

Manna from heaven:
Refuse from an arboreal ant links aboveground
and belowground processes in a lowland tropical forest

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Citation: Clay, N. A., J. Lucas, M. Kaspari, and A. D. Kay. 2013. Manna from heaven: Refuse from an arboreal ant links aboveground and belowground processes in a lowland tropical forest. *Ecosphere* 4(11):141. <http://dx.doi.org/10.1890/ES13-00220.1>

Abstract. Aboveground consumers can shape belowground processes by serving as conduits for resources. Social insects dominate in terms of biomass in tropical forests, but compared to studies on large mammals, or aggregate solitary insects, we know relatively little about the role of social insects as nutrient conduits particularly in complex environments like tropical forests. Social insects like ants in the tropical forest canopy can connect aboveground and belowground food webs by producing a nutrient stream (excreta) from large, long-lived and stationary nests. The excreta, in turn, would create enduring spatial heterogeneity in the forest floor. Here we evaluate this scenario in a lowland Neotropical forest using *Azteca trigona*, a dominant canopy ant that feeds on honeydew and insects and rains refuse out of its hanging nests onto the leaf litter below. We investigate decomposition rates and detrital communities associated with areas near nests versus 10 m away. Further, we directly test refuse's impact on decomposition and detrital communities in a common garden experiment. Relative to leaf litter, refuse is enriched 7-fold in P, 23-fold in K, and 3-fold in N, all elements shown to limit decomposition in this forest. Accordingly, both artificial substrates and natural leaf litter substrates decomposed over 1.5- and 1.2-fold faster respectively below *A. trigona* nests and areas under nests supported more invertebrate detritivores and predators compared to controls 10 m away. These decomposition results were replicated in a 6-wk common garden experiment, but the changes in detrital invertebrate composition were not. Canopy ants like *A. trigona* act as dependable nutritional conduits to patches of the forest floor, transferring significant quantities of aboveground exudates and necromass. The general capacity for such social insect colonies to generate ecosystem heterogeneity remains an open question.

Key words: biogeochemistry; community structure; detritus; food web; frass; landscape heterogeneity; nutrient subsidies.

Received 5 July 2013; revised 30 September 2013; accepted 2 October 2013; **published** 22 November 2013.
Corresponding Editor: U. Nielsen.

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INTRODUCTION

Linkages between above- and below-ground processes have widespread impacts on terrestrial ecosystems (Bardgett et al. 1998, Scheu 2001, Van der Putten et al. 2001). Litterfall is one obvious biochemical flux that connects the canopy to the detrital decomposer microbes and invertebrates (Tian et al. 1992, Cadisch and Giller 1997). Additionally, consumer activity such as insect herbivory in forests can influence belowground processes via changes in vegetation structure and composition (Trumble et al. 1993), nutrient leaching rates (Tukey and Morgan 1963) and the quantity and quality of litterfall (Chapman et al. 2003, Classen et al. 2007, Kay et al. 2008).

Consumer byproducts such as excreta are another important linkage between above- and below-ground systems (Lovett and Ruesink 1995, McNaughton et al. 1997, Reynolds and Hunter 2001, Steinauer and Collins 2001, Mikola et al. 2009, Kagata and Ohgushi 2012) and are a concentrated source of bioavailable nutrients (Ruess and McNaughton 1984, Sørensen et al. 2003). Herbivore byproducts (excreta and cadavers) fall in quantity to the forest floor (Schowalter 2000, Hunter 2001, Frost and Hunter 2004, 2007, 2008) and can accelerate decomposition (Wardle 2002, Frost and Hunter 2004), increase plant growth (Haines 1978, Feeley 2005) and create persistent landscape heterogeneity (Whitford 2000, Fox-Dobbs et al. 2010). However, the ecosystem consequences of insect excreta are often difficult to study experimentally because deposition is frequently diffuse and transitory. This is particularly true in complex environments like tropical forests where these organic inputs may exist as transfers between distant canopy and forest floor layers.

Ants and other social insects are model organisms for examining consumer-mediated above- and below-ground linkages because they regularly concentrate their excreta around large, stationary and long-lived colonies (Weiss 2006). However, surprisingly few studies have examined their ecosystem-level impacts (Wagner 1997, Whitford 2000, O'Dowd et al. 2003, Freymann et al. 2010, Wardle et al. 2011), despite their prominence as consumers in many systems including tropical forest canopies (Fittkau and Klinge 1973) where they dominate in terms of

numbers and animal biomass (Tobin 1997, Dial et al. 2006). Ants have considerable promise as conduits between canopy and litter; they are voracious consumers that concentrate excreta, carcasses, and other 'trash' into refuse piles in or near their nests, which can create nutrient hot spots that increase nutrient mineralization and modify soil biota communities (Rojas 1989, Wagner 1997, Weiss 2006, Fox-Dobbs et al. 2010). Such central place foragers present an opportunity to directly measure connections between above- and below-ground systems even in complex environments like tropical forests where there is a notable gap in our knowledge (Rinker et al. 2001, but see Schowalter et al. 2011). This is particularly germane given much of the terrestrial primary productivity (Melillo et al. 1993) and insect biomass and diversity (Nadkarni 1994) exists in these forests.

In the Neotropics, the canopy ant *Azteca trigona* creates large (~0.5–4 m) hanging, conical-shaped nests (Wheeler 1986) that can persist upwards of 15 years (M. Kaspari, *personal observation*; Fig. 1). The tapered bottom of the nest is open, regularly raining copious amounts of refuse that resembles used coffee grounds down to the forest floor. *Azteca trigona* feeds mainly on hemipteran honeydew and arboreal insects (Wheeler 1986, Adams 1994, Davidson et al. 2004). *A. trigona* colonies are polydomous (having multiple nests per colony) and these nests are abundant; in Barro Colorado National Monument, Panama one of us recorded one *A. trigona* colony with 1–5 large nests every 40 m² (N. A. Clay, *unpublished data*). Given, their abundance and persistence, we hypothesized that *A. trigona* is an important nutrient conduit between the Neotropical canopy and forest floor that stimulates decomposition by enhancing the microbial and invertebrate breakdown of leaf litter.

Here we use multiple experiments to test the hypothesis that *A. trigona* act as nutritional conduits between the canopy and forest floor. Specifically, we test the predictions that (1) *A. trigona* refuse is nutritionally enriched relative to the litter on which it falls, (2) refuse addition stimulates decomposition relative to non-refuse addition plots, and (3) refuse addition further affects invertebrate abundance and community composition of the detrital food webs relative to non-refuse addition plots. Using *A. trigona* as a



Fig. 1. Photo of *Azteca trigona* nest and the experimental bucket setup. Photo by Jane Lucas.

model species we were able to investigate the impact aboveground social insects can have on belowground systems in a complex tropical ecosystem.

MATERIALS AND METHODS

We conducted fieldwork from mid-May to mid-July in 2009, 2010, and 2012 on Barro Colorado Island (BCI), Panama. BCI is managed by the Smithsonian Tropical Research Institute and is a seasonal lowland tropical rain forest

receiving ca. 2600 mm rain annually, the majority of which falls in the rainy season from mid-April to mid-December (Wieder and Wright 1995).

Decomposition experiments

Artificial substrates.—In 2010 we tested whether areas below *A. trigona* nests were associated with higher decomposition rates using standard artificial substrates (wood dowels and filter paper) to facilitate comparison to results from other studies. We located 10 nests and placed 3 decomposition bags at each of 3 locations: directly below the nests, 1 m from below the nest, and 10 m from the nests. For bags placed away from nests, we placed the first bag in a random direction, and then placed the second and third bags at the same distance from nests but at 120° and 240° from the first bag. We constructed decomposition bags using solid polyester material on the bottom and 0.75 cm diameter polyester mesh on the top. This allowed macrofauna access and insured we fully collected all of the remaining substrates on collection days. In each bag we included one pre-weighed wood dowel (white birch: *Betula papyrifera*) and two pre-weighed folded pieces of 9-cm grade P8 filter paper (Fisher Scientific, www.fishersci.com). We collected one decomposition bag from each distance (0, 1 and 10 m) every 2 weeks for 6 weeks; we failed to recover one bag from the 10 m distance. After collection, we gently rinsed dirt and debris from substrates and dried them at 60°C for 48 hr (sufficient time for complete drying).

Natural substrates.—In 2012, we used leaf litter from two temperate North American species not found on BCI: post oak (*Quercus stellata*) and red maple (*Acer rubrum*) and two resident BCI species: *Cecropia peltata* and *Astronium graveolens*. We collected recently fallen post oak litter from Oklahoma and red maple litter from Massachusetts in early fall 2012 and we collected *Cecropia* and *Astronium* litter from the forest floor in early June 2012. We used the temperate species because it allowed us to have large quantities of litterfall of consistent quality. We opportunistically used *Cecropia* and *Astronium* because they, unlike most BCI species, produced significant litterfall in early June (start of our field season). We located 15 nests and placed 8 decomposition bags directly under nests (0 m) and 10 m away

from nests. Decomposition bags were made of 0.75 cm diameter polyester mesh that contained ca. 5 g of dried, sterilized, and pre-weighed leaf litter of a single species. At 3 and 6 weeks we collected 4 decomposition bags (1 of each species) from all 0- and 10-m distances. Litter was extracted, gently rinsed, dried at 60°C until weight stabilized and reweighed. The use of all of these substrates (artificial sources, temperate litter, and native litter) allows us to assess the generality of *A. trigona* nest effects on decomposition.

Common garden.—We conducted a common garden experiment in June 2010 to determine if *A. trigona* refuse addition affects decomposition. We demarcated 45 0.5 × 0.5 m (0.25 m²) plots on the forest floor and assigned plots to one of three treatments: refuse addition, soil addition (a control for the addition of habitat space via particulate matter), or control plots that were unmanipulated. We selected 15 nests not used in the observational study and measured nest length (distance from the nest's point of attachment to the tree to the bottom of the nest) and height above surface (distance from the ground to the bottom of the nest) using a clinometer. We collected refuse from nests by placing 0.7 m (0.39 m²) diameter plastic buckets propped off the ground on 1.5-m PVC poles directly below nests. Bucket bottoms had two 2 cm diameter holes so rain did not gather in buckets and bucket tops were covered in removable fine mesh nylon that collected the falling refuse (Fig. 1). Every 3 days, we removed refuse from the cloth and measured the wet refuse volume for each nest using a graduated cylinder. The 15 refuse addition plots received equal volumetric proportions of refuse pooled from all 15 nests every 3 days. Similarly, 15 soil addition plots received soil (top soil was collected >100 m away from experimental plots) of equal volume as the refuse deposited on refuse addition plots. Prior to treatment, we placed 3 decomposition bags (as described above) on each of the 45 plots (Refuse, Soil and Control). Every 2 weeks for 6 weeks we collected 1 decomposition bag from each plot and cleaned, dried and reweighed wood and filter paper as described above in *Decomposition experiments: Artificial substrates*.

Chemical analysis.—In 2010, we collected refuse using buckets (as described above) from 3 nests

not used in the observational or experimental studies herein. Refuse was analyzed for lignin content, the metals Ca, K, Mg, Na, Fe, Zn, Cu, Mn, Ni, and macronutrients S, C (total C), N (total N) and P. The Soil Analytical Laboratory at Oklahoma State University (Stillwater, Oklahoma, USA) conducted analyses using a combination Lachat QuickChem 8000 flow injection autoanalyzer (Lachat, Loveland, Colorado, USA), Spectro CirOs ICP (Inductively Coupled Plasma) spectrometer (Spectro, Kleve, Germany), and an Ankom fiber analyzer (Ankom, Macedon, New York, USA). Litterfall is a common conduit of nutrients between the canopy and forest floor. Here we compared the decomposition of substrates in leaf litter vs. refuse. Thus, we further compared the chemistry of leaf litter ($n = 25$) and refuse to determine how refuse- and plant-mediated nutrient deposition differed. Leaf litter was gathered from the forest floor in locations throughout the island and analyzed in 2004 as part of a previous study that examined the relationship between litter depth and phosphorous (see Kaspari and Yanoviak 2008 for leaf litter collection and chemistry analysis methods).

Detrital invertebrate communities

Natural communities.—In July 2009 we tested whether *A. trigona* refuse piles were associated with detrital invertebrate communities distinct from those in leaf litter 10 m away from nests. We collected the detrital communities from 0.25-m² (0.5×0.5 m) areas directly below 20 nests and from 0.25-m² areas 10 m from nests in a random direction; these nests were different from those used in the decomposition study. We collected all leaf litter on plots down to the topsoil into a large sifter with a 1-cm² metal mesh. After sifting, we discarded the coarse leaf litter and kept the fine ‘siftate’ containing the invertebrates below the metal mesh (Bestelmeyer et al. 2000). We placed a random 400-ml subset of the siftate into a Berlese funnel and after 24 hr we collected the invertebrates that had fallen into the cup with 95% ethanol at the bottom of the funnel. Invertebrates were identified to at least Class and represented the 33 focal taxa that were most common in this study and others (Wardle 2002, Decaëns 2010). We deposited vouchers in the Museo de Invertebrados Fairchild, Panama and MK’s collection at the University of Oklahoma.

Common garden communities.—We tested whether refuse addition is associated with distinct invertebrate communities within this common garden experiment. After 6 weeks, we harvested detrital invertebrate communities from each plot (Refuse, Soil and Control plots) and extracted and identified invertebrates as described above in *Detrital invertebrate communities: Natural communities*.

Statistical analysis

Artificial and natural decomposition experiments.—We tested for substrate decomposition differences among refuse piles, 1 m and 10 m (artificial substrates) or 0 and 10 m (natural substrates) using Profile Analysis (v. 10.0; SPSS, Chicago, Illinois, USA). Profile Analysis tests three null hypotheses: (1) slopes do not differ from 0 over time (i.e., flatness: a measure of within-group main effect); (2) no difference among groups over time (i.e., equal levels: a measure of between-group main effect); and (3) no difference among slopes over time (i.e., parallelism: a measure of within-group \times between-group interaction). We used arcsine percent mass loss of leaf litter, filter paper or wood as the dependent variable sampled over time (within-group) and distance as the independent (between-group) variables. We used percent mass loss because numerous samples had 0 mass remaining after 6 weeks (our last collection time). In these cases we substituted all 100% mass loss values with $100 - 1/4n$, where n was the sample size (Bartlett 1947, Sahu 2013). We report Wilk’s lambda unless within-subject data did not meet assumptions of sphericity (Mauchly’s test of sphericity: $p \leq 0.05$), in which case we report Greenhouse-Geisser test statistics. If any of these null hypotheses were rejected we performed Tukey HSD (between-group) or ANOVA (within-group) post hoc tests.

Common garden decomposition experiment.—We quantified the effect of nest length and height above surface on the amount of refuse captured in buckets using linear regression. We then tested whether decomposition rates (arcsine percent mass loss of filter paper or wood) sampled over time differed among treatments (Refuse, Soil, or Control) in our common garden experiment using Profile Analysis. We performed post hoc tests when any of the null hypotheses were rejected.

Chemical analysis.—We tested if refuse chemistry differed from leaf litter using GLM-MANOVA in SPSS (v. 10.0). We used a posteriori ANOVAs to determine which chemistry parameters differed between refuse and leaf litter. We had insufficient samples to correct refuse for dry mass so we report results with caution. If refuse has higher nutrient content than leaf litter for a given element, these results are reliable because correcting for percent dry matter increases the relative elemental quantity. Because leaf litter values are already corrected for dry mass, if we could correct refuse for dry mass this would result in an even greater difference between refuse and leaf litter. However, results that indicate no difference or a depletion in a given element should be interpreted with caution.

Natural detrital invertebrate communities.—We tested whether invertebrate communities differed between locations (below nests vs. 10 m away) using Permanova in PC-ORD v. 6 (McCune and Mefford 2011). Permanova is a non-parametric multivariate analysis of variance that was designed for community analyses that violate the assumptions of parametric MANOVAs (Anderson 2001). Permanova tests the null hypothesis of no difference among groups (in this study: 0 vs. 10 m and Block: paired distances) using random permutations of the data. Permanova uses a pseudo-F statistic and tests significance by permuting the data (for details see Anderson 2001). We used Bray-Curtis dissimilarities and 9999 permutations ($\alpha = 0.05$). We used a posteriori Wilcoxon tests to determine which taxa differed.

Common garden detrital invertebrate communities.—We used Permanova to test for differences in invertebrate communities among Refuse, Soil, or Control plots as described above in *Statistical analysis: Natural detrital invertebrate communities*.

RESULTS

We collected refuse from *A. trigona* nests that ranged from 0.7–3.1 m in length and 0.7–3.9 m in height above surface. Together, nest height above surface and length accounted for 64% of the variation in refuse quantity collected below *A. trigona* nests. From a single nest, we captured on average 11.1 ± 9.03 ml (0.69 ± 0.39 g ml⁻¹ wet wt) refuse day⁻¹ nest⁻¹ (an underestimate given

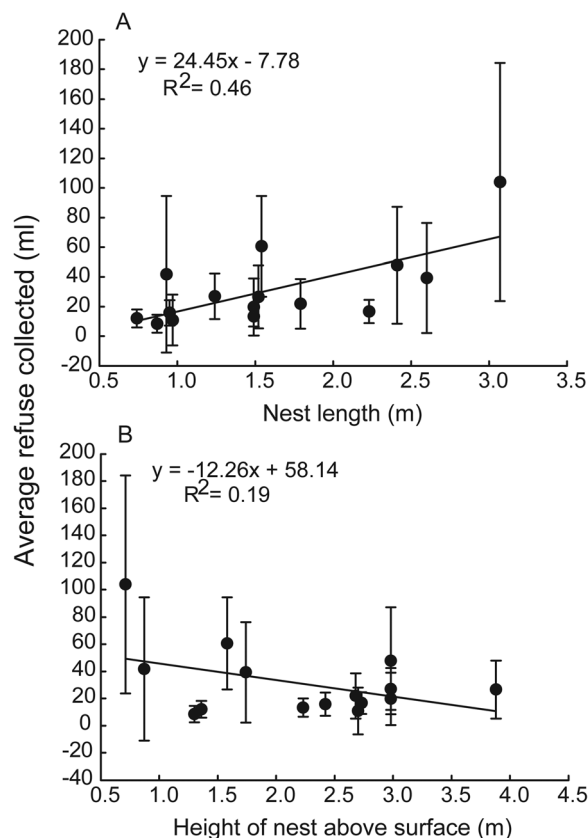


Fig. 2. Amount of refuse collected in buckets propped on 1.5-m poles below 15 *Azteca trigona* nests. Refuse volume (ml) produced from each nest was measured every three days. Each point is the average of all 14 refuse measurements collected over 6 weeks for an individual nest related to that nest's length (A) and height above surface (B). Bars represent standard deviation.

that our apparatus did not collect all refuse, particularly for nests higher in the canopy). The amount of refuse collected in buckets increased with nest length: a proxy for nest size ($p = 0.002$; Fig. 2A), and decreased with nest height above surface: a proxy for how diffusely the refuse fell ($p = 0.031$; Fig. 2B).

Decomposition experiments

Artificial and natural decomposition experiments.—Decomposition rate generally increased with proximity to *A. trigona* nests for artificial substrates (Profile Analysis test of equal levels—main effect of distance: $p \leq 0.014$; Fig. 3) and

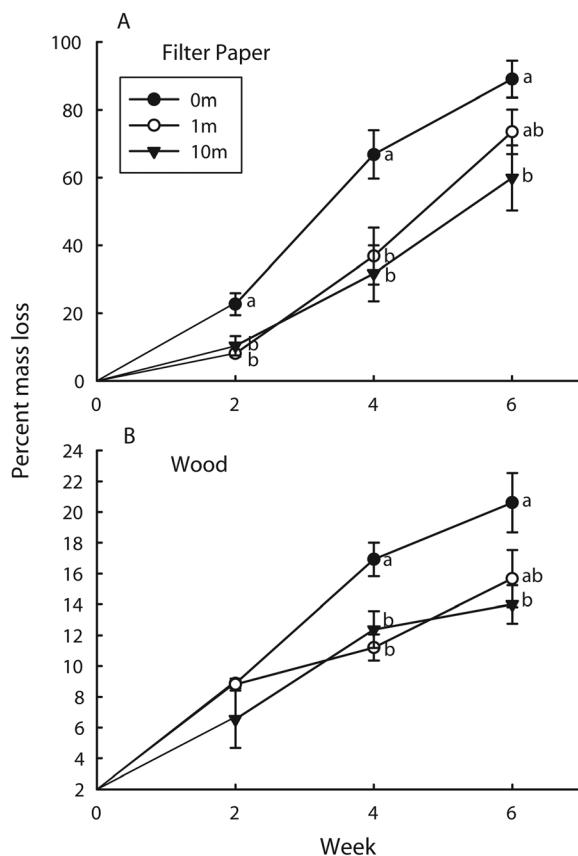


Fig. 3. Average percent mass loss of filter paper (A) and wood (B) directly below *A. trigona* nests (0 m), 1-m or 10-m distance over time. Bars represent standard deviation and letters indicate significant differences among mass loss by distance within a sampling time.

natural substrates ($p \leq 0.058$) except for *Astro-nium graveolens* that had similar decomposition rates between distances and lost very little mass during the 6 week period ($p = 0.462$; Fig. 4, Appendix: Table A1). After 6 weeks, mass loss averaged 1.5-fold higher below nests than 10 m away for artificial substrates (Tukey's HSD: $p < 0.05$) and 1.2, 1.3, and 1.4 for *A. rubrum*, *C. petlata*, and *Q. stellata* respectively. Substrates continued to lose mass over time (Profile Analysis test for flatness—Time: artificial substrates, *A. rubrum*, *C. petlata*, and *Q. stellata* $p \leq 0.001$; Appendix: Table A1) and consistently for artificial and natural substrates (Profile analysis test for parallelism—Time \times Distance: $p \geq 0.074$; Figs. 3 and 4; Appendix: Table A1). Decomposition only increased under nests for *C. petlata* after 3 weeks (p

$= 0.014$). These effects were evident for filter paper after 2 weeks, after 4 weeks for wood (Fig. 3), and after 6 weeks for *A. rubrum*, *C. petlata*, and *Q. stellata* (Fig. 4).

Common garden decomposition experiment.—Over 6 weeks, *A. trigona* refuse added as a fertilizer in a common garden experiment, enhanced filter paper mass loss up to 1.3-fold more than soil addition or control plots (Profile analysis main effect of treatment: $p < 0.001$; Fig. 5, Appendix: Table A2). The ability to detect this effect increased over time (Profile Analysis test for flatness: $p < 0.001$ and parallelism: $p = 0.050$; Appendix: Table A2) and by 6 weeks, filter paper in refuse piles had virtually disappeared (Fig. 5A). Refuse addition marginally enhanced wood decomposition (Profile analysis test of equal levels: $p = 0.068$; Appendix: Table A2). After 4 weeks, wood mass loss was marginally higher in refuse piles ($p = 0.049$) than controls but not soil plots, but treatment effects were smaller ($p > 0.05$) after 6 weeks (Profile Analysis test of flatness: $p < 0.001$ and parallelism: $p = 0.293$; Fig. 5B, Appendix: Table A2).

Chemical analysis.—*A. trigona* refuse was enriched relative to leaf litter ($F_{12,15} = 96.579$, $p < 0.0001$) in a variety of elements shown in other tropical systems to limit decomposition (Table 1). Refuse was nearly 3-fold higher in total N, 6-fold in P, 13.5-fold in K, 9-fold in Na, and 2-fold in S. Refuse was depleted in a variety of nutrients relative to leaf litter: Fe by 41-fold, Ca by 2.5-fold, and Mn by 8-fold. There was no difference between *A. trigona* refuse and BCI leaf litter for Mg, Zn, Cu or Total C (Table 1).

Detrital invertebrate communities

Natural detrital invertebrate communities.—Compared to 10 m away, 14 of the 33 taxa quantified were more abundant in refuse piles and only Thysanoptera was less abundant (Fig. 6). Refuse communities averaged more arthropods (refuse: 736 ± 465 , control: 322 ± 208 ; paired t-test $t_{18} = 3.67$, $p = 0.002$) and 2.4-fold more microbiodetritivores and predators compared to 10 m away (Permanova: $p = 0.0015$; Fig. 6, Appendix: Table A3).

For example, the numerically dominant microbiodetritivores: Oribatids, Collembola and Diptera larvae, were respectively 2.1-, 3.3-, and 5.3-fold more abundant below nests compared to

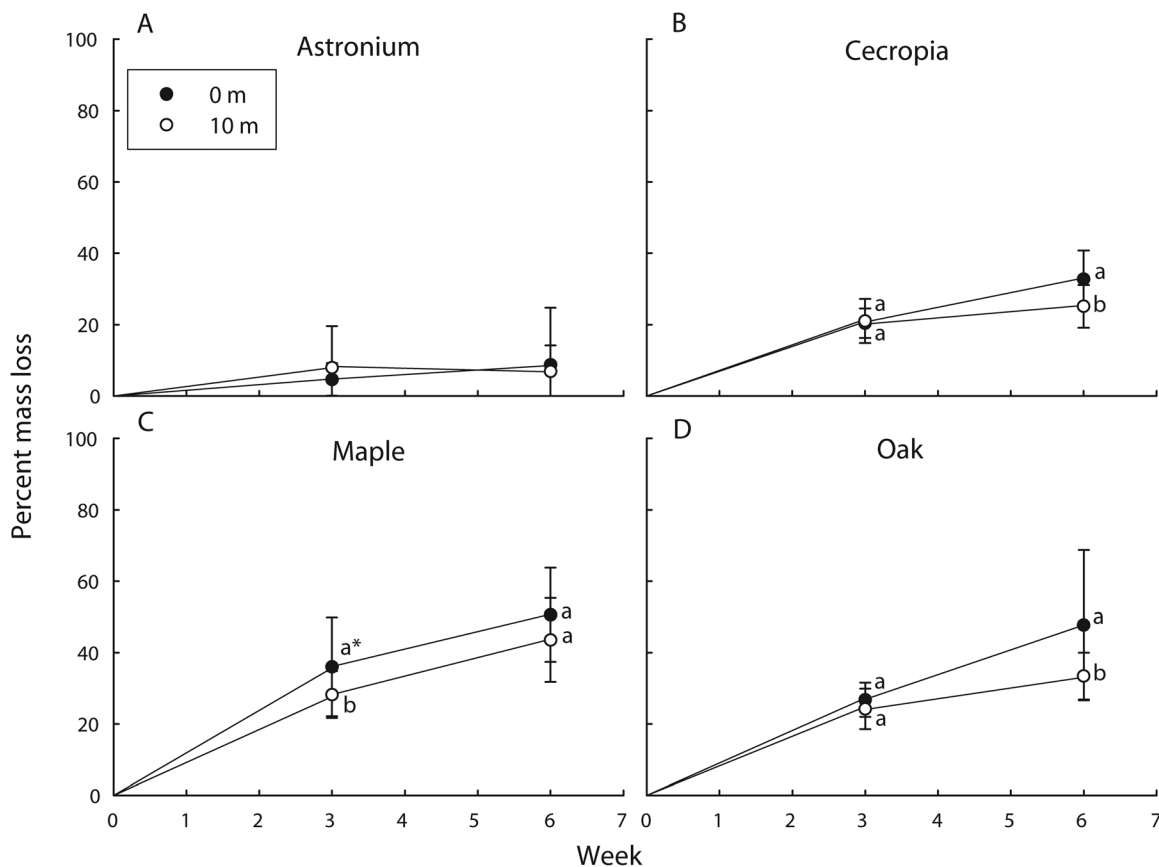


Fig. 4. Average percent mass loss of 2 BCI (A and B) and two temperate (C and D) species. The asterisk in panel C indicates $p = 0.064$. Bars are standard deviation and letters indicate significant differences among mass loss by distance within a sampling time.

paired controls 10 m away (Fig. 6). Likewise, the less abundant Enchytraeids and Lumbricids (Annelida), Lepidoptera larvae and Nematoda also increased at least 3-fold under nests. Results of these latter taxa should be interpreted with caution as Berlese Funnel methods are not typically used to measure their abundance. Of the predators, Pseudoscorpions averaged 8.7-fold more abundant below *A. trigona* nests, and a variety of other predacious taxa were also more abundant, including the generalist ant predator *Wasmannia* (5-fold), Staphylinid beetles (4-fold), spiders (2.7-fold) and a 2.2-fold increase in predatory mites, which included Mesostigmata, Trombidioidea and Prostigmata (Fig. 6).

Common garden detrital invertebrate communities.—The 6 weeks of fertilizing with *A. trigona* refuse did not alter invertebrate communities (Permanova, $p = 0.271$; Appendix: Table A4).

Refuse addition plots trended toward higher arthropod abundance (refuse = 818 ± 642 , soil = 477 ± 348 , control = 422 ± 261 ; Permanova, $p = 0.266$), but with only a small effect size (partial $\eta^2 = 0.055$).

DISCUSSION

Here we demonstrate that social insects can generate long-term, concentrated nutrient conduits between the canopy and litter. We show that the Neotropical ant *A. trigona* produces a stream of C, N, P, K and other nutrients in the form of a rain of refuse that is at least 1.3-fold more concentrated in these decomposition-enhancing nutrients (Kaspari et al. 2008, Kaspari et al. 2009, Barantal et al. 2012) than leaf litterfall. Barro Colorado Island is 1,500 ha; given the density of *A. trigona* (3.7 ± 2.6 large nests 40 m^{-2} ;

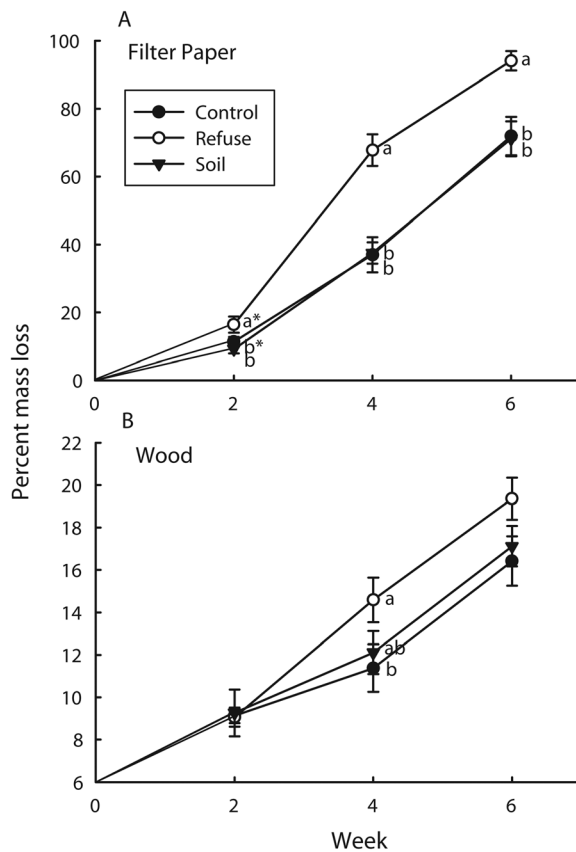


Fig. 5. Average percent mass loss of filter paper (A) and wood (B) in Refuse, Soil, and Control plots over time. Bars represent standard deviation and letters indicate significant differences among mass loss by treatment within a sampling time. Asterisks in panel A indicate $p = 0.057$.

N. A. Clay, *unpublished data*), this suggests that *A. trigona* deposit ca. 10.6 tons day⁻¹ (12,488 liters day⁻¹) of refuse at this site. Litterfall on Gigante Peninsula, part of the Barro Colorado Island National Monument, averages $987.4 \pm 123.9 \text{ g m}^{-2} \text{ yr}^{-1}$ (Sayer et al. 2012): ca. 40.6 tons day⁻¹ on BCI. This suggests that this one species of ant deposits in refuse the equivalent of 25% of the total litterfall of a Neotropical forest! This nutrient stream is associated with a doubling of common microbi-detritivores like Oribatids and Collembolans and predators like Pseudoscorpions and a commensurate doubling of filter paper decomposition, a 1.5-fold increase in wood decomposition, and 1.2–1.4-fold increases in decomposition of three species of leaf litter compared to areas 10 m away. Further, marginally significant effects can extend up to 1 m from nests (Fig. 2) suggesting *A. trigona* produce 3-m² patches of higher activity and abundance on the tropical forest floor. These results suggest that social aggregation in the canopy can generate heterogeneity in consumer productivity on the forest floor below.

The role of social insect nutrient translocation at ecosystem-level spatial scales has received surprisingly little attention (Wagner 1997, Whitford 2000, O'Dowd et al. 2003, Freymann et al. 2010, Wardle et al. 2011) despite other well documented excretion impacts on ecosystem function by consumers occurring in high densities (McNaughton et al. 1997, Beard et al. 2002, Feeley 2005, McIntyre et al. 2008, Atkinson et al. 2013). In kind and similar to insect frass additions in temperate

Table 1. Chemistry results from the MANOVA and univariate post hoc tests of refuse and leaf litter substrates from BCI, Panama (see Kaspari and Yanoviak 2008 for leaf litter collection and chemistry analysis methods). Parentheses next to substrates indicate sample size. Refuse values are uncorrected for percent dry mass. Values for refuse and leaf litter are mean \pm SD. For refuse, $n = 3$; for leaf litter, $n = 25$.

Chemical	Refuse	Leaf litter	F	p
P (%)	0.559 \pm 0.081	0.091 \pm 0.010	960.318	<0.0001
Ca (%)	0.840 \pm 0.074	2.056 \pm 0.536	14.930	0.001
K (%)	2.578 \pm 0.630	0.127 \pm 0.065	468.204	<0.0001
Mg (%)	0.305 \pm 0.044	0.317 \pm 0.126	0.026	0.872
Na (%)	0.074 \pm 0.015	0.008 \pm 0.002	513.693	<0.0001
S (%)	0.360 \pm 0.052	0.188 \pm 0.026	93.494	<0.0001
Fe (ppm)	772.10 \pm 516.77	31547.36 \pm 19190.31	8.230	0.008
Zn (ppm)	67.27 \pm 17.27	77.33 \pm 20.12	0.684	0.416
Cu (ppm)	46.57 \pm 12.88	52.40 \pm 17.63	0.304	0.586
Mn (ppm)	117.60 \pm 41.64	957.22 \pm 600.70	5.667	0.025
Total N (%)	5.032 \pm 0.381	1.717 \pm 0.233	481.422	<0.0001
Total C (%)	44.567 \pm 1.850	39.258 \pm 5.714	2.483	0.127

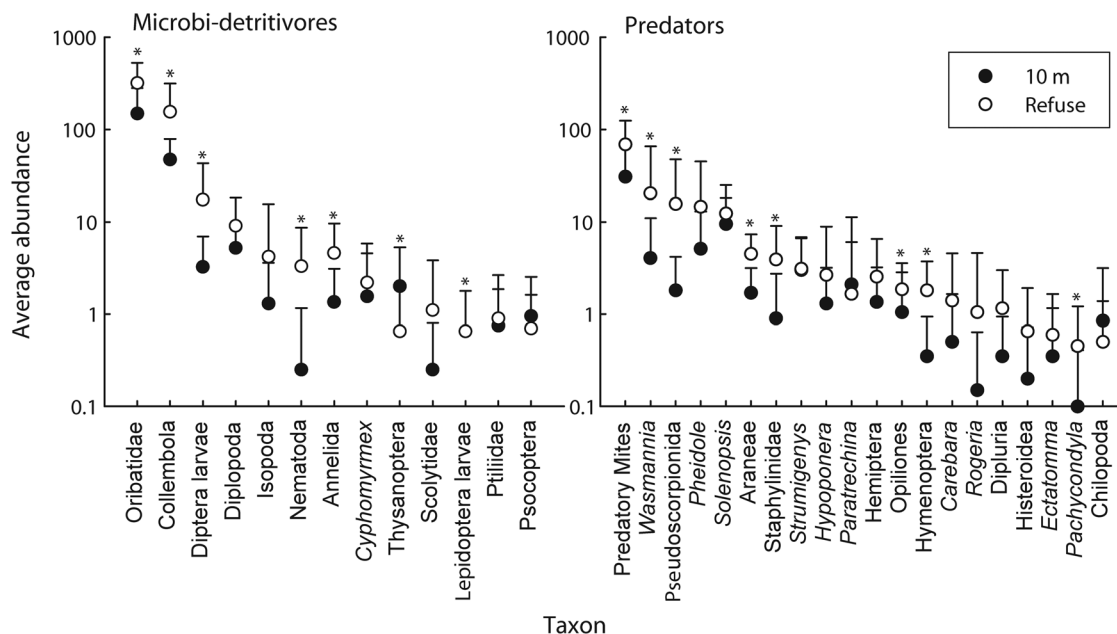


Fig. 6. Average abundance on a \log_{10} scale of the 33 invertebrate taxa collected from 0.25-m² plots below nests in refuse or 10 m away. Taxa are divided into functional trophic groups. Bars represent positive standard deviation and asterisks indicate significant difference in abundance (Wilcoxon, $\alpha = 0.05$) between refuse and 10-m plots.

forests (Lovett and Ruesink 1995, Reynolds and Hunter 2001, Kagata and Ohgushi 2012), our common garden experiment confirmed the stimulatory effects of *A. trigona* refuse on artificial and natural substrate decomposition (Fig. 5). However, ours is one of a subset that follows the nutrient addition through to the decomposer communities themselves (but see Bardgett et al. 1998, Wardle 2002). Refuse piles that have likely persisted for multiple years supported distinct communities (Fig. 6). This was not the case in the experimental refuse addition plots after six weeks. A number of possibilities may account for our ability to replicate decomposition patterns but not invertebrate densities. First, six weeks may have been inadequate time to drive invertebrate population growth and recruitment. Second, it is highly plausible that refuse enhanced microbial activity or biomass (Allen and Schlesinger 2004). Alternatively, increased invertebrate activity could have yielded the same result. More detailed information on refuse biochemistry and detrital community metabolism and composition is needed to identify the aspects of *A. trigona* refuse that impact nutrient cycling in this system.

Many aboveground insects produce excreta in pulses (seasonal or outbreaks: Lam and Dudgeon 1985, Lovett and Ruesink 1995) and are not stationary, however, *A. trigona* nests have been known to persist 15 years or more, and as such, they generate long-standing productivity hot spots, landscape heterogeneity, and are dependable parts of the forest environment. Such dependability should have consequences for the surrounding plants. Accelerated decomposition frees more nutrients from standing crop dead organic matter that can stimulate plant growth and reproduction (Wardle 2002). The majority of *A. trigona* nests are attached near or on tree trunks, and the large quantities of refuse falling are concentrated at the base of host trees (N. A. Clay, *personal observation*). Given that *A. trigona* nests are stationary, long-lived, and nest refuse substantially enhances decomposition, host trees may benefit from their association with *A. trigona* through increased mineralization and nutrient availability. We predict that trees, especially the *A. trigona* nest host tree, will allocate roots to take advantage of these resources. Plants concentrate their nutrient uptake through fine roots and this

response of tree-produced dense fine root mats occurs in howler monkey (*Alouatta*) excreta sites (Feeley 2005). Such nutrient exchange paired with *A. trigona*'s predatory behavior (Adams 1994) could lead to coevolution between *A. trigona* and host trees. However to our knowledge no studies have examined host tree fidelity in this species, but a closely related species *Azteca chartifex* shows preference for *Goupia glabra* (Goupiaceae) trees (Dejean et al. 2008). Further investigation into the relationship between *A. trigona* and host trees will likely reveal complex interactions.

The ecologies of the canopy and of the forest floor are often studied independently; research at the canopy-forest floor interface largely focuses on the roles of plants in litterfall. As important as litterfall chemistry is as a process linking above- and below-ground food webs (Wardle 2002), consumer excreta can also leave a substantial ecosystem footprint (Fonte and Schowalter 2005, Schowalter et al. 2011). The long-term impact of such subsidies from species like *A. trigona* are likely profound, especially when considered collectively with the diverse contributions of excreta from other canopy consumers.

ACKNOWLEDGMENTS

We thank Taylor Zumbusch, David Donsoso, Matt Sweeney, Jon Shik, and Deana Flatt for assistance in the field and D. Flatt and Kendra Tholt for laboratory assistance. We also thank Oris Acevedo and Belkys Jiménez and STRI staff on BCI, Panama, ANAM for permits and OSU soil lab. ZEEB Discussion Group (OU) provided useful comments on earlier versions of the manuscript. Funding was provided by the Zoology Department (OU), the College of Arts and Sciences (OU), Graduate Student Senate (OU), and NSF DEB 0842038 (PI M. Kaspari, A. Kay).

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SUPPLEMENTAL MATERIAL

APPENDIX

Table A1. Results of the Profile Analysis testing *A. trigona* refuse effects associated with nests (Distance) on decomposition using both natural leaf litter (*Astronium graveolens*, *Cecropia peltata*, *Acer rubrum*, *Quercus stellata*), and artificial (filter paper and wood) substrates over Time. When assumptions of sphericity were violated we report Greenhouse-Geisser test statistics.

Source	SS	df	MS	F	p	Partial η^2
Filter paper						
Between subjects						
Distance	1.624	2	0.812	8.811	0.001	0.404
Error _{BS}	2.396	26	0.092			
Within subjects						
Time	8.313	1.458	5.702	76.005	<0.001	0.745
Time \times Distance	0.200	2.916	0.069	0.914	0.441	0.066
Error _{WS}	2.844	37.909	0.075			
Wood						
Between subjects						
Distance	0.087	2	0.044	5.033	0.014	0.279
Error _{BS}	0.226	26	0.009			
Within subjects						
Time	0.297	1.216	0.244	24.819	<0.001	0.488
Time \times Distance	0.026	2.433	0.011	1.105	0.353	0.078
Error _{WS}	0.311	31.627	0.010			
Astronium						
Between subjects						
Distance	0.030	1	0.030	0.556	0.462	0.019
Error _{BS}	1.502	28	0.054			
Within subjects						
Time	0.001	1	0.001	0.017	0.898	0.001
Time \times Distance	0.015	1	0.015	0.365	0.551	0.013
Error _{WS}	1.143	28	0.041			
Cecropia						
Between subjects						
Distance	0.024	1	0.024	4.174	0.051	0.130
Error _{BS}	0.162	28	0.006			
Within subjects						
Time	0.137	1	0.137	30.978	<0.001	0.525
Time \times Distance	0.031	1	0.031	6.949	0.014	0.199
Error _{WS}	0.124	28	0.004			
Maple						
Between subjects						
Distance	0.089	1	0.089	3.893	0.058	0.122
Error _{BS}	0.642	28	0.023			
Within subjects						
Time	0.364	1	0.364	49.881	<0.001	0.640
Time \times Distance	<0.001	1	<0.001	0.047	0.830	0.002
Error _{WS}	0.205	28	0.007			
Oak						
Between subjects						
Distance	0.158	1	0.158	6.551	0.016	0.190
Error _{BS}	0.676	28	0.024			
Within subjects						
Time	0.458	1	0.458	20.182	<0.001	0.419
Time \times Distance	0.078	1	0.078	3.452	0.074	0.110
Error _{WS}	0.635	28	0.023			

Table A2. Results of the Profile Analysis testing *A. trigona* refuse effects (Treatment: Refuse, Soil, or Control) on decomposition in the common garden experiment using artificial (filter paper and wood) substrates over Time. When assumptions of sphericity were violated we report Greenhouse-Geisser test statistics.

Source	SS	df	MS	F	p	Partial η^2
Filter paper						
Between subjects						
Treatment	1.877	2	0.938	18.297	>0.001	0.466
Error _{BS}	2.154	42	0.051			
Within subjects						
Time	14.620	1.618	9.034	220.961	>0.001	0.840
Time \times Treatment	0.355	3.237	0.110	2.679	0.050	0.113
Error _{WS}	2.779	67.970	0.041			
Wood						
Between subjects						
Treatment	0.028	2	0.014	2.860	0.068	0.120
Error _{BS}	0.202	42	0.005			
Within subjects						
Time	0.352	2	0.176	68.716	>0.001	0.621
Time \times Treatment	0.013	4	0.003	1.259	0.293	0.057
Error _{WS}	0.215	84	0.003			

Table A3. PERMANOVA results of BFW observational study comparing communities below nests (Refuse) and 10 m away (Control) (Nest effect: $n = 20$ each) using Bray-Curtis dissimilarities as the distance measure and 9999 permutations ($\alpha = 0.05$).

Source	df	SS	MS	F	p
Nest effect	1	0.821	0.821	6.486	0.002
Block	19	2.274	0.120	0.946	0.589
Residual	19	2.404	0.127		
Total	39	5.499			

Table A4. PERMANOVA results of BFW experimental study comparing communities in Refuse, Soil and Control plots ($n = 15$ each) using Bray-Curtis dissimilarities as the distance measure and 9999 permutations ($\alpha = 0.05$).

Source	df	SS	MS	F	p
Treatment	2	3623.33	1811.67	1.211	0.271
Residual	42	62850.16	1496.43		
Total	44	66473.49			