeys, Nagy & Milton (1979) and Milton *et al.* (1980) found that adult *Alouatta palliata* that were fed on a variety of food sources produced dung that contained 1.8–2.1% nitrogen and 0.3–0.4% phosphorus (based on dry mass measurements). While the exact concentration of nutrients in faeces is highly dependent on the monkey's diet and nutrient intake, these results indicate that monkey faeces typically contain much greater concentrations of nutrients than leaf litter (~ 1% N and 0.04% P for tropical moist forests; Vitousek & Sanford 1986).

In a study investigating the phenomenon of group defecation, Gilbert (1997) found that *Alouatta seniculus* do not defecate at random sites throughout the forest; rather, they tend to repeatedly use specific defecation spots. This latrining behaviour was observed for monkey troops living in both forest fragments as well as contiguous undisturbed forests (Gilbert 1997). In another study looking at primary seed dispersal patterns by *A. seniculus*, Andresen (2002) observed that while individuals would sometimes defecate away from the rest of the group, the monkeys would generally group defecate once in

the morning and once in the evening. The resultant latrine piles covered a median area of 17 m² and had a mean dry weight of 31 g of dung per m² (Andresen 2002). By combining these results with the nutrient concentrations reported above, we find that Andresen's study troops deposited over 0.6 g of nitrogen and 0.1 g of phosphorus per m² of forest floor at each defecation event (not including urine).

Given the high nutrient content of howler monkey faeces and their behaviour to utilize specific locations, it follows that these latrines should create relatively stable areas of high nutrient availability. In this study, I tested soil nutrient content and nutrient availability (N and P) along two transects, each of which crossed through an established latrine of *A. seniculus*.

In addition, I measured fine-root biomass along the two transects in order to determine if plants are in fact utilizing the nutrients made available through the latrine piles. Fine roots (< 2 mm in diameter) are plants' primary sites of nutrient uptake and absorption (Forde & Lorenzo 2001, Gower 1987, Ostertag 2001, Vitousek & Sanford 1986). Previous studies have found that plants are able to exploit patches of high nutrient availability through the phenomenon of 'root foraging', in which the plants will increase the growth of fine roots into the nutrient-rich medium (Gower 1987). I hypothesized that soil nutrient pools, nutrient availability, and fine-root biomass would all increase with proximity to the howler monkey latrines.

The transects used in this study were located on small (≤ 1 ha) land-bridge islands in Lake Guri, Venezuela. Lake Guri is a large hydroelectric reservoir located along the lower portion of the Caroni River in east-central Venezuela. Islands in the lake experience a mean annual temperature of 27.5 °C with an annual rainfall of approximately 1500 mm (the majority of precipitation

Table 1. Characteristics of study islands.

Island	Latitude	Longitude	Area (ha)	Distance to mainland (km)	Number of <i>Alouatta seniculus</i>	Dominant tree species
A	7° 14' 18" N	62° 50' 17" W	0.7	5.5	6	<i>Bourreria cumanensis</i> O.E. Shultz ¹
B	7° 14' 6" N	62° 50' 10" W	1.0	5.7	4	<i>Ocotea glomerata</i> Mez ²

¹ Boraginaceae.² Lauraceae.

occurs between the months of May and October; Alvarez *et al.* 1986). Soils within the region are highly weathered, clay-rich Oxisols derived from the Guiana shield (Alvarez *et al.* 1986). The habitats of the islands used in this study, which shall henceforth be referred to as Islands A and B, are classified as semi-deciduous tropical dry forest (Huber 1986, Terborgh *et al.* 1997). Canopy height is approximately 15–20 m with occasional emergents reaching heights of up to 25 m. Characteristics of the study islands are listed in Table 1.

Islands A and B both support small troops of red howler monkeys with six and four individuals, respectively (J. Terborgh, unpubl. data). While both troops have been observed to utilize several small latrines scattered throughout the islands, each island has a single large centrally located latrine that has remained in approximately the same location for at least the last 4 y. Individuals defecate in these latrines from mid-canopy while perched on vines spanning between trees. The latrine on island A encompasses an area of 9 m² while the latrine on island B is concentrated in an area less than 4 m². These latrines are located at approximately the highest points of the islands and thus any leached nutrients should flow evenly throughout the surrounding soil.

On both islands, I established randomly oriented 30-m-long transects with the latrines located at the midpoints. I collected soil samples at the – 15, – 10, – 5, 0 (latrine), + 5, + 10 and + 15 m marks. At each location, I collected between 10 and 20 soil samples of the top 10 cm of mineral soil using a punch tube soil probe (diameter = 1.75 cm). Within each latrine, dung was removed from the surface prior to sampling the mineral soil. The samples from each site along the transects were combined, mixed and subsampled (Tan 1996). Soil samples were oven dried at 60 °C, and brought to the laboratory for nutrient analysis. Total nitrogen concentrations were determined on 75-mg subsamples of finely ground soil via dry combustion in an automated CHN analyser. Phosphorus concentrations were determined colorimetrically in sodium bicarbonate extracts (1:2 soil solution ratio) on a TRAACS auto-analyser (Tan 1996).

The availability of nutrients for plant uptake was determined using ion exchange membranes (IEM; Binkley & Matson 1983, Bridgham *et al.* 2001, Subler *et al.* 1995). IEMs are small (4 × 2 cm) sheets of crossed-linked polymers with active exchange sites for anions and cations

(Abrams & Jarrell 1992). When placed in the soil, these strips act as infinite sinks for ions that are suspended in the soil solution. By measuring the amount of nutrients absorbed over a set time period it is possible to determine the relative availability of a given nutrient to plants using the equation:

$$B = \pi(N^2)/4tS \quad (\text{Eqn 1})$$

where B is an index of bioavailability, N is the total amount of the nutrient absorbed to the IEM, t is time in h, and S is the surface area of the IEM exposed to the soil (all IEMs used in the study had a surface area of 16 cm²; Abrams & Jarrell 1992).

For this study, I placed an IEM in the top 5 cm of soil at each sample location. After a period of 24 h (t), the IEMs were removed from the soil and kept in a freezer until they could be brought to the laboratory for analysis. In the laboratory, the nutrients adsorbed to the IEMs were desorbed by shaking for 2 h in 50 ml of 2 M KCl solution. Total IEM exchangeable nitrogen (NO₃ + NH₄) and phosphorus concentrations were measured colorimetrically with a TRAACS auto-analyser.

I determined fine-root biomass along the transects by collecting three soil samples of 101.6 cm³ (10 cm deep × 10.2 cm wide × 2.5 cm thick) at each sample location (for a total of 305 cm³ of soil from each location) and removing the roots through repeated washing and sievings. All roots were sorted and the fine roots (< 2 mm) were collected, oven dried at 60 °C until constant weight, and massed.

Laboratory analyses revealed that the concentration of both total nitrogen and bicarbonate extractable phosphorus in the soil underlying the two latrines was substantially higher than in the soil collected at the other sample sites. The total soil nitrogen concentrations in the latrines were 1.6 and 1.7 times greater, on Islands A and B respectively, than the mean concentrations from the other sample sites along the corresponding transects (Figure 1a). The increase in nutrient concentration was even more dramatic with regards to soil phosphorus. On Island A, the concentration of bicarbonate phosphorus under the latrine was 3.8 times greater than in the surrounding soils; on Island B, phosphorus levels were over six times greater (Figure 1b).

In addition to high soil nutrient concentrations under the latrines, I also found corresponding high levels in

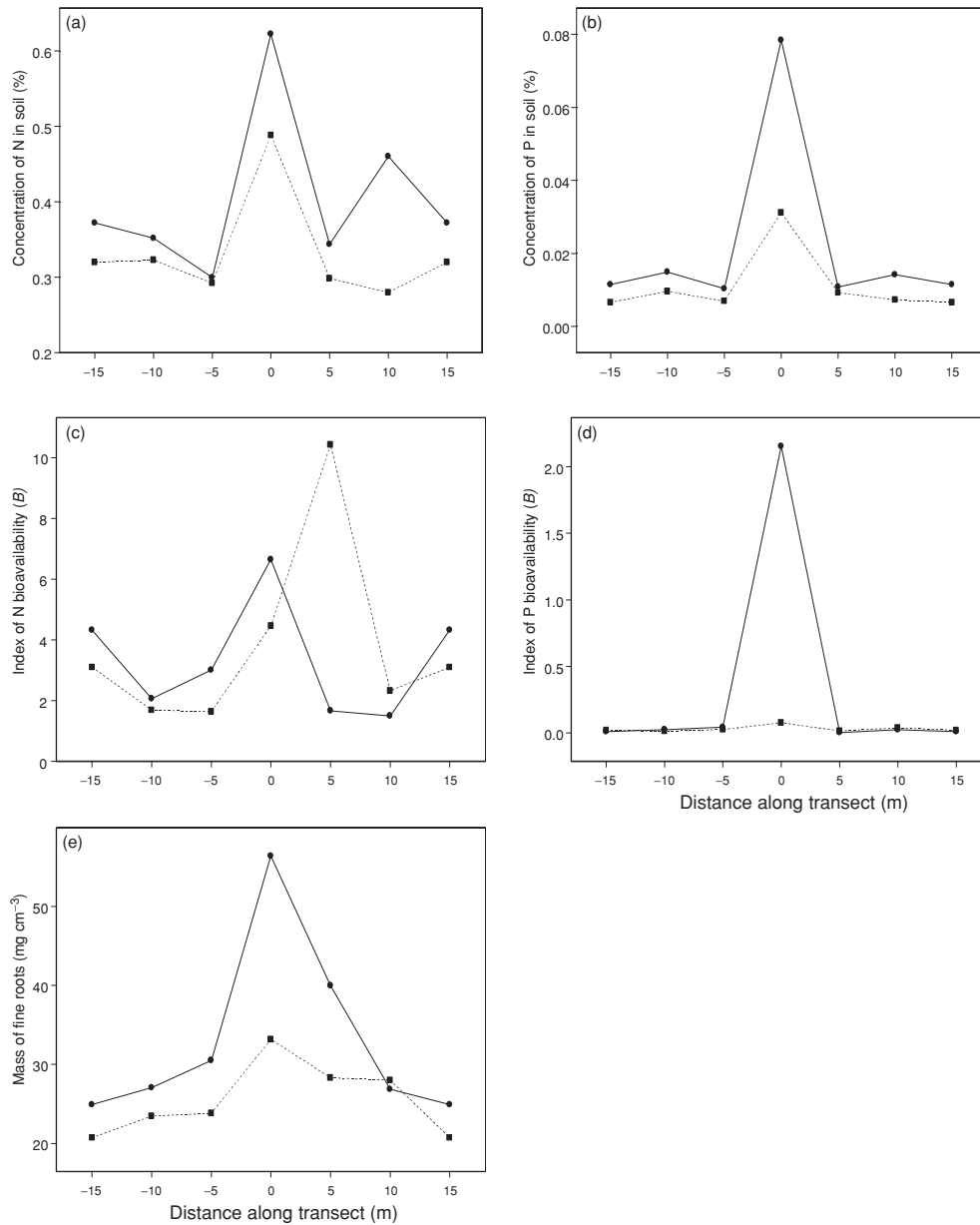


Figure 1. Nutrient concentration and availability both show evidence of local enrichment under *Alouatta seniculus* latrines (latrines are located at the 0 m mark). (a) and (b) depict the concentration (%) of total N and bicarbonate P in the soil, respectively. The corresponding availability of N and P for plant uptake (B , see text) are shown in (c) and (d). Fine-root biomass (mg cm^{-3}) is greatest underneath the latrines (e). Island A = broken line, square symbols; Island B = solid line, circle symbols.

the availability of nitrogen and phosphorus for plant uptake. The index of bioavailability (B) for nitrogen was 1.1 times greater than in the surrounding sample sites on Island A and 3.2 times greater on Island B (Figure 1c). Interestingly, the greatest index of nitrogen availability for Island A was found at one of the sample sites located 5 m from the latrine. The reason for the high nitrogen availability at this site is unknown but may be due to microsite differences and possible differences in soil moisture (i.e. nutrient availability as measured

by the IEMs will increase with increasing soil moisture content; Abrams & Jarrell 1992, Binkley & Matson 1983, Cooperband & Logan 1994). It is also possible that the location of the latrine has shifted slightly over the past several years resulting in the observed pattern.

The availability of phosphorus was dramatically greater under the latrines than at the other sample sites in each transect. On Island A, B for phosphorus in the latrine was 3.4 times greater than the average B derived for the other four sample sites. On Island B, bioavailability

was over 93 times greater in the latrine than outside (Figure 1d).

Finally, it appears that fine-root biomass responds to the high concentrations of soil nutrients in the howler monkey latrines. On Island A, the mass of fine roots was 1.3 times greater in the latrine than in the other sample sites; on Island B, fine-root biomass in the latrine was almost twice that found outside of the latrine (1.8 times greater; Figure 1e). The distribution of fine roots may be responsible for the observation that the concentration of soil nutrients and the availability of nutrients for plant uptake are often lowest along the edges of the latrines (± 5 m). While the input of nutrients is very localized around the centre of each latrine, the increase in fine-root biomass appears to extend beyond the periphery (see Figure 1e). Consequently, the latrine edges may experience high nutrient demands relative to input and thus have lower nutrient concentrations/availability than either the latrine centre or the surrounding soil.

Due to continued loss of habitat and hunting pressure, it is important that we understand the role of herbivores in nutrient cycling. While the findings of this preliminary study are based on a very small sample size, the results clearly support the hypothesis that habitual latrine sites are associated with localized soil nutrient enrichment. Additional research is needed to investigate these patterns using larger sample sizes, test alternative hypotheses, and to address additional questions such as the effects of the spatial distribution of nutrient on plant community composition and structure.

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