



# Biogeographic patterns and conservation priorities for the dung beetle tribe Phanaeini (Coleoptera: Scarabaeidae: Scarabaeinae) in Bolivia

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**Abstract.** 1. The New World Phanaeini are the best known Neotropical dung beetle tribe and a conservation priority among the Scarabaeinae, an ideal focal taxon for biodiversity research and conservation.

2. We compiled a comprehensive distributional database for 39 phanaeine species in Bolivia and assessed patterns of species richness, body size and endemism in relation to abiotic variables and species richness and body mass of medium to large mammals across nine ecoregions.

3. Pair-wise linear regressions indicated that phanaeine richness, mean size and endemism are determined by different factors. In all cases mammal body mass had greater explanatory power than abiotic variables or mammal richness. Phanaeine richness was greater in ecoregions with on average smaller mammals and greater mammal richness. Mean phanaeine size increased with mean body mass of the largest herbivorous and omnivorous mammals. Endemism was greater in ecoregions with on average smaller herbivorous and omnivorous mammals. On average, smaller phanaeines had more restricted distributions than larger species; ecoregional endemism and mean body size were negatively correlated.

4. Large phanaeines probably depend on large mammals to provide adequate food resources. Greater richness of smaller mammal species may allow for greater temporal and spatial resource partitioning and therefore greater phanaeine species richness. Low numbers of large mammal species may favour the persistence of geographically restricted phanaeine species by reducing interspecific competition with larger, more geographically widespread and presumably dominant phanaeines.

5. Cerrado, Southwest Amazonia and Yungas are priority ecoregions for phanaeine conservation due to high total and endemic species richness.

**Key words.** Body size, ecoregions, endemism, macroecology, Neotropics, species richness.

## Introduction

Understanding patterns and processes underlying species distributions is fundamental to ecology and biodiversity conservation. In the highly diverse Neotropics, research on species richness and biogeographic patterns and their

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underlying causes has largely focused on a limited number of higher taxa including vascular plants, birds and mammals (e.g. Rahbek, 1997; Patterson *et al.*, 1998; Pennington *et al.*, 2000; Kessler, 2001; McCain, 2004; Herzog & Kessler, 2006; Young *et al.*, 2009). The same taxonomic bias applies to the identification of priority areas for conservation in and beyond the region (e.g. Myers *et al.*, 2000; Myers, 2003; but see Spector, 2002; Kohlmann *et al.*, 2007). Among invertebrates and particularly insects, which comprise the vast majority of known biodiversity on Earth, some groups have received increasing attention in recent years (e.g. Brehm *et al.*, 2003; Escobar *et al.*, 2007; Kubota *et al.*, 2007), but studies on insect macroecology and conservation biogeography in the Neotropics and elsewhere are still vastly underrepresented (Diniz-Filho *et al.*, 2010).

Scarabaeine dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) have repeatedly been proposed as an ideal focal taxon for biodiversity research and conservation (Halffter & Favila, 1993; Spector & Forsyth, 1998; Spector, 2006). They can be sampled quantitatively with a standardised protocol, are taxonomically relatively accessible, have a broad geographical distribution, display a range of responses to environmental change and habitat disturbance, are of ecological and economical importance and their geographical patterns of species richness and endemism match general trends in overall diversity (Spector, 2006; and references therein). In addition, they are relatively diverse and abundant at most sites, especially in the tropics; sampling is rapid, straightforward, and inexpensive, resulting in high cost-effectiveness of dung beetle surveys (Gardner *et al.*, 2008); they are sensitive to declines in persistently hunted large mammal populations (Andresen & Laurance, 2007; Nichols *et al.*, 2009); and they have been used effectively to identify conservation priority areas (Kohlmann *et al.*, 2007).

The Phanaeini are the best known scarabaeine dung beetle tribe in the Neotropics in terms of their taxonomy and general distribution of species (see Edmonds, 1972, 1994, 2000; Arnaud, 2002; Edmonds & Zidek, 2004, 2010; Philips *et al.*, 2004). They are endemic to the Americas (Davis *et al.*, 2002) and are largely comprised of tunnelers (Davis & Scholtz, 2001; Philips *et al.*, 2004) that bury dung in tunnels excavated directly below droppings. Because of their large average body size relative to species in other dung beetle tribes, phanaeines are likely to be particularly important for ecological processes such as secondary seed dispersal and parasite regulation (Nichols *et al.*, 2008) and for ecosystem functioning (Larsen *et al.*, 2005), making them a conservation priority among the Scarabaeinae. The approximately 160 species of Phanaeini are usually characterised by bright metallic colours, considerable sexual dimorphism and conspicuous cephalic and pronotal armament (Arnaud, 2002; Philips *et al.*, 2004). In part due to their charismatic appearance, phanaeines are relatively well studied and well represented in collections. For Bolivia, a recent extensive review of the distribution and natural history of phanaeines

reported the occurrence of 39 species in the country (Hamel-Leigue *et al.*, 2009).

Analytical studies on Neotropical dung beetle diversity gradients have so far focused on elevational variation in species richness and composition (Lobo & Halffter, 2000; Escobar *et al.*, 2005, 2007). Global-scale studies on dung beetle diversity and historical biogeography (Davis & Scholtz, 2001; Davis *et al.*, 2002) also contributed general insights for the Neotropical region. However, comprehensive analyses for individual Neotropical countries or biogeographic regions are lacking (but see Kohlmann *et al.*, 2007). Similarly, very little has been published on Bolivian dung beetle communities. With the exception of Spector and Ayzama (2003), who examined ecotonal species turnover in far eastern Bolivia, studies published to date reported on inventories from a handful of selected localities (Kirk, 1992; Gutiérrez & Rumiz, 2002; Quinteros *et al.*, 2006; Hamel-Leigue *et al.*, 2008; Vidaurre *et al.*, 2008).

Species distributions are often influenced by abiotic factors, especially temperature and precipitation, which vary across regions. Dung beetle diversity and abundance can also be determined by mammal abundance, diversity and size (Hanski & Cambefort, 1991). In West African savannas, for example the diversity and average size of dung beetles was highest at sites with a diverse mammal fauna and lowest at sites with only small mammals and humans, and the average size of dung beetles was correlated with the average size of mammals (Cambefort, 1991). In Mexican tropical rain forest fragments and agricultural habitats the number of species and individuals of dung beetles correlated closely with the species richness of non-volant mammals (Estrada *et al.*, 1998). However, most evidence indicates that dung abundance is more important than mammal diversity *per se* for sustaining beetle diversity (Hanski & Cambefort, 1991; Estrada *et al.*, 1999). In the Neotropics, no dung beetle species are known to be attracted to the dung of only one vertebrate species (Hidalgo & Cárdenas, 1996; Larsen *et al.*, 2006). Strong species-specific preferences for dung type do not seem to exist, and human dung attracts the same beetles as monkey dung (Howden & Nealis, 1975; Estrada *et al.*, 1993). In addition, large beetle species prefer large dung baits, and small dung may not provide adequate food (Peck & Howden, 1984; Lumaret *et al.*, 1992).

In the present study we assessed biogeographic patterns of species richness, body size, species composition and endemism of Bolivian phanaeines in relation to abiotic variables vs. species richness and body mass of medium to large mammals across nine Bolivian ecoregions (Ibisch *et al.*, 2003). On the basis of biogeographic patterns, we also identify priority ecoregions for conservation. Ecoregions currently represent the smallest spatial scales for which adequate phanaeine sample coverage exists for country-wide analyses (see Hamel-Leigue *et al.*, 2009). Ecoregion classifications are increasingly used for effective conservation planning and management at large spatial scales (Noss, 1996; Olson & Dinerstein, 1998; Olson *et al.*,

2001; Magnusson, 2004; Herzog *et al.*, 2005; Loyola *et al.*, 2007; Larrea-Alcázar *et al.*, 2010; Twedt *et al.*, 2010), and Bolivia is one of few South American countries for which a detailed nation-wide ecoregion classification exists (Ibisch *et al.*, 2003).

## Materials and methods

### Locality data

We compiled a distributional database of the occurrence of 39 phanaeine species based on 178 georeferenced Bolivian collecting localities (see Hamel-Leigue *et al.*, 2009); one additional locality (without information on collecting methods) could not be georeferenced, but was assigned with certainty to an ecoregion and included in the analyses. Five localities that could not be georeferenced or assigned with certainty to a given ecoregion due to ambiguous information were excluded. The minimum distance between localities was 1.0 km; collecting sites or transects with a spatial proximity of <1.0 km were combined to form a single locality.

Data sources included literature accounts (see Hamel-Leigue *et al.*, 2006, 2009), unpublished collecting work and reference collections of the authors, which accounted for 89 (50%) of the 179 localities, and specimens in six museums (see Hamel-Leigue *et al.*, 2009; for details) reviewed by ACHL, DJM and THL. Species determinations were made by ACHL, THL, DJM, BDG and WDE. Geographical coordinates and elevation of localities sampled by the authors were determined in the field using hand-held GPS units and, in some cases, altimeters. Museum specimen and literature localities lacking specific coordinates or elevation were georeferenced based on the site description provided, using topographic maps, Google Earth and gazetteers (e.g. Paynter, 1992), combined with the knowledge of Bolivian geography and topography of the authors.

### Ecoregions

Bolivia covers an area of 1 098 581 km<sup>2</sup> and is located on the transition from tropical to subtropical regions spanning a 1460-km latitudinal gradient from about 9°40' S to 22°52' S. It covers an elevational gradient that ranges from about 80 m in the eastern lowlands to 6542 m in the Andes in the southwest of the country. Consequently, a great diversity of terrestrial ecosystems and habitats exists in Bolivia. We used ecoregion type to describe this diversity, following the ecoregion classification of Ibisch *et al.* (2003; with slight modifications, see below), who recognised a total of 12 Bolivian ecoregions (Fig. 1; Table 1). These ecoregions largely correspond to those of Olson *et al.* (2001; see Table 1) but are mapped at a much finer spatial scale (country vs. global scale respectively). Two ecoregions were excluded: Prepuna, for which we did not

find any evidence of dung beetle sampling, and Southern Puna (situated at elevations above 3500 m a.s.l. on the Altiplano in southwest Bolivia), which appears not to host any phanaeine species based on limited collecting work in this region by ACHL. Due to low sampling intensity and only one recorded species, Northern Puna was excluded from statistical analyses.

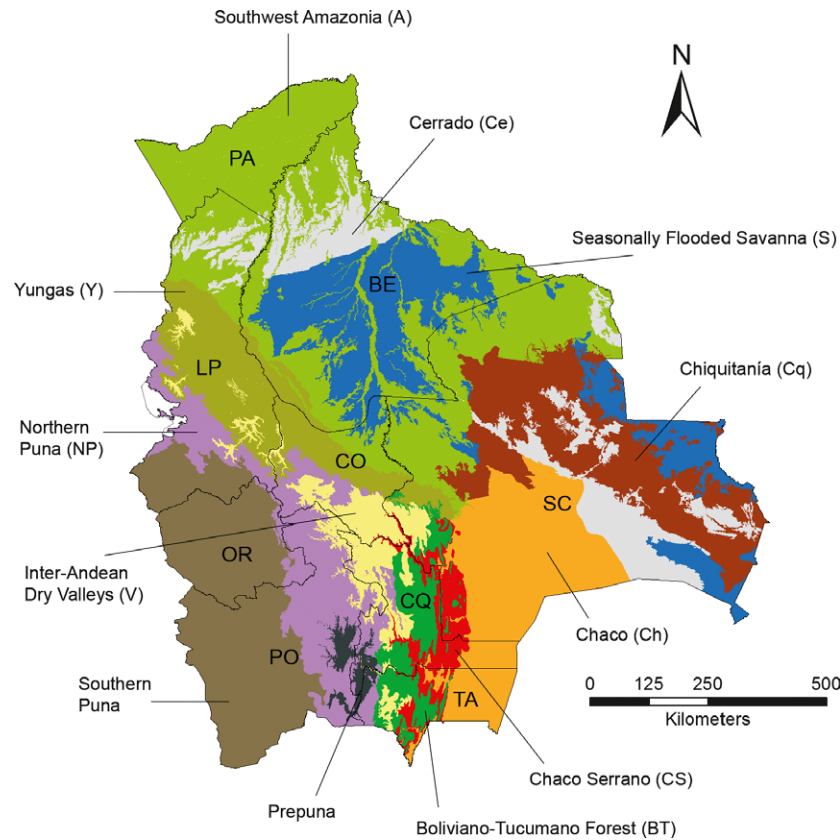
The limit between the ecoregions Southwest Amazonia and Yungas was modified as follows. Ibisch *et al.* (2003) considered the humid Andean foothills (500–1000 m, Sub-Andean Amazonian Forests subecoregion) as part of the Southwest Amazonia ecoregion. However, a newer classification of northern and central Andean ecosystems (Cuesta & Becerra, 2009; Josse *et al.*, 2009) treats these sub-Andean forests as Andean cloud forest ecosystems down to an elevation of 600 m in Bolivia. In addition, in animal taxa such as birds a number of exclusively Andean species extend down to the humid foothills, but are absent from flat Amazonian terrain away from the first Andean ridges (see Hennessey *et al.*, 2003; Herzog *et al.*, 2005). Therefore, we included the Sub-Andean Amazon Forests subregion in the Yungas ecoregion.

### Species richness

Each collecting locality was assigned according to ecoregion. Some localities were situated on the transition between two ecoregions (within *ca.* 5 km of the boundary), and they were assigned to both regions. Based on locality records we determined the presence of all phanaeine species in each ecoregion. Species collected in localities on the transition between two ecoregions were assigned to either region only if they had also been collected in at least one other, non-transitional locality of that region.

Because some data sources (especially museum collections) are likely to provide information only on species presence possibly resulting in false-absence data, we determined the number of localities per ecoregion that were sampled systematically using pitfall trap transects or by intensive manual collecting at dung pats (Table 2) vs. localities with only opportunistic manual collecting or without information on collecting methods. To account for differences in sampling effort and potential differences in heterogeneity between ecoregions, we used incidence-based species accumulation curves combined with species richness estimation for systematically sampled localities in each ecoregion. Sample accumulation order was randomised 50 times and species richness estimates were computed using *EstimateS* 8.0.0 (Colwell, 2006).

We examined the results of six estimators based on the recommendations of Herzog *et al.* (2002) and Hortal *et al.* (2006): incidence-based coverage estimator, Chao 2, Jackknife 1 and 2 (first- and second-order jackknife estimators), Bootstrap and MMMeans (nonparametric Michaelis-Menten estimator). Jackknife 2 and MMMeans were discarded because they produced inconsistent estimates



**Fig. 1.** Distribution of 12 ecoregions in Bolivia based on Ibisch *et al.* (2003). See text for the modification of the limit between Southwest Amazonia and Yungas. Political divisions (departments): BE = Beni; CO = Cochabamba; CQ = Chuquisaca; LP = La Paz; OR = Oruro; PA = Pando; PO = Potosí; SC = Santa Cruz; TA = Tarija.

**Table 1.** Abiotic characteristics of 10 Bolivian ecoregions of Ibisch *et al.* (2003), number of collecting localities and species occurrence records (No. of L & OR;  $N = 179$  and  $473$ , respectively) and corresponding ecoregions of Olson *et al.* (2001; see also <http://www.worldwildlife.org/science/wildfinder/>). The Prepuna and Southern Puna of Ibisch *et al.* (2003) are excluded because we did not find any evidence of dung beetle sampling in these ecoregions. Chaco Serrano was not recognised by Olson *et al.* (2001), but included in Chaco NT0210 and Bolivian montane dry forest NT0206. Yungas includes the subecoregion Subandean Forests, which was included in Southwest Amazonia by Ibisch *et al.* (2003); see text for details. Area values were taken from Ibisch *et al.* (2003). Elevation values are based on elevations of all georeferenced collecting localities of phanaeine dung beetles in the respective ecoregion. Climate variables were extracted from the Bolivian SAGA climate model (Kessler *et al.*, 2007; Soria-Auza *et al.*, 2010) for georeferenced collecting localities. MAP = mean annual precipitation; MAT = Mean annual temperature.

Ecoregion (acronym)	Area (km <sup>2</sup> )	Mean elevation (range) (m)	MAP (range) (mm)	MAT (range) (°C)	No. of L & OR	Olson <i>et al.</i> (2001) ecoregions
Southwest Amazonia (A)	253 018	257 (430)	2050.5 (8002.1)	25.8 (2.8)	65, 230	NT0166
Boliviano-Tucumano Forest (BT)	29 386	1704 (1700)	1175.8 (1165.0)	17.6 (12.1)	7, 12	NT0165
Cerrado (Ce)	84 967	528 (700)	1444.1 (1216.3)	24.2 (4.3)	12, 59	NT0704
Chaco (Ch)	105 006	527 (580)	814.9 (936.0)	24.3 (2.6)	26, 42	NT0210
Chiquitania (Cq)	101 769	271 (210)	1179.9 (483.9)	25.5 (0.7)	7, 20	NT0212
Chaco Serrano (CS)	23 176	855 (700)	829.5 (740.5)	22.6 (3.1)	12, 15	–
Northern Puna (NP)	84 606	3593 (1015)	854.7 (1132.5)	7.1 (5.0)	10, 10	NT1002 & NT1003
Seasonally Flooded Savanna (S)	127 988	163 (90)	1469.5 (879.6)	26.2 (1.3)	19, 55	NT0702 & NT0907
Inter-Andean Dry Valleys (V)	44 805	2223 (2000)	576.9 (501.9)	15.0 (11.0)	21, 30	NT0206
Yungas (Y)	79 085	1035 (1850)	3288.7 (7840.2)	22.0 (11.5)	30, 70	NT0105



**Table 2.** Number of collecting localities, observed and estimated species richness, mean body size (total length) and endemism scores (calculated as the inverse of the mean number of ecoregions inhabited for all constituent species of a given region) of phanaeine dung beetles in each of 10 Bolivian ecoregions. Species richness estimates were computed with *EstimateS* 8.0.0 (Colwell, 2006) using incidence-based species accumulation curves for systematically sampled localities (50 randomisations of sample accumulation order).

Ecoregion (acronym)	No. of localities <sup>†</sup> ( <i>N</i> = 179)	No. of species <sup>‡</sup> ( <i>N</i> = 39)	ICE	Chao 2	Jackknife 1	Bootstrap	Mean estimate	Mean body size (mm)	Endemism score
Southwest Amazonia (A)	65 (43)	22 (22)	22.4	22.0	23.0	23.1	22.6	20.4	0.328
Boliviano-Tucumano Forest (BT)	7 (6)	3 (3)	3.7	3.0	3.8	3.4	3.5	17.5	0.333
Cerrado (Ce)	12 (9)	19 (18)	20.2	19.1	21.6	19.9	20.2	21.1	0.322
Chaco (Ch)	26 (10)	11 (10)	15.1	13.0	14.5	12.0	13.6	22.1	0.297
Chiquitania (Cq)	7 (6)	9 (9)	11.3	9.4	11.5	10.5	10.7	23.1	0.231
Chaco Serrano (CS)	12 (6)	4 (4)	6.4	4.4	5.67	4.8	5.3	24.4	0.250
Northern Puna (NP)	10 (2)	1 (1)	–	–	–	–	–	–	–
Seasonally Flooded Savanna (S)	19 (13)	11 (11)	11.5	11.0	11.9	11.8	11.6	20.2	0.306
Inter-Andean Dry Valleys (V)	21 (10)	3 (3)	3.0	3.0	3.0	3.1	3.0	19.6	0.300
Yungas (Y)	30 (23)	12 (12)	13.4	13.5	14.9	13.3	13.9	17.3	0.353

ICE, incidence-based coverage estimator.

<sup>†</sup>Numbers in parentheses indicate the number of localities inventoried systematically.

<sup>‡</sup>Numbers in parentheses indicate the total number of species recorded in systematically inventoried localities ( $S_{\text{obs}}$ ).

at maximum sample size for some ecoregions, which were either lower than  $S_{\text{obs}}$  or unreasonably high (both in absolute terms and relative to values returned by the other estimators). As an estimate of total species richness in each ecoregion, we calculated the mean of the estimates of the four remaining estimators at maximum sample size (Table 2).

To determine to what degree sampling effort might bias analyses, we examined the relationship of the number of all and of systematically inventoried localities per region with ecoregion area (Pearson correlation).

### Body size

We used length (measured in dorsal aspect from pygidium to anterior margin of clypeus), which is highly correlated with width and depth (A. C. Hamel-Leigue and S. K. Herzog, unpubl. data), as a measure of body size because it is the most accurate predictor of biomass in dung beetles (Radtke & Williamson, 2005). For 24 species we measured (to the nearest 0.1 mm) between 6 and 107 specimens per species using digital callipers, with an approximately equal ratio of males and females, and determined the arithmetic mean for each species (Table 3). For 15 species with <6 specimens available to us (Table 3) we additionally obtained length values from the literature (Olsoufieff, 1924; Blut, 1939; Martínez & Pereira, 1960; Edmonds, 1994, 2000, 2008; Arnaud, 2002; Edmonds & Zidek, 2004) and used the mid-point between the minimum and maximum value (rounded to the nearest 0.5 mm) for each species as a proxy for the arithmetic mean. Based on individual species' means we determined the mean body size of all species (mean of the species means) for each ecoregion.

### Endemism

As an estimate of the level of ecoregional endemism that is independent of species richness we first determined for each species the total number of ecoregions it inhabits, followed by calculating the inverse of the mean number of ecoregions inhabited for all constituent species of a given region. This resulted in low endemism scores for regions with mostly ecoregionally widespread species and high endemism scores for those regions containing more narrowly distributed species.

### Explanatory variables

For each ecoregion we analysed three sets of explanatory variables. The first set included five abiotic variables: area, mean annual precipitation, mean annual precipitation range, mean annual temperature, mean annual temperature range. Area values were taken from from Ibisch *et al.* (2003). Climate variables were extracted from the Bolivian SAGA climate model (Kessler *et al.*, 2007; Soria-Auza *et al.*, 2010) with a resolution of 30 arc s for all georeferenced collecting localities. Because of extreme collinearity between elevation and temperature (Pearson  $r = 1.0$  for mean values, 0.98 for range values) no elevational variables were included.

For the second and third set of explanatory variables we extracted data on the species richness and mean body mass, respectively, as well as diet of medium to large mammal species ( $N = 110$ ) in each ecoregion from Wallace *et al.* (2010). Species richness variables included: total number of species, number of herbivores and omnivores combined ( $N = 72$ ), total number of species in the upper

**Table 3.** Distribution by ecoregion, elevation and mean body size (length measured from pygidium to anterior margin of clypeus) of 39 phanaeine dung beetle species in Bolivia. For ecoregion acronyms see Tables 1 and 2.

Species	No. of locality records	Ecoregions	Elevational range (m)	Mean body size <sup>†</sup> (mm)
<i>Bolbites onitoides</i> (Harold, 1868)	8	Ch	300–800	16.7 (6)
<i>Coprophanaeus acrisius</i> (MacLeay, 1819)	10	A, Ce, S	150–900	27.0 (2)
<i>C. bonariensis</i> (Gory, 1844)	7	Ce, Ch, Cq, CS	200–950	31.9 (7)
<i>C. caroliae</i> (Edmonds, 2008)	1	Y	1250–1350	19.5 (1)
<i>C. cyanescens</i> (Olsoufieff, 1924)	9	A, Ce, Ch, Cq	200–900	22.0 (12)
<i>C. ensifer</i> (Germar, 1821)	14	A, Ce, Ch, Cq	200–800	45.5 (1)
<i>C. ignecinctus</i> (Felsche, 1909)	7	Y	700–1800	19.6 (38)
<i>C. lancifer</i> (Linnaeus, 1767)	8	A	100–300	39.6 (61)
<i>C. magnoi</i> (Arnaud, 2002)	6	S	150–200	20.4 (7)
<i>C. pessoai</i> (Pereira, 1949)	1	Ch	250	17.5 (0)
<i>C. suredai</i> (Arnaud, 1996)	3	A	100–150	18.5 (0)
<i>C. telamon</i> (Erichson, 1847)	38	A, Ce, (Ch), S, Y	100–1150	21.5 (61)
<i>Dendropaemon</i> nr. <i>bahianus</i> (Harold, 1868)	1	A	300	10.3 (0)
<i>D. denticollis</i> (Felsche, 1909)	2	S, A?	150–400	8.0 (1)
<i>D. pauliani</i> (Martinez & Pereira, 1960)	1	Ch	~300–400	13.0 (0)
<i>D. viridis</i> (Perty, 1830)	1	Ce	700–800	18.0 (0)
<i>Diabroctis mimas</i> (Linnaeus, 1758)	15	A, Ce, Ch, Cq, CS, S	100–1300	24.1 (17)
<i>D. mirabilis</i> (Harold, 1877)	1	Ce	700–800	18.5 (2)
<i>Gromphas aeruginosa</i> (Perty, 1830)	8	A, Ch, Cq, S	200–500	13.7 (6)
<i>G. lacordairei</i> Brullé, 1834	6	A, Ch, S	150–600	12.9 (39)
<i>Oruscatus davus</i> (Erichson, 1847)	12	BT, NP, V, Y	2050–4000	17.4 (24)
<i>Oxysternon conspicillatum</i> (Weber, 1801)	55	A, Ce, Ch, Cq, S, (V), Y	100–1150 (~1750–2600)	23.7 (60)
<i>O. lautum</i> (Macleay, 1819)	17	A, S	150–200	22.5 (60)
<i>O. palaemon</i> (Laporte, 1840)	8	A, Ce	200–800	14.3 (24)
<i>O. silenus</i> (Laporte, 1840)	34	A, Ce, Cq, (V), Y	100–1150 (~2400–2600)	16.8 (64)
<i>O. spiniferum</i> (Laporte, 1840)	5	A, Y	250–1300	11.0 (1)
<i>O. striatopunctatum</i> (Olsoufieff, 1924)	2	Ce	450–800	12.0 (2)
<i>Phanaeus alvarengai</i> (Arnaud, 1984)	7	A, Ce	100–450	17.5 (3)
<i>P. bispinus</i> (Bates, 1868)	23	A, Ce, Y	100–800	14.8 (11)
<i>P. cambeforti</i> (Arnaud, 1982)	4	A, Y	100–700	14.2 (6)
<i>P. chalcomelas</i> (Perty, 1830)	44	A, (BT), Ce, Cq, Y	100–1000 (1650)	14.7 (49)
<i>P. kirbyi</i> (Vigors, 1825)	7	A, Ce, Cq	200–900	15.2 (13)
<i>P. lecourti</i> (Arnaud, 2000)	4	Y	1300–1800	18.6 (8)
<i>P. meleagris</i> (Blanchard, 1845)	17	BT, Y	350–1600	15.5 (90)
<i>P. melibaeus</i> (Blanchard, 1845)	2	Ce	450	14.5 (2)
<i>P. palaeno</i> (Blanchard, 1845)	8	A, Ce, S	200–900	15.5 (1)
<i>Sulcophanaeus batesi</i> (Harold, 1868)	30	(A), BT, CS, (S), V	(150–400) 600–3300	19.6 (107)
<i>S. faunus</i> (Fabricius, 1775)	30	A, (BT), Ce, S	100–900 (1650)	33.4 (31)
<i>S. imperator</i> (Chevrolat, 1844)	16	Ch, CS, V	300–2600	21.9 (7)

<sup>†</sup>Numbers in parentheses indicate the number of specimens measured by the authors (ACHL, BDG). For  $N > 5$ , body size values are based exclusively on those measurements. For the remaining species data were supplemented with values from the literature (see text).

body mass quartile (i.e. the largest 25% of all species; body mass range: 8.9–215.0 kg,  $N = 28$ ) and number of herbivores and omnivores in the upper body mass quartile ( $N = 19$ ). The corresponding variables of the third set included mean body mass of all species, of herbivores and omnivores combined, of species in the upper body mass quartile and of herbivores and omnivores in the upper body mass quartile.

For each set of explanatory variables we used Pearson correlations to determine the degree of collinearity between variables. In the first (abiotic) set, three correlations were significant: mean annual temperature vs. mean annual temperature range ( $r = -0.85$ ), mean annual

precipitation vs. mean annual precipitation range ( $r = 0.81$ ) and area vs. mean annual temperature ( $r = 0.69$ ); all other correlation coefficients were  $\leq 0.50$ . In the second set (mammal species richness), all pair-wise correlation coefficients were  $\geq 0.75$  and significant. In the third set (mean body mass of mammals), two pair-wise correlation coefficients were significant: all species vs. herbivores and omnivores ( $r = 0.80$ ) and vs. species in the upper body mass quartile ( $r = 0.73$ ); all other correlation coefficients were  $\leq 0.39$ . Significant collinearity also existed between most abiotic, mammal species richness and mean body mass variables (see Results).

### Statistical analyses

For the analysis of ecoregional patterns, pairwise linear regression was used to determine relationships of species richness, body size and endemism with the three sets of explanatory variables. Similarity in species composition between ecoregions was examined with cluster analysis using Jaccard's coefficient as similarity measure and two different linkage rules based on the recommendations of Legendre and Legendre (1998): Ward's method and the weighted pair-group method using arithmetic averages (WPGMA). Analyses were made using STATISTICA for Windows (StatSoft Inc, 2004). To determine whether differences between clusters were significant we applied the non-parametric one-way analysis of similarities (ANOSIM) of the Paleontological Statistics Software Package (PAST, ver. 2.13; Hammer *et al.*, 2001) with 10 000 permutations and the distance version of Jaccard's coefficient ( $D_{\text{Jaccard}} = 1 - S_{\text{Jaccard}}$ ; see Legendre & Legendre, 1998) as distance measure. ANOSIM was carried out at two different levels of similarity. First, at the lowest similarity after the first branching point (two clusters), for which the original cluster analysis presence-absence matrix at the ecoregion level was used. Second, at intermediate similarity (3–4 clusters depending on the linkage rule), using a presence-absence matrix based on all systematically sampled localities per ecoregion, as use of the ecoregion level matrix would have been nonsensical due to the low number of ecoregions (1–3) per cluster.

Ecoregions are not limited in their spatial extent by political borders. This may potentially influence the regression analysis because local and subregional species richness is often partly determined by regional processes and the regional species pool (e.g. Ricklefs, 1987; Caley & Schluter, 1997; Herzog & Kessler, 2006). However, comparable ecoregion classifications for neighbouring countries and total ecoregion area estimates are unavailable; comprehensive treatments of the distribution of species in neighbouring countries are similarly lacking for several phanaeine genera. To determine potential biases we examined the relationship of the area of Bolivian ecoregions (Ibisch *et al.*, 2003) with that of the corresponding ecoregions of Olson *et al.* (2001; see above), which were correlated significantly and positively (Pearson  $r = 0.67$ ,  $P = 0.049$ ). Cerrado (the largest South American ecoregion) fell well outside the 95% CI, only a small proportion of which (*ca.* 4%) is represented in Bolivia. We therefore consider that the regression analysis is not significantly biased by politically constrained ecoregion area values.

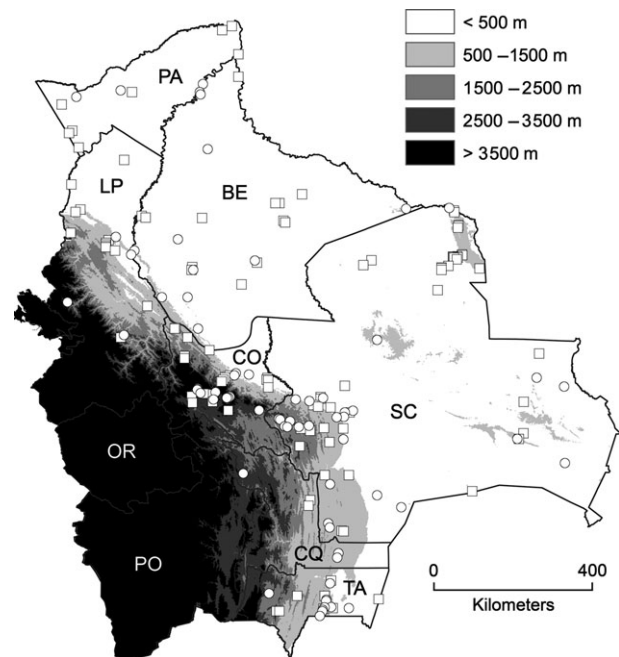
### Results

Our database contained 473 occurrence records of 39 phanaeine species from 179 Bolivian collecting localities, 109 of which were inventoried systematically (Fig. 2). The number of sampling localities per ecoregion (Table 2)

correlated positively with ecoregion area for all localities (Pearson  $r = 0.62$ ) and for systematically inventoried localities (Pearson  $r = 0.71$ ), but only the correlation of systematically inventoried localities was significant ( $P = 0.08$  and  $0.03$  respectively). For all localities, Yungas fell marginally above (significantly oversampled compared to other ecoregions) and Chiquitania below (significantly undersampled) the 95% CI. For systematically inventoried localities, Chiquitania was undersampled and Yungas was more thoroughly sampled than all other ecoregions.

### Species richness

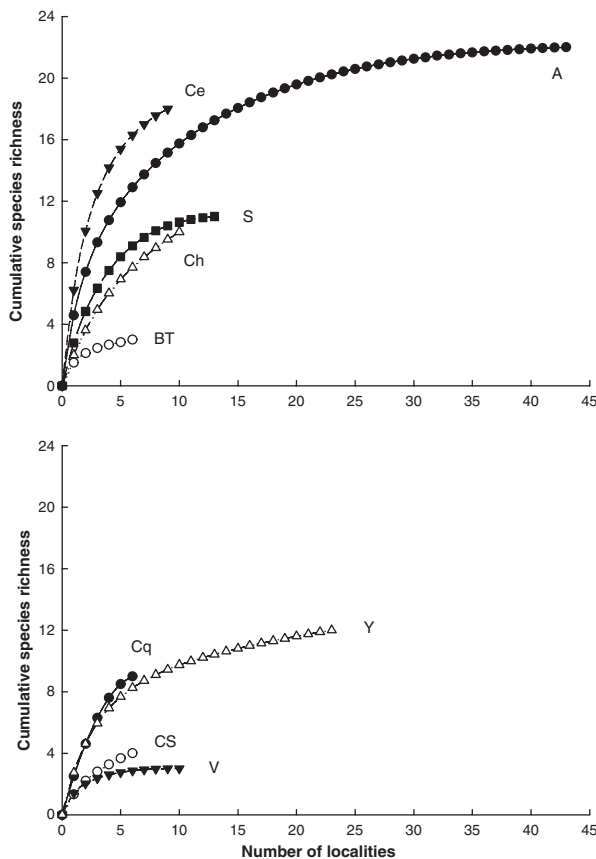
The observed number of species per ecoregion ranged from 1 (Northern Puna) to 22 (Southwest Amazonia) (Table 2). Species richness recorded in systematically sampled localities equalled that of total recorded species richness per ecoregion except for Cerrado and Chaco, where one species each was found only in opportunistically sampled localities (Table 2). Species accumulation curves (Fig. 3) for Southwest Amazonia (A), Seasonally Flooded Savanna (S) and Inter-Andean Dry Valleys (V) approached an asymptote, indicating a high degree of sampling completeness. Species richness estimators also



**Fig 2.** Distribution of 179 collecting localities of phanaeine dung beetles in Bolivia. Squares indicate localities inventoried systematically with baited pitfall traps or by intensive manual collecting at dung pats, circles localities sampled opportunistically or without information on collecting methods. Political divisions (departments): BE = Beni; CO = Cochabamba; CQ = Chuquisaca; LP = La Paz; OR = Oruro; PA = Pando; PO = Potosí; SC = Santa Cruz; TA = Tarija.

suggested that virtually all species present had been detected in these ecoregions (Table 2). By contrast, sampling completeness was lowest in Chaco, Cerrado and Chiquitania as species accumulation curves still rose steeply at maximum sample size (Fig. 3). Species richness estimators suggested that between about 1 and 3 species went undetected in these ecoregions (Table 2). Despite less steeply rising species accumulation curves (Fig. 3), species richness estimators indicated that about 1–2 species went undetected in Yungas and Chaco Serrano (Table 2).

Among abiotic explanatory variables (Table 4), area was the best single-factor predictor of species richness per ecoregion ( $R^2 = 0.68$ ), followed by mean annual temperature ( $R^2 = 0.51$ ) (collinearity between independent variables: Pearson  $r = 0.69$ ); both relationships were positive. Some biotic explanatory variables explained similar proportions of the variance (Table 4). Mean body mass of all mammals was the overall best predictor ( $R^2 = 0.72$ , negative relationship), followed by species richness of all mam-



**Fig. 3.** Incidence-based species accumulation curves for systemically sampled localities of phanaeine dung beetles in nine Bolivian ecoregions (A = Southwest Amazonia; BT = Boliviano-Tucumano Forest; Ce = Cerrado; Ch = Chaco; Cq = Chiquitania; CS = Chaco Serrano; S = Seasonally Flooded Savanna; V = Inter-Andean Dry Valleys; Y = Yungas). Sample accumulation order was randomised 50 times.

mals ( $R^2 = 0.54$ , positive relationship) (collinearity: Pearson  $r = -0.87$ ). In addition, both had high collinearity with ecoregion area (Pearson  $r = -0.92$  and  $0.87$  respectively) and moderate to low collinearity with mean annual temperature (Pearson  $r = -0.61$  and  $0.35$  respectively).

#### Body size

Mean body size (total length) of phanaeine dung beetle assemblages was greatest in Chaco Serrano (24.4 mm) and Chiquitania (23.1 mm) and smallest in Yungas (17.3 mm) and Boliviano-Tucumano Forest (17.5 mm) (Table 2). We found a slight but significant tendency for larger species to inhabit a greater number of ecoregions (Pearson  $r = 0.34$ ,  $P = 0.04$ ) and localities (Pearson  $r = 0.39$ ,  $P = 0.01$ ). Mean body size and mean estimated species richness per ecoregion (Table 2) were not correlated (Pearson  $r = 0.04$ ,  $P = 0.92$ ).

Mean body size had significant relationships with three explanatory variables (Table 4): mean body mass of

**Table 4.** Regression coefficients ( $R$  values) for pairwise linear regressions of estimated species richness, endemism and mean body size (length) of phanaeine dung beetles ( $N = 39$ ) against selected environmental parameters in nine Bolivian ecoregions.

	Estimated species richness	Mean size	Endemism score
<b>Abiotic variables</b>			
Area	0.83**	-0.02	0.20
Mean annual precipitation	0.62	-0.48	0.56
Mean annual precipitation range	0.57	-0.45	0.60
Mean annual temperature	0.72*	0.46	-0.21
Mean annual temperature range	-0.44	-0.79*	0.59
<b>Number of medium to large mammal species</b>			
All species	0.73*	-0.39	0.54
Herbivores & omnivores	0.68*	-0.48	0.60
Upper body mass quartile (all species)	0.41	-0.66	0.56
Herbivores & omnivores in upper body mass quartile	0.26	-0.72*	0.61
<b>Mean body mass of medium to large mammals</b>			
All species	-0.85**	0.25	-0.47
Herbivores & omnivores	-0.68*	0.51	-0.77*
Upper body mass quartile (all species)	-0.48	0.41	-0.37
Herbivores & omnivores in upper body mass quartile	0.02	0.86**	-0.69*

\* $P < 0.05$ , \*\* $P < 0.01$ .

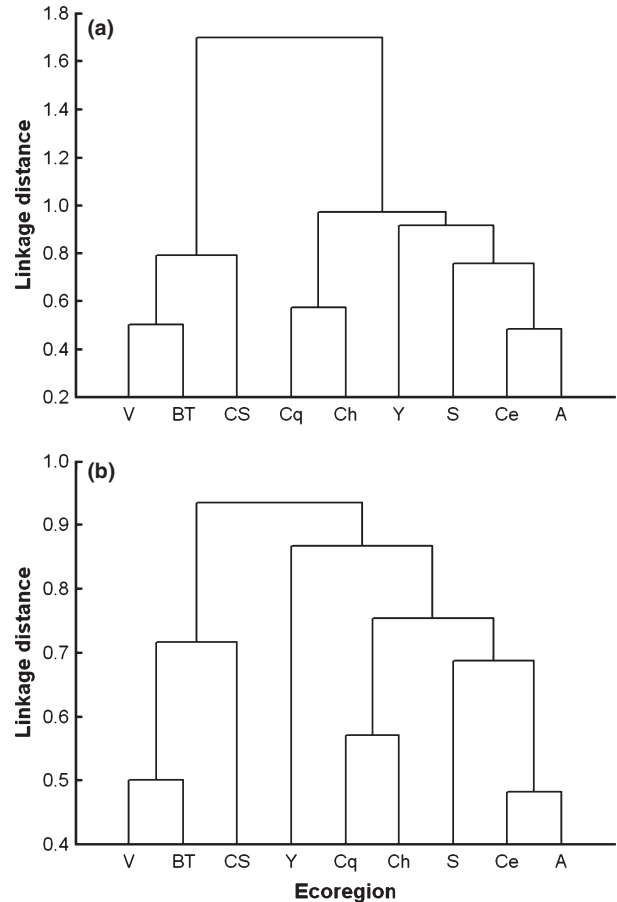


herbivorous and omnivorous mammals in the upper body mass quartile, i.e. mean mass of the largest herbivores and omnivores ( $R^2 = 0.74$ , positive relationship), mean annual temperature range ( $R^2 = 0.63$ , negative relationship) and number of herbivorous and omnivorous mammal species in the upper body mass quartile ( $R^2 = 0.52$ , negative relationship). Collinearity between mean mass of the largest herbivores and omnivores and the other two variables was moderately high (Pearson  $r = -0.69$  and  $-0.70$  respectively); mean annual temperature range and number of herbivorous and omnivorous mammal species in the upper body mass quartile had lower collinearity (Pearson  $r = 0.46$ ).

#### Species composition and endemism

The known distribution of the 39 phanaeine species recorded in Bolivia (Table 3) varied greatly from a single locality and ecoregion (e.g. *Coprophanaeus caroliae* Edmonds, 2008) to 55 localities and six ecoregions [*Oxytetrone conspicillatum* (Weber, 1801)] (Table 3). Cluster analysis produced very similar results with both linkage rules except for the placement of Yungas (Y) (Fig. 4). Both linkage rules separated ecoregions into two major groups based on their similarity in species composition (Fig. 4). The first contained the three species-poor Andean ecoregions Inter-Andean Dry Valleys (V), Boliviano-Tucumano Forest (BT) and Chaco Serrano (CS), whereas the second consisted of the five lowland ecoregions Seasonally Flooded Savanna (S), Chiquitania (Cq), Chaco (Ch), Cerrado (Ce) and Southwest Amazonia (A) plus Yungas (Y) (Fig. 4). The dissimilarity between these two groups was statistically significant (non-parametric one-way analysis of similarities (ANOSIM): mean rank within groups = 10.67, mean rank between groups = 26.33,  $R = 0.87$ ,  $P < 0.05$ ). At an intermediate linkage distance, ecoregions were separated into three significantly dissimilar groups by Ward's method (V, BT and CS; Cq and Ch; Y, S, Ce and A; mean rank within groups = 3126, mean rank between groups = 4856,  $R = 0.44$ ,  $P < 0.001$ ) and into four significantly dissimilar groups by the WPGMA (V, BT and CS; Y; Cq and Ch; S, Ce and A; mean rank within groups = 2769, mean rank between groups = 4542,  $R = 0.45$ ,  $P < 0.001$ ) (Fig. 4). Pairwise (*post-hoc*) ANOSIM comparisons also were significant ( $P < 0.001$ ) in all cases for both linkage rules. Based on the linkage distance at individual branching points, Yungas was the most unique (dissimilar) ecoregion, particularly so with the WPGMA linkage rule. Cerrado and Southwest Amazonia were the two most similar ecoregions (Fig. 4).

Phanaeine endemism was highest in Yungas (Y) and lowest in Chiquitania (Cq) (Table 2). Endemism and mean estimated species richness per ecoregion were not correlated (Pearson  $r = 0.33$ ,  $P = 0.38$ ), but a significant negative relationship existed between endemism and mean body size (Pearson  $r = -0.86$ ,  $P < 0.01$ ). Thirty-eight per cent of Bolivian phanaeines (15 species) appear to be



**Fig. 4.** Similarity of nine Bolivian ecoregions in phanaeine dung beetle species composition as determined by cluster analysis using (A) Ward's method and (B) the weighted pair-group method using arithmetic averages (A = Southwest Amazonia; BT = Boliviano-Tucumano Forest; Ce = Cerrado; Ch = Chaco; Cq = Chiquitania; CS = Chaco Serrano; S = Seasonally Flooded Savanna; V = Inter-Andean Dry Valleys; Y = Yungas).

restricted to a single ecoregion, and 54% were recorded in less than three ecoregions (Table 3), suggesting that most species have rather restricted geographical ranges. Cerrado had the greatest number of ecoregionally endemic species (4), followed by Southwest Amazonia, Chaco, Yungas (3 each) and Seasonally Flooded Savanna (2) (Table 3). With the exception of *Coprophanaeus ignecinctus* (Felsche, 1909), ecoregional endemics also inhabited narrow elevational ranges of 500 m or less, and none were recorded above 2000 m (Table 3). Overall, we found a strong tendency for species with narrower elevational ranges to inhabit a lower number of ecoregions (Pearson  $r = 0.61$ ,  $P < 0.0001$ ) and localities (Pearson  $r = 0.73$ ,  $P < 0.0001$ ).

No significant relationship was found between endemism and any of the abiotic variables, nor with any of the mammal species richness variables (Table 4). Mean body mass of herbivorous and omnivorous mammals was

the best single-factor predictor of endemism per ecoregion ( $R^2 = 0.60$ ), followed by mean body mass of herbivorous and omnivorous mammals in the upper body mass quartile ( $R^2 = 0.48$ ) (collinearity between independent variables: Pearson  $r = 0.39$ ); both relationships were negative (Table 4).

## Discussion

To our knowledge this is one of the first comprehensive studies on biogeographic patterns and conservation priorities of an invertebrate taxon in any Neotropical country or region (but see Kohlmann *et al.*, 2007; Löwenberg-Neto & De Carvalho, 2009). Clear patterns emerged for all parameters despite the relatively coarse spatial resolution at the ecoregion level and the relatively small number of ecoregions. They suggest that species richness, mean body size and endemism of phanaeine dung beetles are influenced by different factors, although in all three cases mean body mass of medium to large mammals had greater explanatory power than abiotic factors.

### *Species richness and body size*

Ecoregional patterns of phanaeine species richness appear to be influenced primarily by mean body mass of medium to large mammals, and perhaps also by mammal species richness, but due to negative collinearity between these variables their relative effects could not be disentangled. In other words, ecoregions with on average smaller mammals and greater mammal richness hold greater numbers of phanaeine species. Phanaeine species richness also increased with increasing ecoregion area (and to a lesser degree with mean annual temperature), but high collinearity between ecoregion area and the two biotic variables above does not allow for further disentangling of these relationships.

Mean body size of the phanaeine assemblage in a given ecoregion appears to be primarily influenced by the mean body mass of herbivorous and omnivorous mammals in the upper body mass quartile. In other words, areas with the largest herbivore and omnivore species also tended to support larger phanaeine species. It is noteworthy that this variable failed to explain species richness patterns, whereas the best predictor variable of phanaeine species richness, i.e. mean body mass of all medium to large mammals, explained little of the variation in phanaeine body size. Thus, different processes appear to determine species richness vs. body size of phanaeine assemblages. In particular, because large beetle species generally require greater quantities of dung at each individual dung pad, the largest coprophagous phanaeine species probably depend on large mammals, as supported by Peck and Howden (1984) and Lumaret *et al.* (1992). Greater richness of smaller mammal species, which can be expected to provide lower dung quantities or abundance but greater

diversity of dung types, may allow for greater temporal and spatial resource partitioning among dung beetle species that specialise on particular types of mammals, thereby facilitating greater phanaeine species richness. This is in disagreement with the hypothesis of Hanski and Cambefort (1991) and Estrada *et al.* (1999) that dung abundance is more important than mammal diversity for sustaining beetle diversity, although this hypothesis may primarily apply to smaller spatial and shorter temporal scales than considered by this study.

No studies seem to exist that are directly comparable to our analysis. At a much smaller spatial scale, Estrada *et al.* (1998) also found a significant positive relationship between the species richness of non-volant mammals and that of dung beetles in Mexican tropical rain forest fragments and agricultural habitats. However, our findings only partly agree with patterns observed in West African savannas, where both dung beetle diversity and average size increased with increasing size of mammals, particularly with the presence of elephants (Cambefort, 1991). Whereas this coincides with our results for mean body size, the species richness pattern of Bolivian phanaeines showed the opposite trend – a decrease with increasing average body mass of mammals. The relationship between body size and distribution also differs sharply between Bolivian phanaeines and West African dung beetles. In the latter, smaller species tend to inhabit a greater number of localities (Cambefort, 1991), whereas in Bolivian phanaeines larger species are more widely distributed both in terms of ecoregions and localities. These differences may in part be related to the restriction of our study to a single dung beetle tribe (made up of comparatively large species) and the concomitant lower number of species (39 vs. 207 respectively), to the small number of study sites (6) examined by Cambefort (1991) or quite simply to the fact that the largest Bolivian mammal, the South American tapir (*Tapirus terrestris*), is much smaller than the African elephant.

### *Species composition*

Cluster analysis identified three robust, statistically significant groups of ecoregions that were diagnosed regardless of the linkage rule: (i) the species-poor Andean ecoregions Inter-Andean Dry Valleys, Boliviano-Tucumano Forest and Chaco Serrano; (ii) the relatively dry southeast Bolivian lowland ecoregions Chiquitanía and Chaco; and (iii) the humid lowland ecoregions Seasonally Flooded Savanna, Cerrado and Southwest Amazonia. Clusters (2) and (3) were more similar to each other than either was to cluster (1).

Only the Yungas ecoregion could not be assigned unequivocally to a specific cluster: using Ward's method, it fell into cluster (3), whereas the weighted pair-group method assigned Yungas to its own cluster. However, regardless of the linkage rule, Yungas was the most unique (dissimilar) ecoregion with the greatest individual

linkage distance. It had the highest proportion (25%) of ecoregionally endemic species and obtained the highest ecoregional endemism score. These characteristics contributed to its dissimilarity in species composition with all other ecoregions.

The distinctive clustering of the three remaining, species-poor Andean ecoregions may reflect the evolutionary history of scarabaeine dung beetles, which are mostly adapted to warm or warm-temperate conditions (Halffter, 1991; Lobo & Halffter, 2000). Speciation in the Andes and colonisation of higher and cooler sites appears restricted to a comparatively small subset of species (Lobo & Halffter, 2000), which is exemplified by the elevational ranges of Bolivian phanaeines (Table 3): only 12 species (31%) regularly occur above 1000 m, and only six (15%) above 1500 m. Greater endemic and total species richness in the Yungas indicate that these processes were more successful in this more humid ecoregion with a larger area and less fragmented distribution than the ecoregions comprising cluster (1) (see Fig. 1; Table 1).

Among lowland ecoregions, the high similarity of Southwest Amazonia and Cerrado is somewhat surprising given the differences in dominant vegetation types (forest vs. savanna respectively) and their structure. However, several factors probably contribute to this similarity. First, these ecoregions notably surpass all others in species richness (Table 2). Second, Cerrado is crisscrossed with gallery forests and speckled with evergreen to semi-deciduous forest islands (Ibisch *et al.*, 2003), and two Amazonian forest specialists (*Phanaeus alvarengai* Arnaud, 1984, *P. bispinus* Bates, 1868) as well as four ecoregionally more widespread forest species [*Coprophanaeus telamon* (Erichson, 1847), *Oxysternon conspicillatum*, *O. silemus* Laporte de Castelnau, 1840, *P. chalconelas* (Perty, 1830)] occur in forest habitats in the Cerrado ecoregion (see Hamel-Leigue *et al.*, 2009). Third, habitat generalists [six species, e.g. *Coprophanaeus cyanescens* (Olsoufieff, 1924), *Diabroctis mimas* (Linnaeus, 1758), *Sulcophanaeus faunus* (Fabricius, 1775); see Hamel-Leigue *et al.*, 2009] make up the biggest proportion of species that Southwest Amazonia shares with the Cerrado ecoregion, and these species appear able to cross boundaries between Amazonian forest and *cerrado* grassland habitats. In addition, both ecoregions share a complex history of rainforest-*cerrado* grassland expansion and retraction dynamics in response to climatic fluctuations at least since the last glacial maximum about 21 000 years ago (Mayle *et al.*, 2004, 2007), which may also have contributed to the similarity in species composition.

Nonetheless, given that the Cerrado ecoregion is divided into four subecoregions composed of fairly disjunct 'islands' (see Fig. 1) that span a wide latitudinal gradient (ca. 11°00'S to 19°30'S; Ibisch *et al.*, 2003), once sufficient sample coverage exists for all four subecoregions, a more detailed analysis may reveal more differentiated patterns. Especially the southernmost Cerrado areas may be expected to have greater similarity in species composition with the surrounding or adjacent Chiquitania

and Chaco ecoregions than with Southwest Amazonia (see Fig. 1).

### Endemism

With the exception of the Chiquitania and the species-poor Chaco Serrano, which obtained the lowest endemism scores, overall variation in phanaeine endemism among ecoregions was relatively small and ranged from 0.35 in Yungas to 0.30 in Chaco and Inter-Andean Dry Valleys (Fig. 4). For determining priority ecoregions for conservation it may therefore be more useful to consider absolute numbers of ecoregionally endemic species, which are most numerous in Cerrado (four), Southwest Amazonia, Chaco and Yungas (three each).

Ecoregional patterns of phanaeine endemism appear to be influenced primarily by the mean body mass of herbivorous and omnivorous mammals. Ecoregions with on average smaller herbivorous and omnivorous mammals have higher levels of phanaeine endemism. The negative correlation of endemism with average mammal body mass suggests that an absence or low numbers of large mammal species may favour the persistence of geographically restricted species by eliminating or reducing interspecific competition with larger, more geographically widespread and presumably dominant phanaeines.

Although non-significant, relatively high positive correlations of endemism with mean annual precipitation range and mean annual temperature range may suggest that topographically complex regions hold greater numbers of geographically restricted species, which has been proposed to apply to South American birds (Rahbek *et al.*, 2007). A more fragmented topography and, at higher elevations, increased climatic harshness result in greater risks of stochastic local extinction, more scattered, isolated populations and correspondingly faster rates of population differentiation (Kessler *et al.*, 2001). Once global range sizes of all species can be estimated reliably, a more refined definition of geographically restricted species (e.g. range-size quartiles; Gaston, 1994) may facilitate testing of this hypothesis for phanaeines and dung beetles in general.

### Conservation implications

Three ecoregions stand out as priority areas for phanaeine conservation in Bolivia: Cerrado, Southwest Amazonia and Yungas each hold peak numbers of ecoregionally endemic species. The former two are also the most species rich ecoregions, whereas Yungas has the most distinctive species composition, high endemism (regardless of how it was measured), and ranks third in species richness. Given the absence of ecoregional endemics above 2000 m, phanaeine conservation efforts in the Yungas should focus on areas below this elevation. The identification of priority areas within the Cerrado and, more specifically, among

its four subcoregions requires additional study (see above). All four Cerrado endemics are so far only known from Cerrado Chiquitano on Serranía de Huanchaca (Hamel-Leigue *et al.*, 2009), a Precambrian sandstone plateau of the Brazilian Shield rising to 900 m in Noel Kempff Mercado National Park in northern Santa Cruz department (Killeen & Schulenberg, 1998). However, this is also the most intensively sampled Cerrado area for phanaeines in Bolivia, and particularly the two northern subcoregions Cerrado Paceño (in La Paz department) and Cerrado Beniano (in Beni department) (see Fig. 1) are highly understudied.

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