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Dung Beetle Communities: a Neotropical-North Temperate Comparison

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ABSTRACT - Dung beetle communities have been compared across north temperate latitudes. Tropical dung beetle communities appear to be more diverse based on studies using different methodologies. Here, we present results from a standardized sampling protocol used to compare dung beetle communities across five neotropical forests in Brazil and Ecuador and two warm, north temperate forests in Mississippi and Louisiana. Species richness in the tropical forests was three to seven times higher than the temperate forests, as would be expected by studies of other taxa across tropical and temperate latitudes. Average body size in the temperate forests was larger than the tropical forests, as predicted by Bergmann's rule. Dung beetle abundance and volume per trap-day were generally higher in Ecuador than Brazil, and higher in Mississippi than Louisiana, but there were no tropical-temperate differences. Species rank-abundance curves were similar within countries and between countries. Rank-volume distributions indicated a smaller range of beetle body sizes in Ecuador versus Brazil or the USA. Community similarity was high within countries and low between countries. Community differences between Brazil and Ecuador sites may be explained by differences in productivity based on geological age of the soils.

KEY WORDS: Abundance, diversity, Scarabaeidae, temperate forest, tropical forest

Ecological differences between tropical and temperate ecosystems have long been of interest to the scientific community. Increases in species richness with decreases in latitude have been documented through meta-analyses for various insect taxa (Willig *et al* 2003) although there are textbook exceptions, such as the Ichneumonidae (Janzen 1981). Here, we present the first standardized tropical-temperate comparison for dung beetles (Coleoptera: Scarabaeidae), a taxon that is an ecologically significant guild and regarded as a bio-indicator for ecosystem health (Halffter & Favila 1993, McGeoch *et al* 2002, Spector 2006). Specifically, we compare and contrast tropical and temperate dung beetle communities from five equatorial wet forests in the Amazon Basin to two warm temperate counterparts in the Southeastern USA. Tropical and temperate comparisons have not been examined for this guild, although latitudinal gradients have been described for Finland (Roslin 2001), and Lobo (2000) has aptly compiled cross-study comparisons for the Nearctic region.

Our hypotheses are based on the general ecology of New World tropical and temperate (northern or southern latitudes) dung beetles. Dung beetles are decomposers and primarily consume animal dung, although carrion, rotting fruit and other decaying material may also be eaten

(Gill 1991). First, we hypothesize that tropical forests will exhibit higher dung beetle species richness (alpha-diversity) than temperate forests, as shown by rarefaction (Buddle *et al* 2005). Second, we expect greater community similarity, measured as rank-abundance distributions, rank-volume distributions and beta-diversity within tropical forests and within temperate forests than between temperate and tropical forests. Third, as Bergmann's rule predicts larger body sizes at higher versus lower latitudes (Cushman *et al* 1993), we compare mean body size with the expectation of larger dung beetles in temperate forests than in tropical forests. Finally, in addition to abundance, we add biomass to our community comparisons within and across latitudes, as biomass is generally a better indicator of the functionality within a community (Saint-Germain *et al* 2007).

Material and Methods

To ensure standardization of sampling, we employed the same method in both north temperate and neotropical forests (Fig 1). The tropical sites, sharing similar climates, were located at equatorial latitudes in the Amazon Basin: in

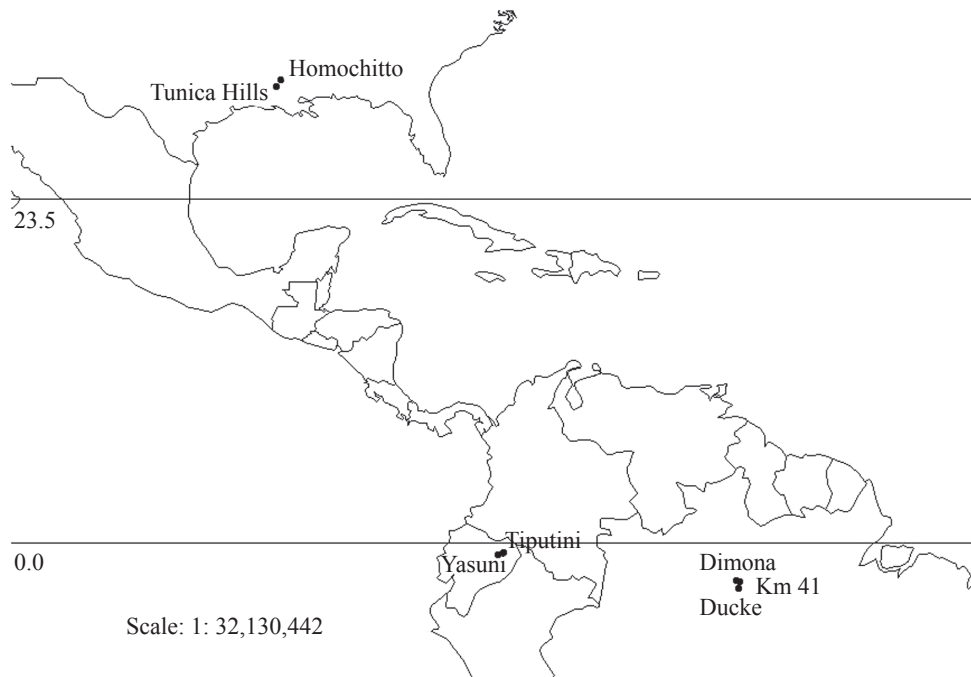


Fig 1 Map of temperate and tropical research stations.

Ecuador we sampled the Tiputini Biodiversity Station ($0^{\circ}37.149'S$ $76^{\circ}09.62'W$; $0^{\circ}37.890'S$ $76^{\circ}08.109'W$; $0^{\circ}37.961'S$ $76^{\circ}08.965'W$) and the Yasuni Research Station ($0^{\circ}40.656'S$ $76^{\circ}24.454'W$; $0^{\circ}40.553'S$ $76^{\circ}23.463'W$), and in Brazil we sampled both the Km 41 Reserve ($2^{\circ}26.952'S$ $59^{\circ}45.872'W$) and Dimona Reserve ($2^{\circ}19.973'S$ $60^{\circ}07.549'W$) at the Biological Dynamics of Forest Fragments Project (BDFFP) and the Adolfo Ducke Reserve ($3^{\circ}00.476'S$ $59^{\circ}56.867'W$; $2^{\circ}55.852'S$ $59^{\circ}58.489'W$). All five sites are closed canopy, *terra firme* (unflooded) forests. Sampling at the tropical sites was conducted during the early and mid-rainy seasons in 2004 and 2005 (see Radtke *et al* 2007 for further details). Temperate sites in the USA were Tunica Hills Wildlife Management Area (Louisiana) and Homochitto National Forest (Mississippi): at Tunica Hills, we sampled the Southeast trail, $30^{\circ}55.797'N$ $91^{\circ}30.568'W$, from 6-9 June 2006 and 19-22 August 2006, and at Homochitto, we sampled the Northwest part of the forest, $31^{\circ}26.546'N$ $91^{\circ}11.568'W$, from 6-9 August 2005. As “upland hardwood” forests, the temperate sites are covered with closed canopy forests that do not flood and are covered by broad-leaved, deciduous trees dominated by *Fagus grandifolia*, *Magnolia grandiflora* and a variety of *Quercus* species. The two sites share similar climates although Homochitto is the cooler site with a mean annual temperature of $19^{\circ}C$, and mean monthly variation of $10-27^{\circ}C$. Annual precipitation is 1500 mm distributed relatively evenly throughout the year (NOAA 1985). The tropical sites are all lowland, wet forest, with mean annual temperatures of $25-27^{\circ}C$ and mean monthly rainfall normally greater than 100 mm. Specific details of the tropical sites can be found in Radtke *et al* (2007). All forest sites, temperate and tropical, had frequent reports of large mammals and were relatively undisturbed large tracts of more than 10,000 ha in size, except for Tunica Hills (2,340 ha), although the latter is

bordered by private primary and secondary forests.

At all sites, beetles were collected in pitfall traps, baited with human dung. Ten traps, consisting of a plastic cup, 88 mm in diameter by 121 mm in height, baited with a 20-30 g ball of human dung wrapped in cheesecloth and covered with a styrofoam plate for protection from precipitation, were spaced 50 m apart along a transect (Larsen & Forsyth 2005). Traps were checked every 24h and re-baited every other day to reduce bait desiccation (Howden & Nealis 1975). A sampling period consisted of four to six days of trapping.

In several instances, more than one transect was sampled at a site, or the same transects were sampled twice, once at the beginning of the rainy season and once during the middle of the rainy season. Although these samples were considered independent of each other given their separation in time (at least one month) or in distance (> 2 km), we pooled them for most analyses. The total number of unpooled transect samples was seventeen: two at Km 41, two at Dimona, two at Reserva Ducke, one at Homochitto, two at Tunica Hills, five at Tiputini, and three at Yasuni.

We used volume as a proxy for biomass because neotropical dung beetle volume accurately predicts biomass ($biomass = 0.20volume + 0.02$) (Radtke & Williamson 2005, Radtke *et al* 2006, 2007). Each specimen's volume was determined by inserting a pin into the elytra and submerging the beetle into a beaker of distilled water resting on a top-loading, battery-powered electronic balance; the change in weight is converted directly into volume ($1\text{ g} = 1\text{ ml}$ of water at sea level) (Radtke & Williamson 2005). Volume was either measured immediately after collection, or following storage in alcohol for a few months; alcohol storage has no effect on volume (Radtke *et al* 2006) although biomass decreases (Howmiller 1972).

Species identifications were made by one of us (MGR)

by comparison with museum specimens (the Collections of Invertebrates at the Instituto Nacional de Pesquisas da Amazônia - INPA, Manaus, Brazil, and the Louisiana State Arthropod Museum - LSAM), keys (Medina & Lopera-Toro 2000), species lists (Klein 1989, Harpootlian 2001, Quintero 2002), and with the help of taxonomic experts. Where specific identifications were not possible, specimens were assigned a morphospecies designation. Specimens are deposited in the Collections of Invertebrates at INPA, Manaus, Brazil; LSAM, Baton Rouge, LA, USA; and the Museum of Invertebrates at Pontificia Universidad Católica del Ecuador, Quito, Ecuador.

To compare species richness among the seven research stations, five tropical and two temperate, we used EstimateS to construct sample-based rarefaction curves (Colwell 2005). The 95% confidence intervals for each curve were graphically reviewed to determine overlap.

To compare the average beetle size among tropical and temperate sites, we used *proc glm* in SAS (SAS Institute 2001). We compared beetle size separately for the entire family, Scarabaeidae, as well as for two genera, *Canthon* Hoffmannsegg (Coleoptera: Scarabaeidae) and *Deltochilum* Eschscholtz (Coleoptera: Scarabaeidae), that were present at all research sites. All samples within a single research station were combined, thereby yielding five tropical and two temperate sites for comparison.

To compare the volume and abundance per trap-day among tropical and temperate sites, we used *proc glm* in SAS. Preliminary analyses showed that a greater volume of beetles was captured on the first day than the second ($P < 0.0001$), so we pooled the data from days 1 and 2, days 3 and 4, and days 5 and 6 of each trapping sequence as our sampling unit for volume and abundance analyses, but report volume and abundance per trap-day. As there were no consistent differences by sampling date, all data from a particular transect were pooled to yield a total of five transects in Ecuador, four transects in Brazil, one transect in Louisiana, and one transect in Mississippi.

We constructed rank-abundance and rank-size curves, and compared frequency distributions via Kolmogorov-Smirnov two-sample tests (Sokal & Rohlf 1995). Rank-abundance curves were derived by ranking species in order from most abundant to least abundant. Rank-size distributions were constructed similarly but by using the average size (volume) of each species, rather than abundance of each species. We made three pair-wise comparisons: Ecuador vs. Brazil, Brazil vs. USA, and Ecuador vs. USA.

Beta-diversity was calculated at the genus and species levels. We chose the quantitative, root transformed Morisita-Horn (RTC_{MH}) index for our comparisons, although we calculated several other indices, all of which produced the same trends (Southwood & Henderson 2000, Magurran 2004). The RTC_{MH} index varies from 0 to 1, spanning no overlap in species composition to identical composition of communities. We calculated beta-diversity values for five pairs of research stations: the three pairs in Brazil (Dimona and Ducke, Dimona and Km 41, Ducke and Km 41), the one pair in Ecuador (Tiputini and Yasuni), and the one pair in the USA (Homochitto and Tunica Hills). Then, we combined data from research stations to calculate beta-diversity for three

pairs of geographical regions (Brazil and Ecuador, Brazil and USA, Ecuador and USA).

Results

We captured a total of 6,381 beetles during 494 trap-days in tropical forests (5,612 beetles during 322 trap-days in Ecuador, and 769 beetles in 172 trap-days in Brazil). In the temperate forest, we collected 523 beetles during 116 trap-days (387 beetles during 38 trap-days in Mississippi, and 136 beetles during 78 trap-days in Louisiana). Species richness was 104 across the tropical forests (80 in Ecuador and 36 in Brazil) and 10 across the two temperate forests (8 in Mississippi and 7 in Louisiana).

EstimateS (Colwell 2005) yielded seven species richness curves (Fig 2). The 95% confidence intervals of the five tropical samples overlapped the means of each other as did the confidence intervals and means of the two temperate samples. None of the temperate means overlapped with the tropical confidence intervals and vice versa; therefore, we conclude that the tropical and temperate species richness estimates are different from each other (Fig 2).

Average beetle body size was significantly different between temperate and tropical sites ($P = 0.027$) and varied among research stations ($P < 0.0001$) (Fig 3a). The largest average body size was 0.80 ml at Homochitto and the smallest average body size was 0.29 ml at Tiputini. For *Canthon*, we found a significant temperate-tropical difference ($P < 0.0001$) and a significant difference among research stations ($P < 0.0001$) (Fig 3b). Homochitto had the largest average body size (0.80 ml), whereas Dimona had the smallest (0.11 ml). For *Deltochilum*, we found a significant body size difference between temperate and tropical sites ($P < 0.0001$) and among research stations ($P < 0.0001$) (Fig 3c). Homochitto had the highest average *Deltochilum* body size (2.1 ml) while Dimona and Ducke had the lowest (0.5 ml).

Testing for beetle abundance per trap-day, we found a significant temperate-tropical difference ($P = 0.0004$) and a significant difference among research stations ($P < 0.0001$)

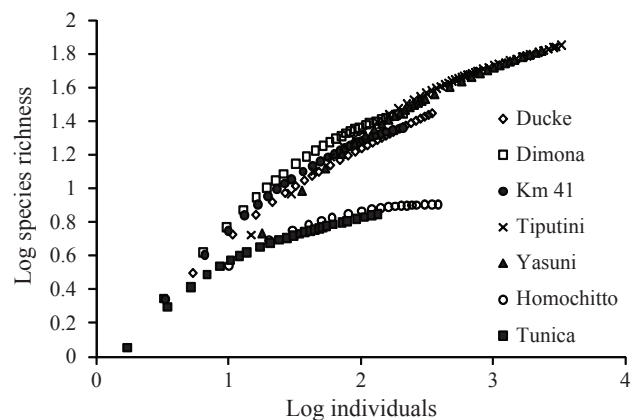


Fig 2 Species accumulation curves, derived by EstimateS, for two temperate and five tropical research stations. Brazil sites are Ducke, Dimona and Km 41, Ecuador sites are Tiputini and Yasuni, and USA sites are Homochitto and Tunica.

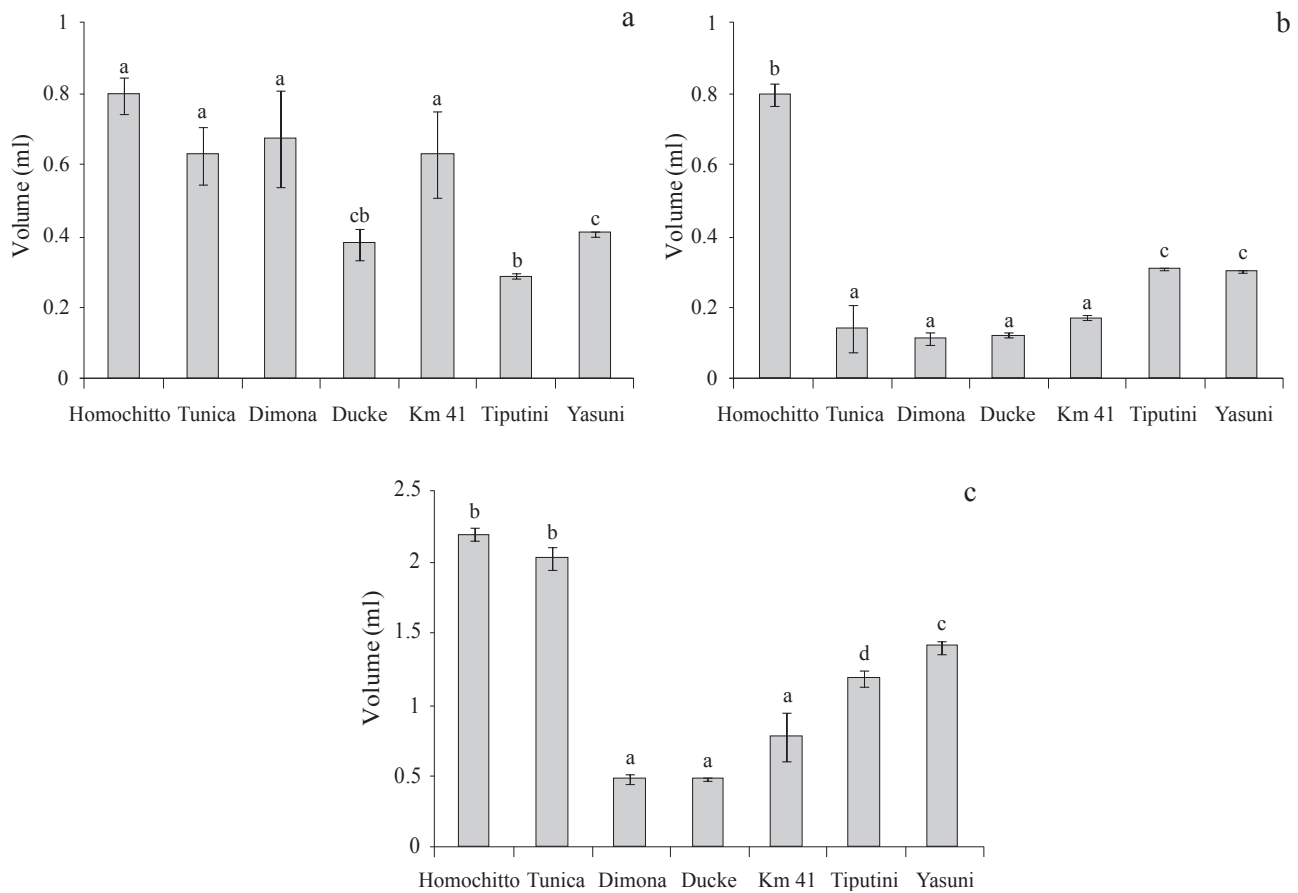


Fig 3 Average beetle body size and SE by research station for a) all beetles, b) *Canthon*, and c) *Deltochilum*. Sites with the same letter are not significantly different ($P > 0.05$) in Bonferroni comparisons.

(Fig 4a). The two Ecuadorian sites, Yasuni and Tiputini, had the highest number of beetles per trap-day, 36.4 and 30.4, respectively. Testing for volume per trap-day, we found a significant difference among research stations ($P < 0.0001$) (Fig 4b). Temperate sites dominated the extremes: Homochitto with 16.4 ml per trap-day and Tunica Hills with 2.2 ml per trap-day. There was not a significant temperate-tropical difference ($P = 0.27$).

We compared the distributions of the rank abundance curves for the following location pairs: Ecuador and Brazil, Brazil and USA and Ecuador and USA. None of the distributions were significantly different from another. Rank-size distributions for the same pairs indicated significant differences between Brazil and Ecuador ($D = 0.48 > D_{.05} = 0.27$), and Ecuador and USA ($D = 0.74 > D_{.05} = 0.46$). The comparison between Brazil

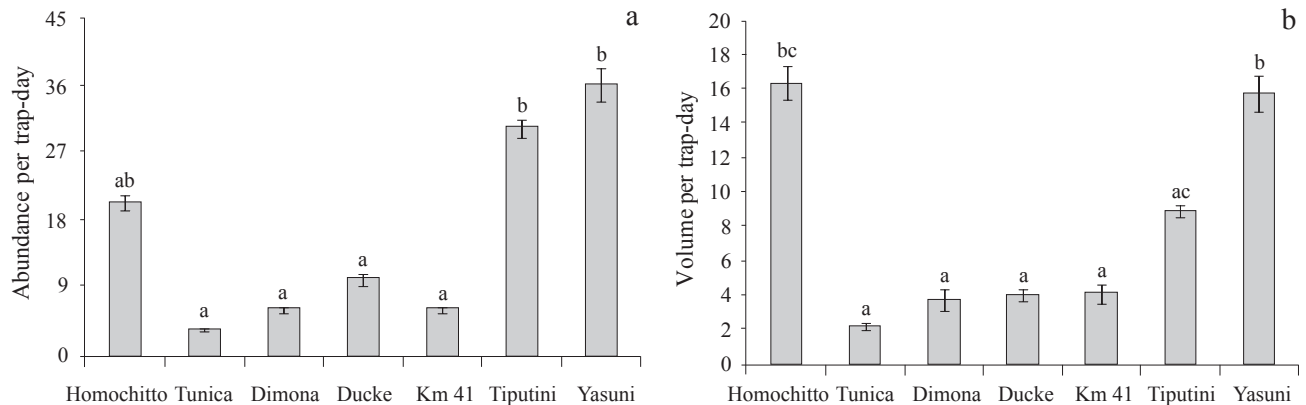


Fig 4 a) Abundance and b) volume per trap-day with SE for research stations. Sites with the same letter are not significantly different ($P > 0.05$) in Bonferroni comparisons.

and USA was not significant ($D = 0.30 < D_{.05} = 0.49$).

Beta-diversity comparisons among research sites within the same geographical region (Ecuador, Brazil, USA) yielded high similarity values. At the species level, RTC_{MH} values ranged from 0.63 to 0.92, and at the genus level, from 0.71-0.98 (Table 1). Across regions, beta-diversity dropped. Brazil and Ecuador showed low similarity at the species level (0.26) but high similarity at the genus level (0.87). Species comparisons between Brazil and USA and between Ecuador and USA were zero at the species level, whereas similarity of genera was 0.38 and 0.33, respectively.

Discussion

One of the greatest challenges in temperate-tropical comparisons is the variation in confounding factors known to influence species richness and composition – namely, habitat heterogeneity, vegetation structural diversity, seasonality, and variation in sampling methods. Here, we tried to minimize such factors by applying a common sampling scheme to dung beetles in closed canopy, old growth forests, only during the growing seasons – the rainy seasons at the tropical sites and the wet, warm summer months in the Southeastern USA.

USA temperate forests had fewer species of dung beetles than Brazilian and Ecuadorian tropical forests, as shown by the actual numbers of species collected and by the rarefaction curves (Fig 2). The curves for Mississippi and Louisiana sites appear to be close to reaching an asymptote with only eight and seven species, respectively, and a combined total of 10 species. These temperate numbers are in line with a secondary forest site slightly south, near Baton Rouge, Louisiana where only 12 species were found after sampling monthly for a full year (Radtke *et al* 2008). Other temperate sites at comparable latitudes in Texas have yielded 8 species in hackberry shrubland, 15 species in live oak/mesquite woodlands, and 16 species in woody shrublands (Nealis 1977; Howden & Scholtz 1986).

Table 1 Beta-diversity calculated as the root transformed Morisita-Horn (RTC_{MH}) values for pairs of research stations and geographical regions by genus and species.

Research station pair	Genus	Species
Within Brazil		
Dimona and Ducke	0.90	0.73
Dimona and Km 41	0.71	0.72
Ducke and Km 41	0.85	0.63
Within Ecuador		
Tiputini and Yasuní	0.98	0.92
Within USA		
Homochitto and Tunica	0.97	0.83
Between countries		
Brazil and Ecuador	0.87	0.26
Brazil and USA	0.38	0
Ecuador and USA	0.33	0

In contrast to nearly complete sampling at the temperate sites, tropical dung beetle richness, ranging from 23 to 71, for research stations in Ecuador and Brazil, was incompletely sampled because the rarefaction curves were still climbing steeply. Such curves are common in tropical diversity studies, where even in extremely large, homogenous tracts, complete community sampling is often impossible. Other studies of dung beetles in *terra firme* tropical wet forests have yielded comparable species richness, from 31 to 54 species per trap day (Peck & Forsyth 1982, Klein 1989, Andresen 2003, Spector & Ayzama 2003, Quintero & Roslin 2005). These studies varied in trap design, season of collection and bait. Still, they confirm our result that lowland, equatorial wet forests, even incompletely sampled, exhibit 3-7 times more species than the warm, temperate forests of the Southeastern USA. Tropical dry forest (cerradão) and savanna (cerrado) in southern Brazil (43°50'W 19°50'S, 900 m a.s.l.) with 13-17 species, exhibit species richness closer to our north temperate forests than to the more proximate Amazon forests (Durães *et al* 2005).

Latitudinal gradients have been observed across many taxa with the predominant pattern being an increase in species richness with decreasing latitude (Willig *et al* 2003). Lobo's (2000) North American dung beetle review is the first study that comprehensively examined dung beetle studies across a large latitudinal gradient, from British Columbia, Canada to Northern Mexico. Accounting for varied methodologies among studies, he documented a latitudinal gradient in species richness from 3 to 28. Furthermore, he showed there was a taxonomic shift in the dominant sub-family, Aphodiinae in the northern latitudes to the Scarabaeinae in the southern latitudes. On a smaller latitudinal scale in Finland, the genus, *Aphodius* Illiger (Coleoptera: Scarabaeidae), has 14 species present in the southern part of Finland and only 4 in the northern regions (Roslin 2001). Our study presents the first standardized tropical versus temperate comparison that includes warm temperate and Equatorial sites and documents that the increase in Scarabaeinae is primarily responsible for the increased diversity at the tropical sites.

One obvious difference between temperate and tropical dung beetle communities is niche specialization, perhaps as a result of competition. Dung beetles specialize on food particle size, location within or under the dung pat, age of dung pat, size of dung pat, dung quality, diel activity, seasonal activity, beetle size, and soil type (Finn & Gittings 2003). Temperate dung beetles compete highly for space below the dung pat whereas tropical beetles appear to be more limited by the food itself (Peck & Forsyth 1982, Gill 1991, Finn & Gittings 2003). Across all latitudes it is advantageous to arrive at the dung pat first to obtain enough resource, be it food or space, for consumption and reproduction. A few species entirely avoid this problem by specializing on rare types of dung, such as sloth, reptile or amphibian dung (Young 1981, Gill 1991), but most species are generalists on mammalian dung. For the vast majority of these, late arrivals have two options. They can abandon the dung pat in search of another because the limiting resource, food or space, has already been preempted by the present occupants, or they can fight for and steal the limiting resource from another beetle — i.e., interference competition. Space is a difficult commodity to steal if a nest has already been built and is

occupied, although a few species (kleptoparasites) do steal space when they parasitize provisioned nests with their own eggs (Cambefort & Hanski 1991). Food, on the other hand, is much more easily taken by force from other beetles, as shown by a number of strategies developed by various species. The different competitive pressures in tropical and temperate dung beetles may contribute to the latitudinal gradient in species richness, although the nature and degree of these interactions is beyond the scope of our study.

In general, our temperate sites had larger average body sizes than our tropical sites (Fig 3a). Tiputini, Ducke, and Yasuni had small body sizes whereas Homochitto had the largest. Tunica, which we expected to have a larger body size than tropical sites, did not differ from tropical Dimona. *Deltochilum* body size indicated a distinct tropical-temperate difference. Both Homochitto and Tunica had significantly larger average body sizes in this genus than did the tropical sites (Fig 3c). For *Canthon*, Homochitto was again the site with the largest average body size, but Tunica Hills was not different than the Brazilian stations (smallest size class). The two Ecuadorian stations were grouped together in an intermediate size class (Fig 3b). Overall, these data support a body size difference between temperate and tropical sites, although there is some variation among individual sites and across genera.

Larger arthropod body sizes in temperate latitudes (Bergmann's rule) are not uncommon. Arthropods with short developmental times relative to season length tend to follow Bergmann's rule whereas arthropods with longer developmental times do not (Blanckenhorn & Demont 2004). Most of the dung beetles in our study fall into the former category as they generally produce more than one generation per year. Second, modern body sizes may be "phylogenetic ghosts" (Cushman *et al* 1993). During the Pleistocene, the temperate forests in our study, although not glaciated, would have been much colder than they are today. Tropical forests were also cooler in the past, but not to the extent of the Southern USA. The larger size of modern beetles in North America may be an adaptation to the prolonged glaciations of the past (Cushman *et al* 1993). Last, large body sizes may be an adaptation to resist starvation in seasonal or unpredictable environments (Cushman *et al* 1993). Both tropical and temperate regions experience seasonality (rainfall and temperature, respectively) and mammals respond by decreasing their activity levels when resources are scarce, but the response in temperate mammals is probably more extreme, especially given that the tropical forests studied here are relatively aseasonal. In temperate climates, many species of dung beetles enter into diapause, a dormancy phase, during the cold months of the year (Hanski & Cambefort 1991). Larger body sizes allow for extra reserve storage and decrease the probability of starvation during times when food is scarce or unavailable (Cushman *et al* 1993).

Two additional untested hypotheses are first, if mammals follow Bergmann's rule, dung pats tend to be smaller in the tropics, so faster resource use (i.e., faster development via a smaller body size) may be more advantageous. Second, even if dung pats are the same size, faster degradation of the resource by fungi and bacteria in the tropics may have selected for faster resource use by dung beetles. Our warm

temperate sites in July and August are as warm as the Equatorial sites, but the temperate dung beetles are active also during many cooler months, March to November, when dung decay by microbes is probably much slower.

There was not a clear tropical-temperate difference for beetle volume and abundance per trap-day (Fig 4). Both Ecuadorian sites and one USA site (Homochitto) had high volumes and abundances per trap-day whereas the Brazilian sites and the other USA site (Tunica Hills) had low volumes and abundances per trap-day. The between site variation of beetle biomass for our temperate forests was as great as variation for our tropical forests. Radtko *et al* (2007) suggested biomass and abundance differences between Ecuador and Brazil may be caused by higher soil minerals and increased productivity in Ecuador, but we had no basis to postulate productivity differences in the temperate forests. Both temperate sites are located on clay and fine silt loess deposits from the Wisconsin glacial period (25,000-50,000 years ago) (Saucier 1974). Homochitto is north of Tunica Hills, but by less than 1° latitude, and the vegetation is similar. Potential productivity indices, based on soil fertility and landscape slope, were similar for several dominant tree species, ranging from 90 to 105 (Morris 1995, McDaniel 2001). Hunting occurs in both temperate reserves, but it is regulated. However, Tunica Hills is partially surrounded by land owned by a private club where hunting regulations may be less enforced, so additional hunting pressure at Tunica Hills may explain the reduced dung beetle abundance and volume relative to Homochitto, although we selected this site on an *a priori* expectation of no significant hunting.

We did not find any differences in the rank-abundance curves between regions (Brazil and Ecuador, Brazil and USA, Ecuador and USA). This was somewhat surprising given the vast differences in number of species collected (10-71). We did find a significant difference in the rank-size curves for Brazil and Ecuador, and Ecuador and the USA, suggesting a variation in beetle size composition within each country. Specifically, Ecuador lacks some of the larger bodied dung beetles that are present in Brazil and the USA. Rates of nutrient recycling (Mittal 1993), secondary seed dispersal (Andresen 2003), and mammal parasite control may be affected by the size of dung beetles in the community (Larsen *et al* 2005); however, forests with small beetles, such as Ecuador, may generate the same overall ecosystem effects if they have elevated numbers of small beetles.

As expected, we found relatively high species similarity between pairs of research stations within each country. Beta-diversity, originally proposed as a measure of diversity along a gradient, has been generalized to a measure of species differences and turnover rates across geographical locations (Veech *et al* 2002). Spector (2002) measured dung beetle beta-diversity across sites in Parque Nacional Noel Kempff Mercado where he found 143 species, but on average, only 29.4 species were present at any single site. Morisita-Horn similarity values for dung beetles between pairs of different forest types at Parque Nacional Noel Kempff Mercado were between 0.64 and 0.97, indicating high community similarity (Forsyth *et al* 1998). Our tropical samples were all from one forest type, lowland rainforest, but they exhibited comparable Morisita-Horn Index values between sites, 0.63-0.73 in Brazil

and 0.92 in Ecuador. Between Ecuador and Brazil, we found much lower similarity, 0.26, so distance is important, even if forest type is constant. Index values between our tropical sites and the USA were zero as there were no species in common; the sites represent different forest types, separated by great distances.

When communities are vastly different, comparisons at the generic level may offer more information about ecological composition than comparisons at the species level (Oliveira & Nelson 2001). At the generic level, similarities between our USA and tropical countries were also low (0.33-0.38) compared to beta-diversity values within temperate or tropical regions (0.71-0.97). Temperate forests supported 10 species in six genera, whereas tropical forests supported 104 species in 18 genera. In all instances where genera were shared, tropical forests had greater species richness than temperate forests. These observations appear to satisfy multiple hypotheses explaining latitudinal gradients in species diversity (Willig *et al* 2003).

Brazil and Ecuador had a similarity index of 0.26. Species overlap –the number of species common to both regions divided by the total number of species– was 9.5%. Studies of Amazonian trees over comparable distances in Peru and Ecuador have indicated greater species overlap– 66% (Pitman *et al* 1999), 33% (Pitman *et al* 2001), and 19-20% (Chave *et al* 2002, Condit *et al* 2002). Seasonality and climate differences have been suggested as causes of high beta-diversity in other tropical forests (Davidar *et al* 2007), but our sites in Brazil and Ecuador were very similar in both factors. We suggest the geology of our sites may explain the low species overlap in dung beetles relative to the tree studies. The aforementioned tree studies were conducted in the Western Amazon where soils are all geologically young; however, tree species composition changes more rapidly from the Western to the Central Amazon than along a North-South gradient within the Western Amazon (Steege *et al* 2000). Several other studies have suggested that the geological age (translates into nutrient availability) of the Amazon may affect regional productivity which in turn affects the local community composition (Emmons 1984, Peres 1997, Peres & Dolman 2000, Radtke *et al* 2007, Stouffer 2007). Species may be adapted for limited productivity in the old Amazon and elevated levels of productivity in the young Amazon. Consequently, the effect of distance on beta-diversity may depend on whether the sites have different or similar geomorphologies. Obviously, more extensive sampling is needed to test these hypotheses.

Overall, the strongest conclusions of our study are that New World dung beetle species richness in wet tropical forests is at least three to seven times that of wet temperate forests and that dung beetle body size is generally larger in temperate regions than tropical regions, following Bergmann's rule. The species richness differences were established by use of taxon sampling curves (Buddle *et al* 2005). These results are reinforced by our use of standardized methodology to collect dung beetles at all sites. Furthermore, our study is one of a handful of community comparisons that incorporate biomass as well as abundance and diversity (Saint-Germain *et al* 2007.) The main weakness of our study is the small number of temperate (2) and tropical (5) sites; more sites would

strengthen our conclusions, potentially resolving conflicting results on beetle volume and abundance. Our study is the first large-scale Scarabaeidae tropical-temperate comparison and fills a void in dung beetle studies. Lobo's (2000) review of North American studies provides greater detail across the cooler latitudes. We expect further research in the tropics to improve our resolution of global patterns.

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