 doi: 10.1111/j.1752-4598.2008.00038.x

Utilisation of introduced Brazilian pastures ecosystems by native dung beetles: diversity patterns and resource use

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Abstract. 1. Cattle pastures dominated by introduced grasses are a characteristic component of many tropical landscapes in Brazil, yet little information is available concerning the insect communities that inhabit these novel ecosystems.

2. Dung beetles are a conspicuous element of pasture insect communities, and make a significant contribution to dung decomposition, parasitic fly control, and soil bioturbation.

3. We sampled dung beetle assemblages in twelve introduced pastures near Viçosa, Minas Gerais, Brazil. We used pitfall traps baited separately with cow and horse dung, and collected a total of 456 dung beetles, comprising 23 species from 13 different genera. We analysed patterns of alpha and beta diversity, community structure, and species composition among pastures and bait types.

4. Cow dung harboured significantly more species, but a similar abundance of dung beetles compared with horse dung. However, both dung types supported species exclusive to that type, and hosted a distinct dung beetle community structure and composition.

5. Although livestock (cattle and horses) was introduced to Brazil less than 500 years ago, our data suggest that novel and well-structured dung beetle communities are actively exploiting these novel food resources in Brazilian pasturelands.

Key words. Biological control, coprophagous insects, pasture, Scarabaeinae.

Introduction

In the last two centuries, several African grass species have been introduced and cultivated in Brazilian pasturelands to feed livestock. These introduced pastures are one of more area-demanding agro-ecosystems in the world, occupying around 99 652 000 ha in 2004 in Brazil alone (IBGE, 2007). Insects are central elements in the functioning of introduced pastures, and these ecosystems likely depend upon as well as play an important role in conservation of native biodiversity.

Our knowledge of dung beetle communities and their ecological function in Brazilian pastures is still embryonic (Mendes & Linhares, 2006; Silva *et al*., 2006). An important step towards a more comprehensive evaluation of the potential for native Brazilian dung beetles to act as effective biological control is to improve our understanding of the distribution and functional roles of native beetle communities in introduced pastures across a range of distinct geographical regions. Such information is fundamental for assessing the impact of new exotic dung beetle introductions, the role of native dung beetles in the control of fly populations, and the impact of introduced livestock on native dung beetle species biodiversity.

Dung beetles (Coleoptera: Scarabaeinae) are detritus-feeding insects, broadly distributed in the tropics (Hanski & Cambefort, 1991). They use mammal dung and other decaying materials to provision both adults and larvae (Halffter & Edmonds, 1982; Hanski, 1987). Dung beetles play a major role in a variety of ecological services in tropical ecosystems (Nichols *et al*., 2008), including secondary seed dispersal (Andresen, 2002; Andresen & Feer, 2005), control of detritus-feeding flies and intestinal parasites (Bryan, 1973; Ridsdill-Smith, 1981; Wallace & Holm, 1983), mixing of organic matter in the soil, soil aeration (Linquist, 1933; Brussaard & Slager, 1986), and nutrient cycling (Yokoyama *et al*., 1989; Bang *et al*., 2005).

Dung beetle communities are affected by several local and regional factors (Menédez & Gutierrez, 1996; Davis *et al*., 2000;

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Scheffler, 2005). Dung quality and type is an important local factor which affects dung beetle larval survival (Owen *et al*., 2006), and it is commonly accepted that dung attractiveness in adult beetles varies across dung types (AlHouty & AlMusalam, 1997). There are significant physical and chemical differences in dung quality between dung types (Gittings, 1998). In addition to dung beetles, several other detritus-feeding insect species use dung pads as food resources (Hanski, 1987; Pinero & Avila, 2004). In many pasture ecosystems, cattle dung are used by blood-feeding flies as a substrate for larval growth. Several economically important fly species generate economic losses through reduced yields of meat and milk in stressed livestock (Fincher, 1990). These include the horn fly (*Haematobia irritans irritans* L.), the African buffalo fly (*Haematobia exigua* De Meijere), the Australian buffalo fly (*Haematobia thirouxi potans* Bezzi), the bush fly (*Musca vetustissima* Walker) and the face fly (*Musca autumnalis* De Geer) (Markin & Yoshioka, 1998).

The effects of dung beetles upon the survival and abundance of livestock parasitic flies are well documented in the scientific literature (e.g. Bergstrom, 1983; Fincher, 1990; Markin & Yoshioka, 1998). Multiple parasitic fly-control programmes have been developed globally, using African species of dung beetles as larval food competitors (Doube, 1986; Fincher, 1990). In Australia, the main justification for dung beetle introductions was that native dung beetles were not capable of using the dung of introduced large mammals (cow, horse, sheep).

In Brazil, using the same methodology as in Australia, the agriculture department (Empresa Brasileira de Pesquisa Agropecuária) introduced the African species *Diginthontophagus gazella* Fabricius as an agent for biological control of dung in the introduced pastures of Mato Grosso do Sul (Miranda *et al*., 1990). This introduction was made before any in-depth knowledge of native dung beetle communities and the potential impacts of *D. gazella* was available.

To contribute to this knowledge gap here, we present patterns in coprophagous beetle communities among 12 introduced pastures in Minas Gerais, Brazil, and provide the first evaluation of differences in attractiveness between cow and horse dung for different species of dung beetle.

Material and methods

Study area

The study was carried out in Viçosa, Minas Gerais (20°45′S, 42°50′W), altitude between 600 and 800 m. The climate is subtropical and moderately humid, with a drier season from May to September (maximum temperature 21 °C) and wetter season from December to May (14 °C) (Cwa in Köppen classification). The region has approximately 1341 mm mean annual precipitation, with a mean annual relative moisture of 80%, and a mean annual temperature of 19 °C.

Cattle rearing in Viçosa is organised in a semi-intensive system, where cattle are pastured for almost the entire year. Most of the rural properties are less than 100 ha in size, and cattle farms and coffee plantations comprise the principal economic activities.

Dung beetle sampling

We sampled 12 introduced cattle pastures (comprised of mixed *Melinis minutiflora* Beauv. and *Brachiaria* spp.) for a 48-h period, January 1994. The sampling unit was a baited pitfall trap composed of a plastic container (diameter 19 cm, height 11 cm) filled with 150 ml of a 5% detergent solution. We placed 200 g of fresh cattle or horse dung bait on a plastic platform 13 cm above the pitfall to attract adult dung beetles.

At each site we set four trap clusters, with each cluster composed of two pitfalls spaced 3 m apart (one baited with cattle dung and one with horse dung), arranged in a square, 30 m on each side. We identified the dung beetles to genera and species, whenever possible, with the help of identification keys and the personal collection of Fernando Z. Vaz de Mello (FZVM). When species identification was not possible, we sorted beetles according to their external morphology. Voucher specimens are housed at the Entomological Collection of the Department of Animal Biology of the Universidade Federal de Viçosa and in the FZVM collection.

Data analysis

We compared patterns of species richness between bait types after standardising for differences in abundance with individual-based rarefaction analysis (Gotelli & Colwell, 2001). Comparisons among bait types were made by visual assessment of overlapping 95% confidence intervals of the rarefaction curves. We assessed the completeness of each sample by calculating the number of observed species as a percentage of the total species richness, which was estimated based on the average of three abundance-based non-parametric estimators – Chao 1, Jack 1, and Boot (Colwell, 2004).

To describe patterns of beta diversity across the pastures, we calculated the average number of species not present in each site defined as $\beta = \gamma - \alpha$, where γ is the number of species sampled in all pastures (gamma diversity) and α is the average number of species present at a given site (alpha diversity). This approach is used as a measure of additive partitioning of diversity (Veech *et al*., 2002) and allows for a direct comparison between alpha and beta diversities in terms of the number of species.

We plotted species-abundance distributions (Whittaker plots) to elucidate dominance patterns within local communities. These curves are cumulative ranked-abundance plots, where the cumulative ranked abundance of each species is plotted against the species rank in order from most abundant to least abundant species.

In order to test the relationship between mean local species abundance and its regional distribution, we performed a simple linear regression, where the mean local abundance of one species was considered a function of the number of sites occupied. A positive relationship is expected if widely distributed species are also locally more abundant than geographically restricted ones.

We used non-metric multidimensional scaling to define the overall differences in community structure within and among bait types. Ordination was undertaken for abundance and data using the Bray–Curtis index. We used analysis of similarities (ANOSIM; Clarke, 1993) to test for significant differences in

Table 1. Capture success, species richness, and sample completeness for dung beetles sampled in introduced pastures in Viçosa, Minas Gerais, Brazil. (a) Number of species observed as a percentage of the average estimated richness; (b) Number of species not found elsewhere as a percentage of landscape total; (c) Number of species observed as a percentage of the landscape total.

Site	No. of individuals	No. of species	Coverage[a]	Exclusive species (percentage)[b]	Completeness (percentage)[c]
P1	20	6	77.8	0.0	26.1
P2	27	9	71.0	0.0	39.1
P3	120	10	78.6	4.3	43.5
P4	17	8	66.7	0.0	34.8
P5	54	9	85.7	13.0	39.1
P6	13	5	66.1	0.0	21.7
P7	26	8	90.1	0.0	34.8
P8	87	4	90.5	0.0	17.4
P9	44	8	68.5	4.3	34.8
P10	21	7	72.8	4.3	30.4
P11	22	6	59.4	0.0	26.1
P12	5	4	49.4	4.3	17.4

multivariate community structure between bait types. This is a non-parametric permutation procedure applied to rank similarity matrices underlying sample ordinations (Clarke, 1993). The closer the global R statistic is to one, the more distinct the differences in communities structure between treatments (Clarke, 1993).

The relative differences between R-values from the ANOSIM tests were used to determine patterns of similarity between dung beetle communities attracted to the two bait types. We used similarity percentage – SIMPER (Clarke, 1993) to determine the contribution that individual species made towards distinguishing differences in community structure among baits. The analysis was performed with PAST (Hammer *et al*., 2001).

Results

Species richness patterns

Across all sampled sites and baits, we collected a total of 456 individuals, comprising 23 species of Scarabaeine dung beetles. On average, our sampling programme captured 73.1% of the expected dung beetle richness at each site (Table 1). The beta-diversity partition was 61% (average of 14 species not present in any given site), implying a potential turnover of 100% in species composition between local communities.

All dung beetle communities were strongly dominated by a single, or at most two species (Fig. 1). Across different site communities, *Dichotomius bos*, *Ateuchus striatulus*, *Dichotomius fimbriatus*, *Onthophagus buculus* alternated as being the locally dominant species (Fig. 1).

There was a positive relationship between local mean abundance and species distribution in the landscape (Fig. 2, $F = 17.02$, $P < 0.0005$, d.f. = 22).

Dung preferences

A significantly greater number of species were attracted to cattle dung (S = 19) compared to horse dung (S = 14) (Fig. 3). Nine

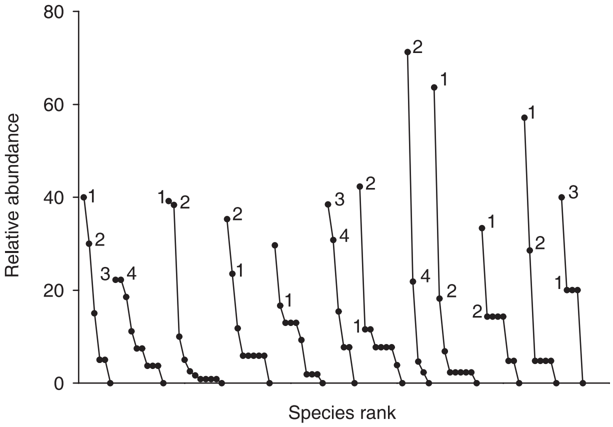

Fig. 1. Rank abundance graphs (Whittaker plots) for dung beetle communities in 12 introduced pastures from southern Brazil. 1) *Dichotomius bos*, 2) *Ateuchus striatulus*, 3) *D. fimbriatus*, 4) *Onthophagus buculus.*

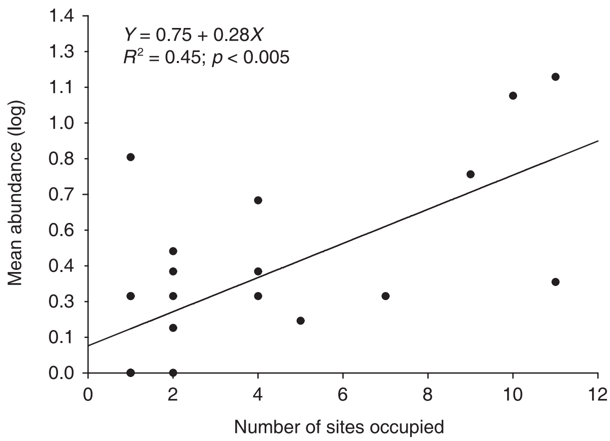

Fig. 2. Relationship between mean local abundance and the number of sites occupied by dung beetle species.

Table 2. Dung beetle average abundance in horse and cattle dung-baited pitfall traps from 12 pasture sites near Viçosa, Minas Gerais, Brazil. The SIMPER analysis illustrates that the community structure of dung beetles in cow dung was distinct from that sampled in horse dung due to changes in average abundance of common species and the presence of exclusive species in both dung types.

Taxon	Mean abundance in cow dung	Mean abundance in horse dung	Contribution	Cumulative percentage
Ateuchus striatulus Laporte, 1840	3.08	10.2	21	26.55
Dichotomius bos (Mannerhein, 1829)	7.83	2.33	18.67	50.15
Onthophagus buculus (Mannerhein, 1829)	4.25	0.25	11.37	64.53
Dichotomius fimbriatus (Harold, 1869)	0.333	1.75	7.228	73.67
Dichotomius nisus (Olivier, 1789)	1.58	0	3.157	77.66
Trichillum externepunctatum (Borre, 1880)	0.25	0.917	2.79	81.18
Agamopus unguicularis (Harold, 1883)	0.167	0.667	2.706	84.61
Dichotomius carbonarius (Mannerhein, 1829)	0	0.667	2.475	87.73
Dichotomius mormon (Ljungh, 1799)	0.333	0.333	2.078	90.36
Chalcocopris hesperus (Olivier, 1789)	0.5	0	1.045	91.68
Canthidium aterrimum (Harold, 1868)	0.583	0	0.9796	92.92
Anomiopus sp.	0.0833	0.0833	0.7495	93.87
Deltochilum sp.	0.167	0	0.7444	94.81
Ontherus appendiculatus (Mannerhein, 1829)	0.0833	0.25	0.7205	95.72
Sulcophanaeus menelas (Laporte, 1840)	0.25	0.167	0.6792	96.58
Canthon lituratum (Germar, 1824)	0.0833	0	0.6318	97.38
Eurysternus jessopi (Martinez, 1989)	0	0.167	0.4587	97.96
Onthophagus rubrescens Blanchard, 1843	0	0.25	0.45	98.53
Dichotomius assifer (Eschschz., 1822)	0	0.0833	0.3883	99.02
Canthon sp.	0.0833	0	0.3454	99.45
Eurysternus hirtellus (Dalman, 1824)	0.0833	0	0.1903	99.7
Canthon septemmaculatum (Laporte, 1840)	0.0833	0	0.1399	99.87
Trichillum hirsutum (Boucomont, 1928)	0.0833	0	0.1013	100

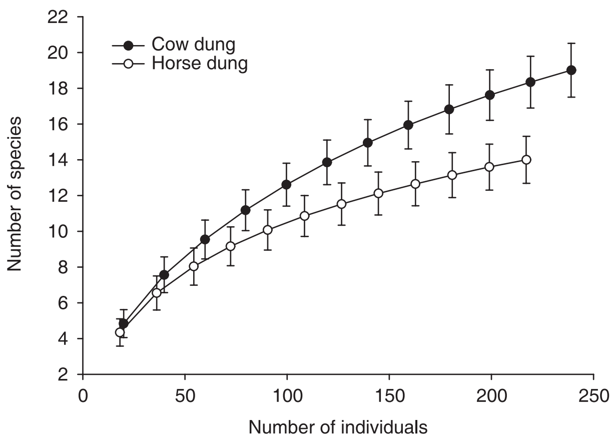

Fig. 3. Individual-based rarefaction curves for dung beetle assemblages within introduced pastures in Viçosa, Minas Gerais, Brazil. Data are pooled from multiple sampling sites. The bars are 95% confidence intervals.

species were captured exclusively in cattle dung baited pitfall traps, while only four species were attracted exclusively to horse dung. Both cow dung (mean = 4.98; SD = 6.39) and horse dung (mean = 4.52; SD = 4.98) attracted similar numbers of dung beetle ($t = 0.37$; $P = 0.71$; d.f. = 11). Of the 456 individuals collected in the sampling programme, 217 were captured in horse dung, while the remaining 239 were attracted to cattle dung. Only five species (*A. striatulus*, *D. bos*, *O. buculus*, *D. fimbriatus* and *Dichotomius nisus*) contributed 83.1% of the total sampled individuals considering all sites and baits. *Ateuchus striatulus* was dominant in horse dung, comprising more than half the number of individuals, and *D. bos* (39.2%) followed by *O. buculus* (21.3%) in cattle dung.

The dung beetle communities sampled in horse and cow dung exhibited differences in community structure (Fig. 4a; ANOSIM $R = 0.29$; $P < 0.0001$). Six species (*A. striatulus*, *D. bos*, *O. buculus*, *D. fimbriatus*, *D. nisus*, and *T. externepunctatum*) contributed to more than 80% of the observed differences in community structure (Table 2).

Discussion

Dung beetle diversity in the pastureland

We observed relatively few dung beetle species in pastures in Viçosa, in contrast to introduced pasture systems elsewhere in Brazil (Table 3), and no evidence of *D. gazella* was found in any of the pasture systems sampled. However, at the regional scale, observed species richness is equivalent to other Brazilian pastures, indicating a large effect of species turnover on regional diversity in our study sites.

Most of the dung beetle communities sampled in individual sites were dominated numerically by few species, with other

Table 3. Studies examining the diversity of dung beetle communities (Scarabaeinae, Aphodiinae, or both) in introduced and native pastures across Brazil.

Vegetation type	Location	Altitude	Mean annual temperature	Mean annual precipitation	Dung beetle sampling method	Sample period	*N*	Species		Reference
								Scarabaeid	Aphodiid	
Northern Brazilian 'Tabuleiro' – open habitat growing on sandy oligothrophic soil	Mamanguape, Pernambuco Pernambuco (06°44′S, 35°08′W)	NS	26 °C	1700 mm	Baited pitfall traps with human dung and decomposing liver bait	1 year	2235	25	NS	Endres *et al*. (2007)
Pasture close to forest	Caruaru, Pernambuco Pernambuco (08°42′S, 35°15′W)	660 m	24 °C	609 mm	Baited pitfall traps with human dung and bovine decomposing meat bait	10 months	1540	28	NS	Silva *et al*. (2007)
Introduced pasture of *Brachiaria decubens*	20°27′S, 54°37′W	NS	NS	NS	Baited pitfall traps with cow dung bait	3 years	56 255	40	15	Koller *et al*. (2007)
Introduced pasture of *Brachiaria brizantha*	Itumbiara, Goiás (20°22′S, 51°22′W)	NS	24.4 °C	NS	Cow dung pads dissection	1 year	4885	4	7	Marchiori (2000)
Introduced pasture *of Cynodon* sp.	Coronel Pacheco, Minas Gerais (21°35′S, 43°15′W)	NS	19.5 °C	NS	Baited pitfall traps with cow dung bait	1 year	1124	8	6	Monteiro *et al*. (2006)
Introduced pasture of *Brachiaria decubens*	Campo Grande, Mato Grosso do Sul	NS	NS	NS	Cow dung pads and soil dissection	2 years	18 844	23	14	Koller *et al*. (1999)
Cattle pasture, probably *Brachiaria* sp.	Pará state (7°50′S, 50°16′W)	NS	NS	1855 mm	Baited pitfall traps with human dung bait	1 month	3732	14	1	Scheffler (2005)
Introduced pasture of *Brachiaria decubens*	Aquidauana, Mato Grosso do Sul	NS	NS	NS	Baited pitfall traps with cow dung bait	48 weeks	3229	19	4	Aidar *et al*. (2000)
Wild grasslands	Bajé, Rio Grande do Sul	NS	NS	NS	Baited pitfall traps with human dung bait	5 months	NS	16	NS	Silva *et al*. (2006)
Introduced pasture of *Brachiaria brizantha*	Itumbiara, Goiás	NS	24.4 °C	NS	Cow dung pads dissection	1 year	488	4	11	Marchiori *et al*. (2001)
Introduced pasture	São Carlos, São Paulo (21°01′S, 47°03′W)	856 m	NS	NS	Baited pitfall traps with cow dung bait	3 months	4124	7	4	Oliveria *et al*. (1996)
Introduced pasture of *Brachiaria decubens* and *Andropogon gayanus*	São Carlos, São Paulo (21°01′S, 47°03′W)	856 m	NS	NS	Cow dung pads and soil dissection	1 year	13 460	17	5	Mendes & Linhares (2006)
Introduced pasture of Coast-cross grass	Piracicaba, São Paulo	NS	NS	NS	Baited pitfall traps with cow dung bait	10 months	934	5	6	Rodrigues & Marchini (1998)
Introduced pasture of *Panicum maximum*	Ilha Solteira, São Paulo (20°22′S, 51°22′W)	335 m	25 °C	1330 mm	Cow dung pads dissection	3 month	NS	9	6	Flechtmann *et al*. (1995a)
Introduced pasture of *Brachiaria decubens*	São Luís, Maranhão	NS	NS	NS	Baited pitfall traps with cow dung bait	3 months	1717	8	1	Pereira *et al*. (2003)
Introduced pasture	Itumbiara, Goiás (20°22′S, 51°22′W)	NS	NS	NS	Cow dung pads and soil dissection	9 months	3229	7	7	Marchiori (2003)
Introduced pasture	Selvíria, Maranhão	NS	NS	NS	Light trap and cow dung pad dissection	1 year	NS	16	11	Flechtmann *et al*. (1995b)
Introduced pasture of *Axonopus affinis* or *Paspalum notatum*	Jaraguá do Sul, Santa Catarina (26°29′S, 49°04′W)	30 m	22 °C	2200 mm	Cow dung pad dissection	5 days	NS	4	4	Flechtmann & Rodrigues (1995)

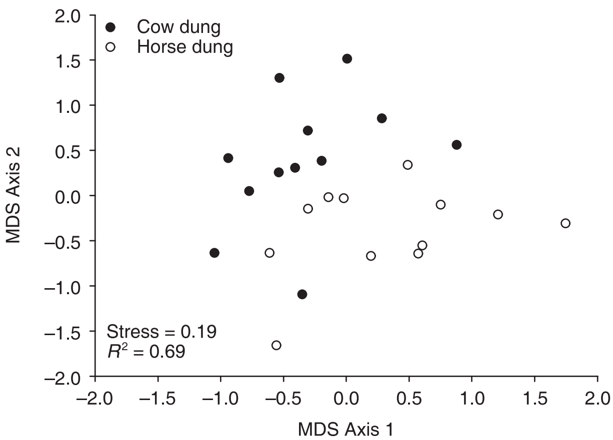

Fig. 4. Non-metric multidimensional scaling (MDS) ordination of the dung beetle community in each pasture as sampled by cow dung and horse baited pitfall traps. Non-metric multidimensional scaling is based on a distance matrix computed with Bray–Curtis similarity index. (a) community structure (quantitative data) and (b) Composition (qualitative data).

species being rare. This pattern is relatively common in open and climatically instable habitats (Magurran, 1988), and illustrates the frequently unpredictable nature of introduced pastures in relation to original forest habitats in the region. For example, Louzada & Lopez (1997) found a much more even species-abundance curve for a dung beetle community from a large Atlantic forest fragment in the same region.

A relatively small number of dung beetle species occurred in Brazilian-introduced pastures compared to forest and savanna-like ecosystems (Howden & Nealis, 1975; Louzada & Lopez, 1997; Milhomem *et al*., 2003; Scheffler, 2005; Gardner *et al*., 2008). Here we observed a positive relationship between species regional distribution and local abundance, illustrating the link between colonisation ability and the capacity for local population growth (Holt *et al*., 2002). In our data, only five species were both locally abundant and distributed across introduced pasture sites. Species that are both broadly distributed in the landscape and exhibit high local abundances in a given site are probably most adapted to open habitats, and horse and bovine dung as a food resource. Those species potentially represent the best options for future use on dung flies biological control programmes focused exclusively on Brazilian native dung beetle species. Because we did not find evidence of *D. gazella* establishment, and there are no reports of horn fly attacks to livestock in the pasture sites we sampled, it appears that native dung beetle communities are effective both in removing the dung produced by the livestock, as well as controlling fly populations.

Dung beetle diversity between dung types

Baited pitfall traps are usually employed for sampling dung beetles in tropical ecosystems. However, this sampling approach has been criticised because of the difficulty in interpreting results and the limited information it yields on dung community processes (Giller & Doube, 1989). Here we use dung-baited pitfall traps to infer dung beetle food preferences, assuming that the differential attractiveness of individuals and species to dung baits are equivalent across communities sampled in different sites. We made no inference about the subsequent residence time in the dung pile by any of the species, but this approach is appropriate for assessing the potential use of cow and horse dung by native dung beetles.

One of the primary aims of this study was to enhance our knowledge of native Brazilian dung beetles concerning the pattern of bovine and equine dung use. Since cattle and horses were introduced to Brazil within the last 500 years, we did not expect to encounter a large number of species using cattle and/or horse dung as food. However, contrary to the situation observed in Australia where native dung beetles were unable to utilise cow dung, the Brazilian dung beetle communities in our study region are able to exploit both introduced dung types. In fact, there is a diverse array of dung beetle communities active in introduced pastures from several Brazilian regions (Table 3).

Our data show a pattern of differential use of cow and horse dung by Scarabeine dung beetles active in introduced Brazilian pastures. Several species utilise both cow and horse dung, but the differences in the identity of the more abundant species between the two dung types clearly distinguishes different beetle communities (Fig. 4). It is possible that different dung kinds have different effects on individual fitness due to inherent differences in quality. If this occurs, we would expect that the proportion of individuals that use this resource increases, but also that the populations do not lose their ability to exploit sub-optimal resources in the form of other dung types if intra-specific competition plays an import regulatory role. The physical properties of horse dung (low water and high fibre content) would reduce the duration of the attractive period to dung beetles, which could explain our lower species capture rate of beetles in this bait type.

There are relatively few records of the species composition of the dung beetle assemblages in Brazilian pastures. An outstanding question is the relative contribution of forest, grasslands and savanna habitats to the total (native) species pool found in anthropogenic pastures. We observed exclusive species captured in both cow and horse dung, thus it is possible to speculate that a maintenance of more than one species of livestock in pasture-lands can potentially enhance the dung beetle biodiversity and associated ecological services, while acting as a conservation tool for introduced pastures. This kind of artificial manipulation of alimentary resource heterogeneity is worthy of further evaluation through direct manipulation of resource supply in different pasture sites, including abandoned pastures.

Acknowledgements

We thank Liz Nichols, Toby Gardner and two anonymous referees for helpful comments on the manuscript.

References

Aidar, T., Koller, W., Rodrigues, S.R., Correa, A.M., Da Silva, J.C.C., Balta, O.D.S., De Oliveira, J.M. & De Oliveira, V. (2000) Coprophagous beetles (Coleoptera: Scarabaeidae) collected in Aquidauana, MS, Brazil. *Anais da Sociedade Entomologica Brasileira*, **29**, 817–820.

AlHouty, W. & AlMusalam, F. (1997) Dung preference of the dung beetle *Scarabaeus cristatus* Fab (Coleoptera-Scarabaeidae) from Kuwait. *Journal of Arid Environments*, **35**, 511–516.

Andresen, E. (2002) Dung beetles in a Central Amazonian rainforest and their ecological role as secondary seed dispersers. *Ecological Entomology*, **27**, 257–270.

Andresen, E. & Feer, F. (2005) The role of dung beetles as secondary seed dispersers and their effect on plant regeneration in tropical rainforests. *Seed Fate: Predation, Dispersal and Seedling Establishment* (ed. by P.M. Forget, J.E. Lambert, P.E. Hulme & S.B. Vander Wall), pp. 331–349. CABI International, Wallingford, Oxfordshire, UK.

Bang, H.S., Lee, J.H., Kwon, O.S., Na, Y.E., Jang, Y.S. & Kim, W.H. (2005) Effects of paracoprid dung beetles (Coleoptera : Scarabaeidae) on the growth of pasture herbage and on the underlying soil. *Applied Soil Ecology*, **29**, 165–171.

Bergstrom, R.C. (1983) *Aphodius* beetles as biological control agents of elk lungworm, *Dictyocaulus hadweni*. *Proceedings of the Helminthological Society of Washington*, **50**, 236–239.

Brussaard, L. & Slager, S. (1986) The influence of soil bulk density and soil moisture on the habitat selection of the dung beetle *Typhaeus typhoeus* in the Netherlands. *Biology and Fertility of Soils*, **2**, 50–58.

Bryan, R.P. (1973) The effects of dung beetles activity on the numbers of parasitic gastrointestinal helmintic larvae recovered from pasture samples. *Australian Journal of Agricultural Research*, **24**, 161–168.

Clarke, K.R. (1993) Nonparametric analyses of changes in community structure. *Australian Journal of Ecology*, **18**, 117–143.

Colwell, R.K. (2004) *EstimateS: Statistical Estimation of Species Richness and Shared Species from Samples. User's guide and application*. University of Connecticut, Storrs, Connecticut.

Davis, A.J., Huijbregts, H. & Krikken, J. (2000) The role of local and regional processes in shaping dung beetle communities in tropical forest plantations in Borneo. *Global Ecology and Biogeography*, **9**, 281–292.

Doube, B.M. (1986) Biological control of the buffalo fly in Australia: the potential of the southern African dung fauna. *Biological Control of Muscoid Flies* (ed. by R.S. Patterson & D.A. Rutz), pp. 16–34. Miscellaneous Publications of Entomological Society of America, Hyattsville, Maryland.

Endres, A.A., Creão-Duarte, A.J. & Hernández, M.I.M. (2007) Diversidade de Scarabaeidae *s.str.* (Coleptera) da Reserva Biológica de Guaribas, Mamanguape, Paraíba, Brasil: uma comparação entre Mata Atlântica e Tabuleiro Nordestino. *Revista Brasileira de Entomologia*, **51**, 67–71.

Fincher, G.T. (1990) Biological control of dung-breeding flies: pests of pastured cattle in the United States. *Biocontrol of Arthropods Affecting Livestock and Poultry* (ed. by D. Rutz & R. Patterson), pp. 137–151. Westview Press, Boulder, Colorado.

Flechtmann, C.A.H. & Rodrigues, S.R. (1995) Insetos fimícolas associados a fezes bovinas em Jaraguá do Sul/SC. I. Besouros coprófagos (Coleoptera, Scarabaeidae). *Revista Brasileira de Entomologia*, **39**, 303–309.

Flechtmann, C.A.H., Rodrigues, S.R. & Gaspareto, C.L. (1995b) Biological control of horn fly (Haematobia irritans irritans) in Selviria, Mato Grosso do Sul State: 6. Population dynamics of fimicolous insects except for coprophagous Scarabaeidae. *Revista Brasileira de Entomologia*, **39**, 287–296.

Flechtmann, C.A.H., Rodrigues, S.R., Araújo, S.D. & Wenzel, R.L. (1995a) Levantamento de insetos fimícolas em Ilha Solteira, São Paulo, Brasil. *Revista Brasileira de Entomologia*, **39**, 115–120.

Gardner, T., Hernández, M.M.I., Barlow, J. & Peres, C. (2008) The value of primary, secondary and plantation forests for a neotropical dung beetle fauna. *Journal of Applied Ecology*, **45**, 883–893.

Giller, P.S. & Doube, B.M. (1989) Experimental analysis of inter- and intraspecific competition in dung beetle communities. *Journal of Animal Ecology*, **58**, 129–142.

Gittings, T. (1998) Resource quality and the colonization and succession of coprophagous dung beetles. *Ecography*, **21**, 581–592.

Gotelli, N.J. & Colwell, R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, **4**, 379–391.

Halffter, G. & Edmonds, W.D. (1982) *The Nesting Behavior of Dung Beetles (Scarabaeinae): an Ecological and Evolutive Approach*. Instituto de Ecología, México, D.F.

Hammer, Ø., Harper, D.A.T. & Ryan, P.D. (2001) PAST: paleontological statistics software package for education and data analysis. *Palaeontologia Electronica*, **4**, 1–9.

Hanski, I. (1987). Nutritional ecology of dung and carrion feeding insects. *Nutritional Ecology of Insects, Mites and Spiders* (ed. by J.F. Slanky & J.G. Rodriguez), pp. 837–884. Wiley, New York.

Hanski, I. & Cambefort, Y. (1991) *Dung Beetle Ecology*. Princeton University Press, Princeton, New Jersey.

Holt, A.R., Gaston, K.J. & He, F.L. (2002) Occupancy-abundance relationships and spatial distribution: a review. *Basic and Applied Ecology*, **3**, 1–13.

Howden, H.F. & Nealis, V.G. (1975) Effects of clearing in a tropical rain forest on the composition of the coprophagous scarab beetle fauna (Coleoptera). *Biotropica*, **7**, 77–83.

IBGE (2007) *Levantamento Sistemático da produção Agrícola Brasileira*. Instituto Brasileiro de Geografia e Estatística (IBGE), Rio de Janeiro, Brazil.

Koller, W., Gomes, A., Rodriguez, S. & Oliveiera, R. (1999) Besouros coprófagos (Coleoptera: Scarabaedae) coletados em Campo Grande. *Anais da Sociedade Entomológica do Brasil*, **28**, 403–412.

Koller, W.W., Gomes, A., Rodrigues, S.R. & Goiozo, P.F.I. (2007) Scarabaeidae e Aphodiidae coprófagos em pastagens cultivadas em área do cerrado sul-mato-grossense. *Revista Brasileira de Zoociências*, **9**, 81–93.

Linquist, A. (1933) Amounts of dung buried and soil excavated by certain Coprini (Scarabaeidae). *Kansas Entolomogical Society*, **6**, 109–124.

Louzada, J.N.C. & Lopez, F.S. (1997) The dung beetle community from an Atlantic forest fragmentation. *Revista Brasileira de Entomologia*, **41**, 117–121.

Magurran, A.E. (1988) *Ecological Diversity and Its Measurement*. Princeton University Press, Princeton, New Jersey.

Marchiori, C.H. (2000) Espécies de Scarabaeidae (Insecta: Coleoptera) coletadas em fezes bovinas e carcaça de suínos em Itumbiara, Goiás, Brasil. *Pesquisa Agropecuária Tropical*, **30**, 1–4.

Marchiori, C.H. (2003) Insects (Arthropoda: Insecta) collected on bovine feces after different times of field exposure in Itumbiara, Goias, Brazil. *Arquivos do Instituto Biológico*, **70**, 377–380.

Marchiori, C.H., Oliveira, A.T. & Linhares, A.X. (2001) Artrópodes associados a massas fecais bovinas no sul do estado de Goiás. *Neotropical Entomology*, **30**, 19–24.

Markin, G.P. & Yoshioka, E.R. (1998) Biological control of the horn fly, *Haematobia irritans* L., in Hawaii (Diptera: Muscidae). *Proceedings of the Hawaiian Entomological Society*, **33**, 43–50.

Mendes, J. & Linhares, A.X. (2006) Coleoptera associated with undisturbed cow pats in pastures in southeastern Brazil. *Neotropical Entomology*, **35**, 715–723.

Menédez, R. & Gutierrez, D. (1996) Altitudinal effects on habitat selection of dung beetles (Scarabaeoidea: Aphodiidae) in the northern Iberian peninsula. *Ecography*, **19**, 313–317.

Milhomem, M.S., De Mello, F.Z.V. & Diniz, I.R. (2003) Collection techniques of dung beetle in the Cerrado, Brazil. *Pesquisa Agropecuaria Brasileira*, **38**, 1249–1256.

Miranda, C.H.B., Nascimento, Y.A. & Bianchin, I. (1990) Desenvolvimento de um programa integrado de controle dos nemat¢deos e a mosca-dos-chifres na região dos cerrados. Fase 4. Contribuição de *Onthophagus gazella* para a fertilidade do solo pelo enterrio de fezes bovinas. *Pesquisa em andamento. EMBRAPA*, **43**, 1–5.

Monteiro, C.M.O., Koller, W.W. & dos Reis, E.S. (2006) Besouros coprófagos (Coleoptera: Scarabaeoidea) presentes nas pastagens do campo experimental da Embrapa gado de leite, no município de Coronel Pacheco, Minas Gerais. *XXXIX Semana de Biologia e XII Mostra de Produção Científica – UFJF* (ed. by Editoria UFJF), Vol 1, pp. 29–33. Diretório Acadêmico de Ciências Biológicas, Juiz de Fora, Brazil.

Nichols, E., Spector, S., Louzada, J., Larsen, T., Amezquita, S., Favila, M. & Network, T.S.R. (2008) Ecological functions and ecosystem services of Scarabaeine dung beetles: a review. *Biological Conservation*, **141**, 1461–1474.

Oliveira, G.P., Silva, A.L., Mendes, J. & Tavares, L.N.J. (1996) Insetos associados a fezes de bovinos na região de São Carlos, São Paulo. *Ciência Agronômica*, **27**, 39–42.

Owen, W.K., Lloyd, J.E., Legg, D.E. & Kumar, R. (2006) Endocoprid activity of Aphodius fossor (Coleoptera: Scarabaeidae) related to bovine dung decomposition in a mixed grass prairie. *Journal of Economic Entomology*, **99**, 2210–2215.

Pereira, C.C.A., Chaves, D.P., Koller, W.W., Conceição, W.L.F., Rodrigues, S.R., Gomes, A. & Costa-Junior, L.M. (2003) Ocorrência de coleópteros Scarabaeidae (coprófagos e necrófagos), Aphodiidae, Histeridae e Hydrophilidae em fezes bovinas na ilha de São Luís, Maranhão, Brasil – resultados preliminares. *Revista Universidade Rural*, **23**, 327–328.

Pinero, F.S. & Avila, J.M. (2004) Dung-insect community composition in and zones of south-eastern Spain. *Journal of Arid Environments*, **56**, 303–327.

Ridsdill-Smith, T.J. (1981) Some effects of three species of dung beetles (Coleoptera: Scarabaeidae) in south-western Australia on the survival of the bush fly, *Musca vetustissima* Walker (Diptera: Muscidae), in dung pads. *Bulletin of Entomological Research*, **71**, 425–433.

Rodrigues, S.R. & Marchini, L.C. (1998) Besouros coprófagos (Coleptera, Scarabaeidae) coletados em Piracicaba, SP. *Scientia Agricola*, **55**, 53–58.

Scheffler, P.Y. (2005) Dung beetle (Coleoptera: Scarabaeidae) diversity and community structure across three disturbance regimes in eastern Amazonia. *Journal of Tropical Ecology*, **21**, 9–19.

Silva, F.A.B., Hernandez, M.I.M., Ide, S. & de Moura, R.D. (2007) Comunidade de escarabeíneos (Coleoptera, Scarabaeidae) copro-necrófagos da região de Brejo, Caruaru, Pernambuco, Brasil. *Revista Brasileira de Entomologia*, **51**, 228–233.

Silva, P.G., Garcia, M.A.R., Audino, L.D., Nogueira, J.M., Moraes, L.P., Ramos, A.H.B., Vidal, M.B.U. & Borba, M.F.S. (2006) Besouros rola-bosta: insetos benéficos das pastagens. *Revista Brasileira de Agroecologia*, **2**, 1428–1432.

Veech, J.A., Summerville, K.S., Crist, T.O. & Gering, J.C. (2002) The additive partitioning of species diversity: recent revival of an old idea. *Oikos*, **99**, 3–9.

Wallace, M.M.H. & Holm, E. (1983) Establishment and dispersal of the introduced predatory mite, *Macrocheles peregrinus* Krantz, in Australia. *Australian Journal of Entomology*, **22**, 345–348.

Yokoyama, K., Kai, H., Koga, T. & Kawaguchi, S. (1989) Effect of dung beetle *Onthophagus lenzii* H. on nitrogen transformation in cow dung and dung balls. *Soil Science and Plant Nutrition*, **37**, 341–345.

Accepted 15 October 2008
First published online 26 November 2008

Editor: Simon Leather
Associate editor: Donald Quicke