

## The Old and Young Amazon: Dung Beetle Biomass, Abundance, and Species Diversity

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### ABSTRACT

The Amazon Basin can be divided into two geomorphological regions based on the age of its soils: young (< 30 mya) and old (> 300 mya). We tested the effects of soil age on dung beetle communities by comparing biomass, abundance, and species between reserves in Ecuador on young soils and reserves in Brazil on old soils. Beetle biomass in the old Amazon was one-third that in the young Amazon, and beetle abundance in the old Amazon was one-fourth that in the young Amazon. Species richness, rarefied to equal sample sizes, was not significantly different between old and young soils. These data suggest young soils of the Amazon support a significantly greater biomass and abundance of dung beetles than old soils, but that species richness across the Basin is similar. As dung beetles are bio-indicators of mammals, our data support previous studies indicating a greater biomass of mammals on young versus old Amazon soils.

Abstract in Portuguese is available at <http://www.blackwell-synergy.com/loi/btp>.

*Key words:* Brazil; Ecuador; Neotropics; productivity; richness; Scarabaeidae; tropical wet forest.

THE AMAZON BASIN IS GEOGRAPHICALLY ENORMOUS AND BIOTICALLY DIVERSE. Two factors contributing to its diversity are size and geomorphology. On a grand scale, these factors are confounded because the geologically young Amazon, containing soils of very recent origin (< 30 mya), and the geologically old Amazon, harboring ancient soils (> 300 mya), are separated along geographic axes (Jordan 1985, Sombroek 2000). The young soils originated from the Andean uplift in the Western Amazon during the Cenozoic, whereas the old soils dominate the Central and Eastern portions of the Basin, having originated in the Paleozoic and Mesozoic (Jordan 1985, Sombroek 2000). This vast difference in bedrock age between the West, draining the Andes, and the Central/East, draining the Guianan Shield and the Brazilian Highlands, demarcates differences in forest dynamics (Williamson *et al.* 2005). Plant productivity on older, weathered soils is much lower than on younger mineral-rich soils (Sombroek 2000), and turnover rates for large trees on older soils are only half those on younger soils (Phillips *et al.* 2004).

How such differences in primary production reverberate up the food chain to higher trophic levels is largely unexplored (Henderson & Crampton 1997, Kay *et al.* 1997). Studies of specific vertebrate taxa have shown greater abundances in the regions of young versus old soils of the Amazon (Emmons 1984, Allmon 1991, Peres & Dolman 2000). As mammalian excrement is the limiting factor for dung beetles in the tropics (Peck & Forsyth 1982, Gill 1991) and as changes in dung production are known to affect dung beetle communities (Kadiri *et al.* 1997, Carpaneto *et al.* 2005, Ponce-Santizo *et al.* 2006), we applied a standardized methodology in Brazil and Ecuador to test for differences among dung beetle communities.

Our hypothesis was that geologically young soils in the Western Amazon (Ecuador) would sustain a greater biomass and abundance of dung beetles than old soils in the Central Amazon (Brazil).

Further, we do not hypothesize a difference in species richness between Ecuador and Brazil. Modern floristic studies for the two regions have indicated comparable species richness (Oliveira & Mori 1999, ter Steege *et al.* 2000). However, for mammals, plant productivity can potentially generate diversity differences if population densities are reduced below the viable population thresholds (Wright 1983, Kay *et al.* 1997). Applicability of this productivity argument to dung beetles is doubtful because scarab population densities are much larger than primate densities. Also, scarabs are not known to depend on one particular mammal species' dung, although they may specialize on herbivore, carnivore, or omnivore dung (Gill 1991, Ponce-Santizo *et al.* 2006). Here, we test for differences in dung beetle biomass, abundance, and diversity across the young and old soils, and then discuss the implications for conservation.

### METHODS

We chose three sites in the Central Amazon on old soils and two in the West on young soils (Sombroek 2000). In the Central Amazon of Brazil we sampled in Reserva Adolfo Ducke and the reserves Dimona and Km 41 in the Biological Dynamics of Forest Fragments Project (BDFFP). In the Western Amazon of Ecuador, we sampled at Tiputini Biodiversity Station and Yasuní Research Station. Maps of these sites can be found in Ribeiro *et al.* (1999), Tuomisto *et al.* (2003), and Valencia *et al.* (2004). These reserves have similar elevations, latitude, and climate, but differ geomorphologically in

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soil age. For example, at all reserves mean monthly rainfall is generally > 100 mm, although annual totals vary as follows: 3500 mm at Tiputini, 2826 mm at Yasuní, 2651 mm at BDFFP, and 2100 mm at Ducke (Lovejoy & Bierregaard 1990, Gascon & Bierregaard 2001; Tiputini Research Station Records, Yasuní Research Station Records). Likewise, all reserves harbor evergreen, lowland rain forest, although duration of the rainy season varies somewhat: 10 mo in Ecuador (February through November) and 7 mo (November through May) in Central Brazil. Average temperature is nearly uniform: 27°C at Tiputini, 25°C at Yasuní, 26°C at BDFFP, and 27°C at Ducke (Bruna 2002; Tiputini Research Station Records, Yasuní Research Station Records). Elevations where we sampled are around 200 m in Ecuador and around 100 m in Brazil (Lovejoy & Bierregaard 1990, Gascon & Bierregaard 2001; Tiputini Research Station Records, Yasuní Research Station Records).

The Brazilian reserves are in the old Amazon landform classified as the “Eastern Sedimentary Uplands,” which consist of fluvatile sediments (xanthic ferralsols, also called yellow latosols) that were preweathered during the Cretaceous and Tertiary (Sombroek 2000, Fearnside & Filho 2001). In Ecuador, the reserves are located on a young landform classified as “Western Sedimentary Uplands,” which are also fluvatile deposits (red clays, brown or gray alluvium) that were much less preweathered at the time of their deposition in the Miocene (Sombroek 2000, Tuomisto *et al.* 2003). Soil textures differed somewhat as young soils had a larger proportion of silt (~50%) with clays and sands contributing approximately 25 percent each (Tuomisto *et al.* 2003), whereas weathering of old soils has resulted in clays dominating ridges and plateaus and sands occurring near streams (Chauvel *et al.* 1987, Rebelo & Williamson 1996, Fearnside & Filho 2001, Powers 2004). All sampling was done on upland soils dominated by clay and silt.

All sites are currently protected reserves at least 10,000 ha in size, and all have been reported to contain populations of large mammals with no record of species' extirpations (Emmons 1984, Peres 1997, Vulinec 1999, Peres & Dolman 2000). Mammalian faunas across the sites are quite similar (Peres 1997). Although floristics vary among sites, forest structure is similar with canopy emergents reported to reach 45 m in height (Rankin-de-Mérona *et al.* 1992, Harms *et al.* 2004; Yasuní Research Station Records).

Using pitfall traps baited with human dung, we sampled dung beetles during the rainy seasons at all sites. Along transects located at least 1 km from reserve edges, ten traps were spaced 50 m apart parallel to trails in a closed forest (Larsen & Forsyth 2005). Each trap consisted of a plastic drinking cup, 88 mm in diameter and 121 mm in height, with a Styrofoam plate suspended over it to protect the trap from rainfall. Traps were baited with 20–30 g of dung, a quantity sufficient to attract the largest dung beetles at the sites (Peck & Howden 1984). We collected the contents from the traps daily for four to six consecutive days at approximately 24 h intervals. Traps were rebaited every other day to avoid substantial desiccation (Howden & Nealis 1975). Sampling occurred at the beginning and middle of the rainy season, with five samples taking place during both time periods. A preliminary analysis showed no correlation between samples taken at different times in the rainy season; therefore, these samples were considered independent of each other. Four trails were sampled once, and five other trails were

sampled twice using the same trap locations. In the young Amazon, we sampled along three different trails at Tiputini, and two trails at Yasuní. In the old Amazon, we sampled one trail at Dimona, one trail at Km 41, and two trails at Reserva Ducke (Appendix S1).

We used volume to determine biomass because volume is easier to obtain in the field and it is an extremely accurate predictor of biomass for dung beetles (Radtke & Williamson 2005). We measured volume by inserting the tip of a number 2 insect pin into the elytron of a beetle. We then submerged the beetle in distilled water in a beaker resting on an electronic top-loading balance. The change in mass on the balance (*i.e.*, the force of the beetle to displace the water) was recorded and converted into the volume of a beetle (1 g = 1 ml of water at sea level) (Radtke & Williamson 2005, Radtke *et al.* 2006). Volume measurements were generally performed on fresh specimens immediately after collection; however, in some instances specimens were stored in 70 percent ethanol until measurements could be taken at a later time. Short-term (less than 1 yr) storage in alcohol does not affect dung beetle volume (Radtke *et al.* 2006).

We identified species using collections at BDFFP, keys and species lists (Medina & Lopera-Toro 2000, Quintero 2002), and taxonomic experts. Where specific identification was not possible, specimens were identified to genus and then assigned to a morpho-species. Specimens were deposited at the Collection of Invertebrates at the Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil and the Museum of Invertebrates at Pontificia Universidad Católica del Ecuador, Quito, Ecuador.

We examined species diversity by individual-based and sample-based rarefaction. For individual-based rarefaction, we randomly selected 90 beetles from each sample, choosing this number because it is less than the lowest number of beetles collected at any site. A Ranuni number generator was used to ensure the randomness of the rarefaction (SAS Institute 2001). We repeated this process 20 times, each time using a different seed number for the number generator. Then we took the average to arrive at a final rarefied species number for each sample. We also rarefied by sample, using EstimateS (Colwell 2005).

We used an ANOVA model to test for differences in beetle biomass and species richness between young and old soils. For beetle biomass analyses, the trap-day was considered the sampling unit. We tested for differences in the volume of beetles collected during the first and second days after adding fresh bait to a trap. A greater volume of beetles was captured on the first day than the second ( $P < 0.0001$ ). Therefore, we pooled the data from days 1 and 2, days 3 and 4, and days 5 and 6 of a trapping sequence for analysis. Biomass analyses were carried out pooling all data from each soil age class (young vs. old) for a total of nine samples (five from young soils and four from old soils). For sample-based rarefaction of species richness, we graphically compared 95% CI of the estimated species richness curves (eight in the young and six in the old Amazon).

## RESULTS

A total of 5612 beetles were trapped on young soils during 322 trap-days, whereas 769 beetles were captured during 172 trap-days on

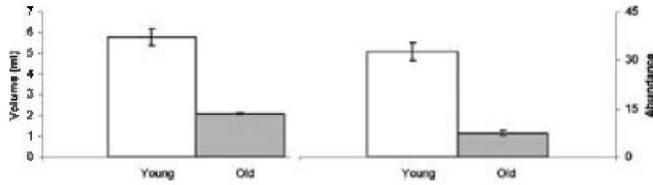


FIGURE 1. Mean  $\pm$  SE for beetle volume (ml) per trap-day (left axis) and abundance per trap-day (right axis) for geomorphologically young and old soils of the Amazon Basin.

old soils. At 17.4 beetles/trap-day, young soils supported nearly four times as many beetles as old soils at 4.5 beetles/trap-day. Curves of the number of species versus sampling effort indicated that species accumulation had slowed considerably after 4–6 d of sampling.

The ANOVA for beetle volume as a function of soil age (young or old), was significant ( $F_{1,245} = 19.5, P < 0.0001$ ). Overall beetle volume and SE for young soils was  $5.5 \pm 0.41$  ml/trap-day versus  $2.1 \pm 0.05$  ml/trap-day for the old soils. Individual sites varied: the means ranging from 3.6 to 9.3 ml/trap-day in the young Amazon and 1.3 to 3.7 ml/trap-day in the old Amazon (Fig. 1; Table 1).

Using the same ANOVA model for abundance, we found a significant difference between the abundance of dung beetles on young and old soils ( $F_{1,245} = 43.3, P < 0.0001$ ). Overall beetle abundance and SE for young soils was  $17.4 \pm 1.8$  beetles/trap-day versus  $4.5 \pm 0.4$  beetles/trap-day on old soils. Sites varied: the means

ranging from 14.0 to 20.0 beetles/trap-day on young soils and 2.2 to 7.0 beetles/trap-day on old soils (Fig. 1; Table 1).

Although we collected 80 species in the young Amazon and 36 in the old Amazon, different abundances mandated comparisons by rarefaction. Individual-based rarefied species number did not differ between young and old soils. Young soil sites ranged from 18 to 27 rarefied species per site whereas old soil sites ranged from 13 to 23 species (Table 1).

For sample-based rarefaction, we graphically compared the 95% CI from the 14 samples, using curves from EstimateS (Colwell 2005). Of 91 possible pairwise comparisons, only one pair exhibited nonoverlapping confidence intervals—the richest sample with the most depauperate sample, so statistically, the species richness estimates were not different among the 14 samples ( $1/91 = 0.01$ ).

## DISCUSSION

**BIOMASS AND ABUNDANCE.**—Our results indicate that young soils in the Amazon support 2.6 times as much dung beetle biomass as old soils. Abundance was even more exaggerated in the young Amazon, being 3.9 times that in the old Amazon. One large species, *Coprophanaeus lancifer* L., collected by us only in the old Amazon, reduced the magnitude of the biomass difference vis-à-vis the abundance difference.

For dung beetles, the samples on young Amazonian soils were more variable than samples on old soils (Fig. 1; Table 1). Trail “Chorongo1” in Yasuní yielded a much higher average beetle volume

TABLE 1. Dung beetle volume per trap-day, abundance, raw and rarefied species numbers, by sampling site.

Soil	Site	Volume per trap-day (ml)	Abundance per trap-day	Raw spp. number	Rarefied spp. number
Young	Maquisapa (early)	5.09	21.50	54	22
	Maquisapa (mid)	1.72	12.65	38	27
	Harpia (early)	4.45	21.10	52	18
	Harpia (mid)	5.81	17.25	40	21
	Chorango2	4.71	13.78	38	23
	Chorango1 (early)	2.33	4.02	25	18
	Chorango1 (mid)	18.1	43.05	52	20
	Peru	4.01	14.02	43	23
	Old	Km 41 (early)	1.80	3.77	22
Km 41 (mid)		2.44	3.46	18	18
Dimona (early)		2.03	2.82	23	23
Dimona (mid)		2.46	4.35	24	22
Station		2.59	6.97	24	19
Cidade de Deus		1.34	5.65	14	13
Young Soils Overall			5.54	5612	80
Old Soils Overall		2.12	769	36	n/a

(9.3 ml/trap-day) than did the other four volume samples taken on young soils (3.6–5.2 ml/trap-day); however, beetle volumes on old and young soils were still significantly different with 'Chorongo 1' removed from the data set ( $F_{1,201} = 20.0$ ,  $P < 0.0001$ ).

The variation among samples within a soil age may be a function of the phenology of different dung beetle species. Timing of rain, temperature, and seasonal conditions can greatly influence the dung beetle population, causing surges and declines of particular species from one week to the next (Hanski & Cambefort 1991). We tried to control for rain and seasonal differences by limiting our sampling to the early and mid-rainy seasons on each soil type. (*n.b.*, the rainy season in the Central Amazon normally begins in November, but was late in 2004, not arriving until January 2005.) We also acknowledge the difference in length of the rainy season, 7 versus 10 mo, between sites in the old and young Amazon, but we were not able to reconcile it in our sampling design. With more field research, this problem may be reduced by sampling across more old and young soil sites or sampling monthly at our sites.

Dung beetles are often considered as a bio-indicator for mammals as they rely directly on mammal excrement for food and nesting material (Gill 1991, Halffter & Arellano 2002) and respond to environmental changes (Lumaret *et al.* 1992, Favila & Halffter 1997, Carpaneto *et al.* 2005). Environmental monitoring programs have been developed with dung beetles as the focal group in some areas of the Neotropics (Celi & Davalos 2001). In this context, the greater dung beetle biomass in the young versus old Amazon may reflect differences in mammal biomass. Most dung beetle studies in the Amazon have been limited to only old or young soils, but Vulinec (1999, 2000) collected dung beetles at three sites in the Brazilian Amazon, one on young soils, and two on old soils. Beetle biomass from the young soil site was four times the biomass at her old sites, generally supporting our hypothesis. Furthermore, Vulinec *et al.* (2006) found an even larger biomass difference between várzea (generally young soil sediments) and terra firme old soils.

Several researchers have suggested similar variation in mammalian taxa. For nonvolant mammals, Emmons (1984) noted abundances of smaller species varied dramatically, generally following soil type and productivity (quantity of fruitfall), but changes in large mammal abundances were much less pronounced. Peres (1997), after surveying primate abundances across the Amazon, concluded that the geochemical gradient determining soil fertility was the best single predictor of howler monkey density, although for this taxon, he suggested low soil fertility leads to poor foliage quality, the primary food source. Total primate biomass for old soils ranged from 81 to 324 kg/km<sup>2</sup> whereas it was 590 kg/km<sup>2</sup> on young soils (Peres & Dolman 2000). Clearly, more studies of mammals, jointly with dung beetles, are needed (Vulinec 1999, 2000; Vulinec *et al.* 2006).

Abundance of other taxa also may be related to productivity of soils in the Amazon Basin. Karr *et al.* (1990) and Stouffer (2007) have noted that some bird territories are much larger in the Western Amazon than in the Central Amazon. Allmon (1991) found densities of forest floor frogs in the Central Amazon to be one-third of that at sites on young soils. Becker *et al.* (1991) noted the Central Amazon had the lowest abundances of Euglossine bees compared to young soils in Panama, Costa Rica, and Peru.

Our beetle results together with studies of other fauna suggest that young soils in the Amazon support a greater biomass and abundance of organisms than older Amazonian soils. Fluvatile sediments in the old Amazon are physico-chemically inactive and lack a weatherable mineral reserve (Sombroek 2000). In contrast, the fluvatile deposits in the young Amazon have a higher ion-exchange capacity and a reserve of weatherable minerals (Sombroek 2000, Tuomisto *et al.* 2003). Consequently, the young soils of the Amazon have the potential to be more productive. Tree turnover rates are higher in the young Amazon, which supports the hypothesis of increased productivity in the Western Amazon (Emmons 1984, Phillips *et al.* 2004). We could not examine the link between productivity and mammals and dung beetles in our study because mammal biomass is unknown for our sites; however, abundances recorded by other researchers generally conform to differences between young and old soils (Emmons 1984, Peres 1997, Peres & Dolman 2000).

**SPECIES RICHNESS.**—Individual- and sample-based rarefaction indicated no differences in beetle diversity between soils. Historically, the Western Amazon was regarded as more speciose for some taxa than the Central Amazon (Gentry 1988, Valencia *et al.* 1994). However, comparable sampling efforts in the old and young regions have demonstrated similar species richness (Cohn-Haft *et al.* 1997, Oliveira & Mori 1999, ter Steege *et al.* 2000).

We interpret our comparisons based on soil ages, as the soils of Ecuador differ in time of origin from those in Central Brazil. Soil age is determined geomorphologically and is a broad geographic feature, so it is impossible to sample both young and old soils in both the Western and Central portions of the Basin. We chose our sample sites to be comparable in other ecological factors, but it is not possible to find exact replicates in this regard. For example, our sites on young soils are wetter and slightly higher in elevation than our sites on old soils. Rainfall can increase dung beetle abundance by providing optimal reproductive and feeding conditions (Gill 1991) or decrease abundance by reducing available flight time (Peck & Forsyth 1982). In this regard, our study should be considered preliminary until the Amazon Basin can be sampled more widely.

Overall, our findings may bear importance for conservation. Current deforestation rates are much higher in the old Amazon than the young (Soares-Filho *et al.* 2006), and as continuous forests become fragmented, only remnants above threshold sizes will harbor viable populations of some mammals. Viable population sizes will depend not just on fragment size, but also on productivity. If higher productivity generates higher abundances, then proportionally larger reserves in the old Amazon will be required to sustain population sizes of mammals comparable to smaller reserves in the young Amazon.

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## SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article online at: [www.blackwell-synergy.com/toc/btp](http://www.blackwell-synergy.com/toc/btp).

Appendix S1

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