Temporal patterns of nutrient availability around nests of leaf-cutting ants (*Atta colombica*) in secondary moist tropical forest

Theresa M. Hudson [a,1], Benjamin L. Turner [b,*], Hubert Herz [b,c], James S. Robinson [a]

[a] Department of Soil Science, School of Human and Environmental Sciences, University of Reading, Whiteknights, Reading RG6 6DW, UK
[b] Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancon, Republic of Panama
[c] Biology Department, San Francisco State University, 1600 Holloway Avenue, San Francisco, CA 94132, USA

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ABSTRACT

Leaf-cutting ants consume up to 10% of canopy leaves in the foraging area of their colony and therefore represent a key perturbation in the nutrient cycle of tropical forests. We used a chronosequence of nest sites on Barro Colorado Island, Panama, to assess the influence of leaf-cutting ants (*Atta colombica*) on nutrient availability in a neotropical rainforest. Twelve nest sites were sampled, including active nests, recently abandoned nests (<1 year) and long-abandoned nests (>1 year). Waste material discarded by the ants down-slope from the nests contained large concentrations of nitrogen and phosphorus in both total and soluble forms, but decomposed within one year after the nests were abandoned. Despite this, soil under the waste material contained high concentrations of nitrate and ammonium that persisted after the disappearance of the waste, although soluble phosphate returned to background concentrations within one year of nest abandonment. Fine roots were more abundant in soil under waste than control soils up to one year after nest abandonment, but were not significantly different for older sites. In contrast to the waste dumps, soil above the underground nest chambers consistently contained lower nutrient concentrations than control soils, although this was not statistically significant. We conclude that the 'islands of fertility' created by leaf-cutting ants provide a nutritional benefit to nearby plants for less than one year after nest abandonment in the moist tropical environment of Barro Colorado Island.

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1. Introduction

Leaf-cutting ants (genera *Atta* and *Acromyrmex*) are a common feature in neotropical forests, savannahs and grasslands. Nests are built underground with a surface area of between 50 and 160 m² (Farji Brener and Silva, 1995a) and a single mature colony can harvest annually between one and two tonnes of fresh plant material (Folgarait, 1998) to feed a saprophytic basidiomycete fungus, which in turn feeds the colony. The harvested material can represent up to 10% of the total forest canopy foliage in the foraging area, which can extend hundreds of meters from the nest (Wirth et al., 2003). *Atta* harvest only live, nutrient-rich leaves, flowers, fruits and seeds (about one quarter of the harvest is non-leaf material), but three-quarters of the material is not metabolized by the fungus and is discarded as waste, along with dead ants and fungus (Abril and Bucher, 2004; Wirth et al., 2003).

In most ant species, waste material is placed in detrital chambers within the nest, which can increase the concentration of nutrients in deep soil horizons. This has been demonstrated for, among others, *Formica polyctena* (Kristiansen and Amelung, 2001), *Formica perpilosa* (Wagner, 1997), *Atta sexdens* (Moutinho et al., 2003; Verchot et al., 2003) and *Atta laevigata* (Farji Brener and Silva, 1995a,b). In species such as *Pogonomyrmex barbatus* that deposit waste material on the soil surface and relocate nest sites infrequently (Gordon, 1992), nutrient accumulation continues for decades (Wagner et al., 1997, 2004) and can persist for considerable time after abandonment. For example, in a deciduous temperate forest the influence of European red wood ants (*F. polyctena*), a mound-forming species with below-ground nests, on soil nutrients is still detectable >20 years after abandonment (Kristiansen and Amelung, 2001). Such species can therefore have a lasting impact on nutrient heterogeneity in the landscape.

Atta colombica is somewhat different from other ant species, because colonies appear to relocate nests relatively often, to the extent that up to 25% of the total population of all colonies may move to a new nest each year (Wirth et al., 2003). Although colonies sometimes move to a previously abandoned nest, the limited

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life-span of an active nest means that the influence of the ants on nutrient cycling may be much more spatially extensive than for more sedentary species. Waste is discarded in surface mounds, which can be >2 m in diameter and are located up to 12 m, and usually down-slope, from the nest (Hart and Ratnieks, 2002). The waste material is enriched in a number of elements compared to surrounding soils (Haines, 1978), which can contribute directly to plant nutrition through enhanced growth of fine roots into the waste material (Haines, 1978; Farji-Brener and Medina, 2000; Sternberg et al., 2007). These nutrient patches may have ecological significance; for example, they have been implicated in the regeneration of the small-gap specialist *Miconia argentea* on BCI (Dalling and Wirth, 1998; Farji-Brener and Medina, 2000).

Previous studies of the influence of *A. colombica* on nutrient dynamics have investigated only active nests (Haines, 1978; Farji-Brener and Medina, 2000), so there is no information with which to assess the persistence of changes in nutrient concentrations after nest abandonment. To address this, we measured temporal changes in nutrient availability in soil and waste material in a chronosequence of *A. colombica* nests in a tropical moist forest on Barro Colorado Island, Panama. Our aim was to determine the extent to which perturbation of nutrient availability persists following nest abandonment in moist tropical forest.

2. Materials and methods

2.1. Study site

Barro Colorado Island (BCI) is situated in Gatun Lake, central Panama (09°09′N, 79°51′W). The mean annual temperature is 26 °C and varies by only 1 °C on a monthly basis, while mean annual rainfall is 2600 mm with a four month dry season from December to April (Windsor, 1990). The entire 1564 ha island is covered with semi-deciduous tropical moist forest.

The soils of BCI were recently assessed in detail (Baillie et al., 2007). The current study was restricted to an area close to the Smithsonian Tropical Research Institute laboratories that included the Fairchild and Standley soil classes – these freely-draining, dark-brown silty-clay loams overlie volcanic bedrock of the Bohio formation. As they are morphologically similar and developed on the same geological substrate, we did not attempt to stratify nest selection on the basis of soil type.

On average, *A. colombica* colonies on BCI move nest sites approximately every four years, which allowed us to identify a series of twelve nest sites of varying ages using a long term (12 year) record of colony dynamics on BCI (Wirth et al., 2003; H. Herz, unpublished data). Nests were selected for their age and proximity to minimize differences in soil and plant species composition and were separated into three groups: (i) active nests, (ii) nests abandoned within one year, and (iii) nests abandoned between one and three years previously. All nests were in late-successional forest and each group contained four 'replicate' nests. For mature colonies of *A. colombica* on BCI, herbivory rates are 266 ± 38 kg biomass per colony per year, which represents approximately 2% of the total foliage (Herz et al., 2007). Refuse production per colony varies markedly between 34.3 and 399.4 kg per year on a dry weight basis (Herz et al., 2007).

2.2. Sampling

Samples were taken after the beginning of the wet season between May and June 2005. *A. colombica* nests consist of underground nest chambers containing fungus gardens and a conspicuous aboveground waste dump, usually sited several meters down-slope of the nest area. For each nest, the following samples were taken:

i.   Soil from directly above the underground nest chambers.
ii. Soil from a control area (approximately 5 m × 5 m) located approximately 5 m upslope of, and in an area apparently uninfluenced by, the nest.
iii. Fresh organic waste material taken directly from the upper few cm of the waste mound of active nests.
iv. Soil from directly underneath the waste mound.

At six of the abandoned nest sites the waste material had completely decomposed, so soil was sampled from the area where the waste garden was previously located and was classified as soil under waste.

Two sets of soil samples were taken. For soil chemical analysis, three replicate cores were taken to 10 cm using a 5 cm diameter hand-corer and bulked. For root biomass measurements, three replicate cores were taken to 10 cm using a 10 cm diameter corer with a hammer. Only a single active nest was sampled using this technique, because disturbance of the nests by the drop-weight aggravated the ants and made sampling virtually impossible. Samples were sealed in plastic bags, returned to the laboratory (<4 h) and refrigerated at 4 °C until analysis. Subsamples of fresh soil were dried (60 °C, 48 h) and milled to a fine powder for elemental analysis.

2.3. Analytical

The moisture content of fresh soil was determined gravimetrically by oven drying at 105 °C for 24 h. Soil pH was measured on fresh soils in both deionized water and 10 mM $CaCl_2$ (1/4 soil to solution ratio) using a glass electrode. Soluble nutrients were extracted from fresh soil and waste material (sieved <4 mm) by shaking for 1 h in 0.01 M $CaCl_2$ at a 1/4 soil to solution ratio. Each extract was vacuum-filtered through a Whatman GF/A glass microfiber filter paper and analyzed for phosphate, nitrate and ammonium by automated colorimetry. Phosphate was determined by molybdate reaction, nitrate by sulphanilamide reaction after reduction to nitrite using a cadmium catalyst, and ammonium by salicylate–nitroprusside reaction. Total carbon and nitrogen were determined using a Flash EA1112 analyser (CE Elantech, New Jersey, USA). Total phosphorus was determined by digestion in concentrated sulfuric acid with selenium catalyst (Parkinson and Allen, 1975), with detection as phosphate by automated molybdate colorimetry. Root biomass samples were washed on a 50 μm sieve using deionized water and separated into three size classes: fine roots (<2 mm diameter), small roots (2–5 mm diameter) and large roots (>5 mm diameter). Samples were dried (60 °C, 48 h) and weighed.

2.4. Statistical analysis

Soil data were log_{10} transformed to meet parametric assumptions. Root data did not require transformation. To account for the unbalanced data set (older nests did not have waste mounds) we used a split-plot factorial analysis with repeated measurements for correlation between sample type (nest soil, waste, soil under waste, and control soil). One-way analysis of variance was used to assess the significance of differences. All statistical analysis was performed using SAS 9.1 (SAS Institute Inc., Cary, NC, USA).

3. Results

3.1. Soil pH and moisture content

The pH for control (non-nest) soil was 6.0 ± 0.7 in water and 5.3 ± 0.9 in 10 mM $CaCl_2$ and did not differ significantly among the

nest sites ($P > 0.05$, df = 11). Values were greater in waste material (6.1 ± 1.0 in water), especially that of active nests, and least in soil above the nest chambers (5.7 ± 0.5 in water), although the latter were not significantly different from the control soil ($P > 0.05$, df = 23). Moisture content of soils ranged between 30 and 52%, although there were no significant differences between age of nest or type of sample ($P > 0.05$, df = 41).

3.2. Total nutrient concentrations

Control soils contained 36.0 ± 14.6 g C kg^{-1} of total carbon, 3.34 ± 1.18 g N kg^{-1} of total nitrogen, and 0.419 ± 0.109 g P kg^{-1} of total phosphorus, and did not differ significantly among the nest sites ($P > 0.05$, df = 11) (Fig. 1). Concentrations were significantly higher in the waste mounds than in soil (carbon: $F = 57.1$; nitrogen: $F = 52.2$; phosphorus: $F = 47.6$; $P < 0.001$, df = 41), and significantly higher in soil under waste than in control soil and soil above the nest chambers (carbon: $F = 14.8$; nitrogen: $F = 15.6$; phosphorus: $F = 19.7$; $P < 0.0001$, df = 35) (Fig. 1).

Waste material from active nests contained around a five-fold greater concentration of total nutrients than control soils, although concentrations declined in recently abandoned nests (Fig. 1). In active and recently abandoned nests, soil above the nest chambers contained lower total nutrient concentrations than in control soils, although this was not significant ($P > 0.05$, df = 15). In long-abandoned nests, there were no significant differences in total nutrient concentrations among control soils, soil above the nest chambers, and soil under (decomposed) waste ($P > 0.05$, df = 11).

3.3. Soluble nutrients

Ammonium concentrations in control soils were 0.73 ± 0.83 mg N kg^{-1} and were not significantly different among sites. There were significantly higher levels of soluble ammonium in the waste material in both active and recently abandoned nests ($F = 11.4$, $P < 0.001$, df = 25), with concentrations up to 548 mg N kg^{-1} (Fig. 2). Soils under waste contained greater ammonium concentrations (mean 12.9 ± 15.0 mg N kg^{-1}) than control soil or soil above nest chambers for all nest ages including the oldest nest sites ($F = 42.6$, $P < 0.0001$, df = 23). There was no significant difference between control and nest soils for any nest age.

Nitrate concentrations in control soils were 23.2 ± 10.2 mg N kg^{-1} and were not significantly different among sites. Concentrations were significantly higher in waste material (mean 345 ± 196 mg N kg^{-1}) and soil under waste (mean 95 ± 118 mg N kg^{-1}) in both active ($F = 22.0$, $P < 0.001$, df = 15) and recently abandoned nests ($F = 22.8$, $P < 0.001$, df = 13) (Fig. 2). For all nest ages, soil under waste contained significantly greater nitrate concentrations than both nest and control soils, while nest soils (mean 9.5 ± 5.8 mg N kg^{-1}) contained significantly lower concentrations than control soils ($F = 18.9$, $P < 0.0001$, df = 35). Nitrate concentrations decreased with nest age for all types of sample except control soils ($F = 18.5$, $P < 0.001$, df = 41).

Soluble phosphate was present at undetectable concentrations in control and nest soils (limit of detection 0.04 mg P kg^{-1} soil). Waste material contained significantly more soluble phosphate than all other samples, although this was true only of active nests ($F = 10.2$, $P < 0.05$, df = 15), because older waste material, soil above nest chambers, control soils, and soil under waste material all contained low, often undetectable, phosphate concentrations (Fig. 2).

3.4. Root biomass

Fine root biomass in control soil was 1.23 ± 0.60 kg m^{-3} for the nine control sites and differed significantly between recently
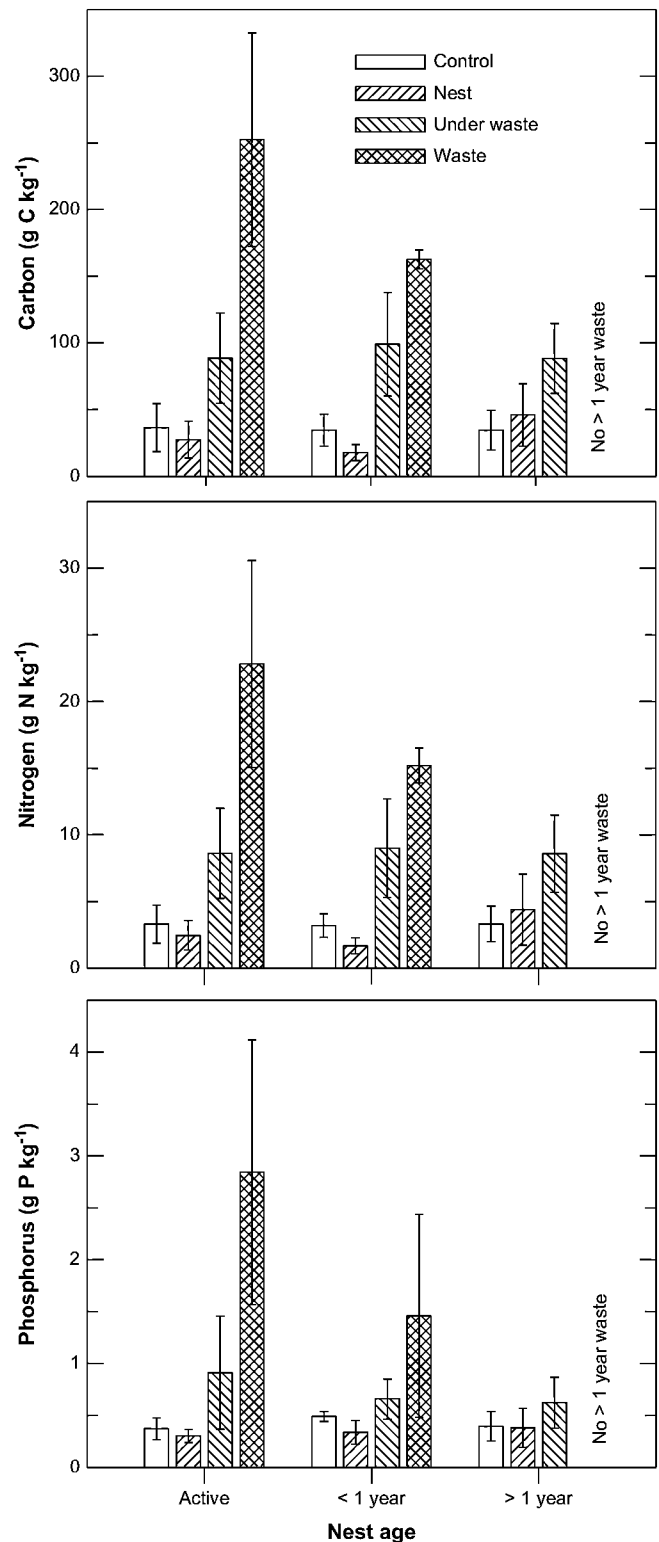

Fig. 1. Total carbon, nitrogen and phosphorus concentrations in soils and waste material from a chronosequence of *Atta colombica* nest sites on Barro Colorado Island, Panama. Active = active nests, <1 year = recently-abandoned nests, >1 year = long-abandoned nests. Values are the mean ± standard deviation of four replicate nests except for <1 year waste ($n = 2$).

abandoned (<1 year) and long-abandoned (>1 year) nest sites ($P < 0.05$, df = 23). Waste material in recently abandoned nests contained a relatively high concentration of roots (2.05 ± 0.17 kg m^{-3}). Soil under waste in recently abandoned nests
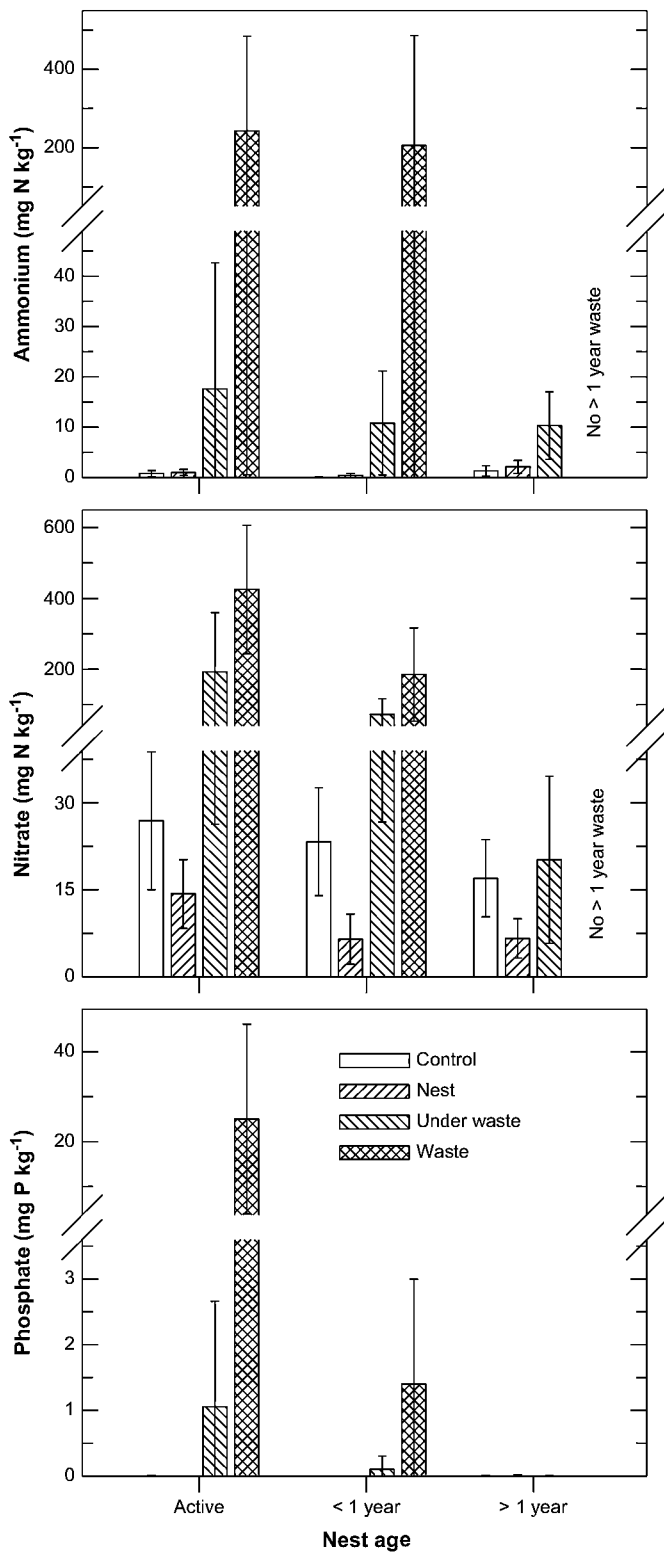
Fig. 2. Soluble, ammonium, nitrate and phosphate concentrations extracted in 10 mM CaCl₂ from soils and waste material from a chronosequence of *Atta colombica* nest sites on Barro Colorado Island, Panama. Active = active nests, <1 year = recently-abandoned nests, >1 year = long-abandoned nests. Values are the mean ± standard deviation of four replicate nests except for <1 year waste (*n* = 2).

contained more fine root biomass than both control soil and soil above nest chambers ($F = 15.7$, $P < 0.0001$, df = 23). The latter contained less fine root biomass than control soils for all nest ages, although this was significant only for recently abandoned sites (Fig. 3). In long-abandoned nests, fine roots decreased in soil under waste compared to recently abandoned nests to a level that was not significantly different from the control soil ($P > 0.05$, df = 17). There were no significant differences in root biomass in the 2–5 mm and >5 mm diameter root size classes (data not shown).

4. Discussion

The term 'islands of fertility' was originally used to describe the effect of vegetation patches in desert ecosystems (Schlesinger et al., 1996). However, it is equally appropriate when describing the concentration of nutrients created by the action of leaf-cutting ants in neotropical forests. Haines (1978) reported that waste from active nests sampled in the dry season (and therefore presumably not extensively leached) was considerably enriched in a series of elements including nitrogen, sulfur, potassium, and phosphorus. Based on these values, he calculated that the flow of nitrogen and phosphorus through the waste mound on an aerial basis was 75 and 93 times that in the forest in general. The local vegetation clearly exploits the patches of nutrients generated by the ant waste material, because fine roots grow rapidly into the waste and underlying soil (Haines, 1978; Farji-Brener and Medina, 2000), even growing directly from tree trunks into waste mounds. Sternberg et al. (2007) recently demonstrated direct connectivity between waste mounds and nearby plants using ¹⁵N labelled nitrate, although neither the foliar concentrations of nitrogen nor phosphorus were greater than control plants. Leaves were enriched only in calcium, which is surprising given that Haines (1978) previously reported calcium to be one of only two elements (the other being sodium) that were not enriched in waste mounds relative to nearby soils. It therefore remains unclear whether access to nutrients in waste mounds benefits nearby plants.
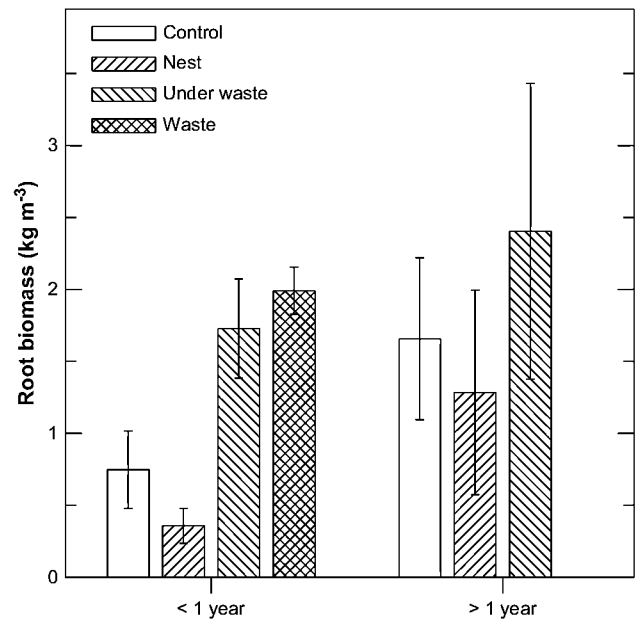

Fig. 3. Fine root biomass in waste material, soil under waste and soil above nest chambers from a chronosequence of *Atta colombica* nest sites on Barro Colorado Island, Panama. Values are for recently abandoned (<1 year) and long-abandoned (>1 year) nest sites, and are the mean ± standard deviation of four replicate nests, with each replicate nest being the mean of three replicate cores.

Despite the large increases in nutrients around the nests of leaf-cutting ants, the effect appears to be transient, because nutrient concentrations returned to background levels in nest sites abandoned for more than one year. This was especially so for soluble phosphate, which declined rapidly after nest abandonment to undetectable concentrations. Changes in soluble inorganic nitrogen fractions were longer lived, with ammonium concentrations remaining high even in the wast of nests abandoned for more than one year. Plant uptake is likely to be an important factor in the depletion of the nutrient patches, although leaching may be significant for nitrate and organic phosphorus, especially during the wet season. Inorganic phosphate, in contrast, would be expected to be stabilized rapidly by sorption in these soils, which are rich in iron and aluminium oxides (Baillie et al., 2007).

Root biomass values in control soils were similar to those reported previously for forest on BCI; for example, Haines (1978) recorded 1.43 kg m^{-3} to 20 cm depth in soil, while Farji-Brener and Medina (2000) reported 0.51 kg m^{-3} to 10 cm depth (the latter study used a 1.5 mm upper diameter to define fine roots). Both these authors recorded a considerably greater (four- to five-fold) mass of fine roots in waste material compared to non-nest soils. However, differences in fine root biomass in long-abandoned nests studied here were not significant, indicating that the nutrient-enriched parts of A. colombica nest sites provide a nutritional benefit for plants for no more than one year after abandonment.

As well as creating patches of high nutrient concentrations, A. colombica also create areas of low nutrients. Such islands of infertility may be caused by the movement of nutrient-poor subsoil excavated during the creation of the nest chambers to the surface of the nest (Farji-Brener and Illes, 2000), as indicated by the lower total phosphorus concentration in freshly excavated soil analyzed separately. Leaf-cutting ants also maintain the surface area of the nest free of vegetation (Garrettson et al., 1998), which is likely to reduce nutrient inputs from litter and fine root turnover, root exudates, and microbial activity. Soil above nest chambers from recently abandoned nests contained significantly less fine roots than control soils, while Haines (1978) also reported slightly lower (but not significantly so) fine root biomass around the nest area.

Farji-Brener and Illes (2000) argued that Atta species have ecological significance by creating gaps in the forest, similar to tree fall gaps, by providing seedlings with an area of forest rich in nutrients and free from competition for light and water. The fact that leaf-cutting ants are typically abundant in regenerating or disturbed forests (Haines, 1978) suggests that they may have an important influence on the trajectory of succession (Farji Brener and Silva, 1995a). As well as providing a source of available nutrients to existing plants, waste mounds of A. colombica nests provide ideal areas for the establishment of new seedlings, particularly where the waste is not discarded next to a tree. Farji-Brener and Medina (2000) reported the presence of seedlings of 60 species in waste material on Barro Colorado Island and suggested that the waste mounds contributed to the regeneration of small-gap specialists such as M. argentea, due in part to the presence of large numbers of seeds of this species in waste material.

A second leaf-cutting ant species on Barro Colorado Island, Atta cephalotes, has subterranean waste dumps, but information on the influence of these species on forest nutrient cycles is limited. However, deep soils (>1 m) around A. sexdens nests, a species that forms underground waste chambers and is common in secondary forest in the Eastern Amazon, contain higher concentrations of cations, inorganic nitrogen, and organic matter than surrounding soil (Moutinho et al., 2003; Verchot et al., 2003). Fine roots also proliferate in the deep soil around the nest chambers, indicating that the higher concentrations of nutrients are exploited by the local vegetation (Moutinho et al., 2003). It might be expected that

shallow-rooted seedlings would be unlikely to benefit from nutrient enrichment in the nests of such leaf-cutting ant species (Verchot et al., 2003). However, for A. cephalotes, a species with subterranean waste chambers and a relatively long residence time (10–20 years), abandoned nest sites at La Selva Biological Station in Costa Rica contained a much greater diversity and abundance of small plants compared to adjacent areas of the forest floor (Garrettson et al., 1998). Given that nutrient enrichment in A. cephalotes or A. sexdens nests does not occur at the soil surface, the simple clearance of vegetation by the ants is likely to be of importance in promoting understory diversity.

5. Conclusions

The leaf-cutting ant A. colombica perturbs nutrient cycles and contributes to the spatial heterogeneity of nutrient availability in secondary tropical rainforest. Waste mounds clearly provide patches of high nutrient concentrations that can be exploited by nearby plants, although the effects are relatively transient and soluble nutrient concentrations decline to background levels within one year of the abandonment of the nest site. However, the spatial extent of the influence of A. colombica nests is amplified by the relatively high frequency of colony relocation on Barro Colorado Island.

Acknowledgements

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