ORIGINAL ARTICLE

Local and regional ecological morphology of dung beetle assemblages across four biogeographic regions

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ABSTRACT

Aim Niche partitioning within species assemblages is thought to influence species packing and/or total niche space occupied. The evolution of dung beetles (Scarabaeinae) is likely to have been strongly influenced by inter-specific competition, leading to niche partitioning. We consider whether local-scale processes leave a signature in regional patterns of functional diversity in dung beetle assemblages, and investigate the correlation between total exploited ecomorphological space and density of species packing with increased species richness. We test whether ecomorphological space occupied by local assemblages reflects that of their regional species pool, and the extent to which ecomorphological space is convergent or divergent within functional groups across regional pools.

Location Neotropics, Africa, Australia and Madagascar.

Methods Dung beetle assemblages were collected in a standardized manner from four biogeographic regions. Ecomorphological similarity among the assemblages was assessed by multivariate analysis of 19 linear measurements for 300 species and three functional nesting types (roller, tunneller or dweller), firstly on a local level within the Neotropics and Afrotropics, and then between the regional species pools.

Results Key body measurements, in particular the hind tibia, separated rollers and tunnellers into largely non-overlapping entities along the first three axes of the shape analysis. Three Neotropical assemblages, which vary widely in species numbers, each harboured a similar amount of morphometric variation, resulting in increasingly dense species packing with greater species richness. Similar findings were obtained in two South African assemblages. Assemblages in the four biogeographic regions showed largely similar distributions of ecomorphological variation, including the separation of rollers and tunnellers, despite their distant phylogenetic relationships. Ecomorphological similarity among regions was particularly high in tunnellers, whilst the rollers exhibited greater regional differentiation.

Main conclusions Local assemblages evidently represent the full diversity of functional groups available in the regional pool, even in species-poor assemblages. There is a strong trend towards convergence in morphology separating tunnellers and rollers in phylogenetically independent lineages. The ecomorphological similarity of regional assemblages suggests that morphological convergence is the result of common selective forces active within the assemblages themselves. This lends support to the widely hypothesized effect of inter-specific interactions and niche partitioning in determining assemblage composition and lineage evolution in the Scarabaeinae.

Keywords
Assemblage structure, convergence, dung beetles, ecomorphology, functional morphology, niche partitioning, Scarabaeinae.

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INTRODUCTION

How species within natural assemblages subdivide resources and occupy niche space, and the extent to which niche space occupancy is determined by regional species pools, are questions that have long interested ecologists and biogeographers (e.g. MacArthur, 1972; Lawton, 2000). Ecomorphological analyses have proven to be a powerful means of testing the relative prevalence of two opposing processes (e.g. Travis & Ricklefs, 1983; Richman & Price, 1992; Wainwright & Reilly, 1994; Aguirre *et al.*, 2002; Bellwood *et al.*, 2002): limiting similarity (driven by inter-specific competition) maintaining differences in niche position between species (e.g. May & MacArthur, 1972); and environmental filtering, a process that sets the boundaries of potential niche space outside which species are no longer adapted to their local environments (Lawton, 2000). It has been argued that niche partitioning results in a positive relationship between species richness and the ecomorphological diversity of animal assemblages (Ricklefs & Miles, 1994). Here we examine an insect assemblage long considered to be influenced by the impact of inter-specific competition, the dung beetles (Scarabaeinae).

Dung beetles are a model group for comparative studies of niche partitioning and functional structure of natural assemblages. Since dung tends to be patchy in distribution and ephemeral, competition for it as a food source and/or breeding substrate is likely to have strongly influenced the evolution of assemblage diversity and structure in dung beetles (e.g. Peck & Forsyth, 1982; Hanski & Cambefort, 1991a; Giller & Doube, 1994; Finn & Gittings, 2003; Horgan & Fuentes, 2005). In the tropics, the Scarabaeinae usually comprise the dominant dung-feeding insects (Hanski, 1991a). Scarabaeinae are well studied in terms of their natural history and are an accepted monophyletic group (Janssens, 1949; Balthasar, 1963; Cambefort, 1991a), while recent studies have improved our understanding of their phylogenetic relationships (e.g. Philips *et al.*, 2004; Monaghan *et al.*, 2007) and historical biogeography (Davis *et al.*, 2002). Moreover, the composition of a scarabaeine assemblage can be sampled efficiently by trapping with various baits (e.g. Hanski, 1983).

Based upon nesting and feeding strategies, dung beetle species can be classified into three functional groups: 'rollers' (telecoprids), 'tunnellers' (paracoprids) or 'dwellers' (endocoprids). The latter nest and feed within the dung pat or at the interface between the dung pat and soil surface, and lay eggs within a simple nest. Tunnellers and rollers move dung underground for feeding and breeding. Burrows are excavated for this purpose directly beneath the resource by tunnellers, whilst rollers fashion balls of dung and roll them away for burial elsewhere.

The Scarabaeinae are well suited for global comparisons of niche partitioning and functional structure, as phylogenetically distinct assemblages are present in the major biogeographic realms, in particular in sub-Saharan Africa, the Neotropics, the Oriental Region, Australia and Madagascar. This was confirmed by molecular phylogenetic analyses of Scarabaeinae (Monaghan *et al.*, 2007), which revealed endemic clades in each region. However, the range of nesting and feeding behaviours in each region is strikingly similar, while many phylogenetically independent taxa also show remarkable morphological similarity. The phylogenetic studies also confirm the non-monophyly of the nesting strategies, contrary to the assumption of early classifications (e.g. Balthasar, 1963). Nesting types appear to be evolutionarily plastic, including the presumably derived rolling behaviour, which was inferred to be present early in the evolution of Scarabaeinae but was lost and gained on multiple subsequent occasions (Philips *et al.*, 2004; Monaghan *et al.*, 2007).

Competition is often invoked as a selective force leading to resource partitioning in communities (e.g. Ricklefs & Miles, 1994). Hence, while actual species interactions, and competition in particular, are difficult to detect and measure, evidence of niche partitioning may reflect the 'ghost of competition past' (Connell, 1980). Morphological traits are an important manifestation of the niche position of species and can therefore be used in studies of niche partitioning within assemblages. The ecomorphological approach (Reilly & Wainwright, 1994) used in the present study assumes that differences in the species ecology and behaviour are reflected in body size and allometric shape variation (e.g. Ricklefs & Travis, 1980; Travis & Ricklefs, 1983; Douglas & Matthews, 1992; Ribera *et al.*, 1999; Melville *et al.*, 2006). If inter-specific competition is indeed shaping the composition of assemblages, coexisting species are expected to show ecomorphological differences that reflect niche partitioning (e.g. Richman & Price, 1992; Ricklefs & Miles, 1994). Ecological niche partitioning is believed to occur in numerous ways in dung beetle assemblages, e.g. through differentiation in body size, diet choice, diel activity, endothermy and behavioural or reproductive (nesting) strategy (e.g. Hanski, 1991b; Krell-Westerwalbesloh *et al.*, 2004; Verdú *et al.*, 2007). Much of this ecological diversity is likely to be reflected in the functional morphology of dung beetles; yet we understand little of how niche partitioning influences species packing and total ecomorphological space occupied in local dung beetle assemblages, where current ecological traits rather than lineage history could be expected to be the major influence. Furthermore, in a system in which evolutionary diversification is likely to have been strongly influenced by inter-specific competition, we now have an opportunity to investigate how processes considered to operate at local scales may also influence regional patterns of diversity (reflected in total regional ecomorphological niche space).

In this study we use multivariate analysis of measurements of external body shapes to investigate how species within local dung beetle assemblages occupy niche space (Wainwright & Reilly, 1994). Specifically, we test for evidence of two alternative scenarios of community assembly: (1) whether an increase in species richness is associated with an increase in ecomorphological space occupied, while maintaining constant species packing density; or (2) whether species richness increase is reflected in a greater density of species packing rather than an expansion of ecomorphological space. We test

this using three Neotropical assemblages differing in species richness, and briefly compare the findings with local assemblages in the southern Afrotropics. We go on to compare four biogeographically distinct regional dung beetle assemblages (representing different regional pools), and assess the extent to which they share similar occupancy of ecomorphological space. We investigate how the three major functional groups (rollers, tunnellers and dwellers) occupy this space in different biogeographic regions, and whether occupancy of ecomorphological space reflects convergent evolution by phylogenetically distinct taxa, niche conservatism among closely related taxa or divergent evolution (e.g. Bellwood *et al.*, 2002; Melville *et al.*, 2006).

MATERIALS AND METHODS

Study sites and trapping protocol

Dung beetle assemblages were collected at nature reserves in Belize, Ecuador, South Africa and Madagascar (Inward, 2002), and additionally in Australia by G. Monteith (Queensland Museum). Sites were chosen to be minimally affected by human disturbance. Collecting was timed to coincide with the period of highest activity; generally in the early part of the 'rainy season' (Janzen, 1983; Davis, 1987; Doube, 1991), except in the Western Cape, South Africa, where peak abundance is in the spring/early summer, following the winter rainfall period (Davis, 1987, 2002). A standardized trapping protocol was designed to enable quantitative comparisons of species composition by collecting the majority of species in an assemblage (Inward, 2002). This method consisted of baited pitfall traps deployed along a series of six transects (>500 m apart), of 10 traps each, for each bait type used (60 traps in total). The basic protocol used fresh cattle dung and carrion to attract coprophagous and necrophagous beetles, respectively, with additional bait types deemed most appropriate for the region (detailed below). Necrophagy (carrion feeding) is a widespread behaviour, occurring in most tropical scarabaeine assemblages and taxonomic groups to some extent, often as part of a generalist-type diet (e.g. Matthews, 1974; Hanski, 1983; Gill, 1991; Feer, 2000; Inward, 2002; Tshikae *et al.*, 2008). Traps were left for 2 days, the catch collected and preserved in ethanol, and the dung-baited traps were then re-baited with fresh dung to retain their attractiveness for a further 2 days. This gave a trapping effort of approximately 240 trap-days for each bait type. Additionally, two flight intercept traps (FITs), an effective method of capturing actively foraging dung beetles (Hill & Cermak, 1997), were set up locally and run for approximately 2 weeks, to collect diet specialists (e.g. feeding on decaying fungi and fruit, or small-sized dung pellets). These methods collect species from all feeding groups. Many taxa exhibit generalist tendencies, and species are rarely so closely associated with one resource that a few specimens are not collected with other bait types. Given the lack of clear functional divisions based on feeding substrate, we analysed individuals from all trap types together.

The effectiveness of the pitfall trapping protocol was tested at the sampling site in Belize; a variety of species richness estimates were calculated from the individual trap data using ESTIMATES v. 8.2 (Colwell, 2009), including the Chao 1 and Chao 2 estimators considering rare species occurring once or twice, abundance- and individual-based coverage estimators (ACE and ICE) considering species occurring 1–10 times, and jackknife and bootstrap resampling analyses. These returned estimates suggesting that between 75% (Chao 1 and 2) and 94% (bootstrap) of species had been collected from the moist forest assemblage by the baited traps (mean of all estimators 85%). Similarly, estimates were 88–95% of species sampled in Ecuador, and 91–97% in the Kruger National Park (South Africa).

We investigated local-scale assemblage structure in three Neotropical assemblages from distinct forest types. The most northerly was Mountain Pine Ridge (MPR) in the Cayo region, Belize (17°03′ N, 88°56′ W), a relictual area of natural pine–oak forest. Broadleaf moist forest was sampled some 50 km south of MPR at the Las Cuevas Field Research Station (16°44′ N, 88°59′ W) in the Chiquibul forest reserve. Both sites are at elevations of 400–600 m. In addition to cattle dung and carrion, fresh horse and tapir (non-ruminant) dung was used to contrast with the cattle (ruminant) dung, but proved less attractive, dried out quickly and did not collect any additional species to the cattle dung sample (Inward, 2002). Human dung was also used as a substitute for other omnivore dung types, such as peccaries and monkeys (e.g. Howden & Nealis, 1975; Feer, 2000). It was also used in baited canopy traps, similar to those employed by Davis *et al.* (1997), to target canopy specialists feeding on primate dung. These sites experience moderate seasonality in rainfall, and standardized collecting was conducted during the wetter period. An additional collection of dung beetles during the drier period found, however, that although abundance is reduced, species composition of the assemblage was little affected (Inward, 2002).

A third Neotropical study site was located at the Tiputini Biodiversity Station in the Yasuni Forest Reserve, Napo region, Ecuador (0°38′ S, 76°09′ W). This is primary lowland tropical rain forest, at an elevation of 250 m. Species diversity is known to be high in this region; 473 species of tree have been recorded in a single 1-ha plot in Amazonian Ecuador (Valencia *et al.*, 1994). This wet forest site is relatively aseasonal in its rainfall, and the dung beetles also exhibit reduced seasonality (Peck & Forsyth, 1982). As well as cattle dung and carrion, human dung was again employed at ground level and in canopy traps, as was rotting fruit.

Trapping in South Africa was conducted in Kruger National Park, in thornveld savanna with patches of *Acacia* woodland, south-east of Skukuza (24°50′ S, 31°35′ E). This is floristically rich with an abundant and intact mammal fauna, and represents one of the most species-rich dung beetle assemblages in sub-Saharan Africa. In addition to cattle dung and carrion, fresh elephant dung (a non-ruminant type) was also used here to reflect the diversity of herbivore dung types

available. Hand-collecting from a variety of dung types enabled the collection of species that were not otherwise attracted to pitfall traps, such as the large tunnellers of the genera *Heliocopris* and *Heteronitis*, which presumably require a larger resource than the baits provided, and the flight intercept traps yielded species such as the mycetophagous *Coptorhina nitidipennis*. A contrasting mediterranean-type African assemblage was sampled at the West Coast National Park (33°10′ S, 18°05′ E) in the Western Cape province of South Africa, where the scarabaeine fauna includes some phylogenetically distinctive groups (Cambefort, 1991b; Philips *et al.*, 2004; Monaghan *et al.*, 2007). Again, cattle dung and carrion baits were employed, whilst horse dung was substituted for the elephant dung, as the only regularly available large non-ruminant mammal dung. An additional bait of millipede carrion (family Spirostreptidae) was used here to target *Sceliages*, which specialize on this resource (Bernon, 1981). The 'strandveld' vegetation of this site is dominated by sclerophyllous shrubs such as *Euclea*, and marine-influenced dune thicket.

Three species-rich dung beetle assemblages were sampled in Madagascar (Monaghan *et al.*, 2009) from rain forest habitats in the east, in Ranomafana National Park (21°16′ S, 47°25′ E), Mantadia-Andasibe (Perinet) National Park (18°49′ S, 48°26′ E) and the Makira reserve (15°2′ S, 49°34′ E). Assemblages were also collected from two dry, seasonal forests in the north, in Montagne d'Ambre National Park (12°32′ S, 49°10′ E) and Ankarana special reserve (12°56′ S, 49°04′ E). Owing to the importance of lemur dung in these habitats, this dung type was mimicked by additionally trapping with human dung.

The richest scarabaeine fauna in Australia is found in the tropical rain forest of northern Queensland (Matthews, 1974), to which many of the endemic canthonine species are restricted. This was represented by two sites: Bloomfield Road (lowland rain forest, 15°48′ S, 145°19′ E), and Charmillin Creek (upland rain forest, 17°42′ S, 145°31′ E). Another important dung beetle habitat in Australia is the open (sclerophyllous) forest dominated by *Eucalyptus*, here represented by assemblages from Hartleys Creek (lowland open forest; 16°40′ S, 145°34′ E) and Ravenshoe Road (upland open forest; 17°38′ S, 145°30′ E). Although not collected using our standardized protocol, trapping for this region was considered to be of equal effort, with the same aim of collecting all species present (G. Monteith, pers. comm.).

For comparison of the regional faunas, the dung beetle assemblages of distinct and complementary habitats were pooled to represent the ecomorphological range of dung beetle species present in each region. Thus the Neotropics was represented by the beetles collected at the three forest sites, Africa by a lowland savanna and a Cape fynbos habitat, Australia by two rain forest and two open forest sites, and Madagascar by three rain forest and two dry forest sites. In general, the Neotropical and African dung beetle assemblages are considerably more species rich than those of Madagascar and Australia, so the number of assemblages included reflects an attempt to best represent the overall ecomorphological diversity of each region, while keeping the numbers of species measured at least broadly similar.

Functional group classification and representation

All species were categorized by functional group according to Cambefort (1991b), who distinguishes rollers, tunnellers and dwellers based on the observed or assumed nesting behaviour of each scarabaeine genus, and assumes that all members of each genus retain the same broad functional type. Our classification deviates from Cambefort (1991b) in a few cases, including the Neotropical species of *Eurysternus*, which are often considered to be rollers (e.g. Cambefort, 1991b) but here are designated as dwellers. *Eurysternus* feed from within the dung resource (Halffter *et al.*, 1980) and although females form balls for reproduction, they remain within the dung pats and no rolling has ever been observed. Finally, kleptoparasites are treated as a subgroup of tunnellers, because their use of dung gathered by other larger species may be an opportunistic use of a resource rather than a distinct adaptive strategy (Martín-Piera & Lobo, 1993). Kleptoparasitism appears largely restricted to the African scarabaeines (Halffter & Matthews, 1966; Hammond, 1976; Endrödy-Younga, 1982; Cambefort & Hanski, 1991), with a few in the Neotropics and Australia (Halffter & Matthews, 1966; Verdú & Galante, 2001).

Morphometric variables

For all species collected, 19 linear measurements were recorded from the body and hind leg for three specimens each (wherever available) (Table 1; illustrated in Appendix S1 in Supporting Information). Measurements were chosen to reflect various facets of their functional ecology, and to best represent the diversity of morphology within the group. Photographs were taken dorsally, laterally and of the hind leg, using Auto-Montage v. 3.03 software (Synoptics Ltd., 2000) to produce multilayered composite digital images with the entire specimen in focus. To avoid any potential bias caused by sexual dimorphism, only females were used. A total of 300 species were measured, including 107 Neotropical, 98 African, 57 Australian and 38 Madagascan (Appendix S2).

Analysis of morphospace

Principal components analysis (PCA) was used to describe the morphological space occupied by local dung beetle assemblages or regional faunas. Each raw measurement was log-normalized, and for each species the mean values from the three specimens calculated. To remove the confounding effects of body size (Reilly & Wainwright, 1994), by partitioning the size and shape elements from one another, residual values were calculated from a regression of the species log measurement values against corresponding mean body size. This was carried out in STATISTICA v. 5.5 (StatSoft Inc., 1999), using a body size index (the sum of lengths of elytra + pronotum). The residuals

Table 1 Description of the 19 linear morphometric measurements recorded from the body and hind leg of dung beetle specimens.

Dorsal measurements	
1	Length of pronotum
2	Length of elytra
3	Maximum width of pronotum
4	Distance from (3) to anterior of pronotum
5	Maximum width of elytra
6	Distance from (5) to posterior apex of elytra
7	Width of head (inter-ocular distance)
Lateral measurements	
8	Length of head from clypeus to carina of temple
9	Maximum height of elytra from side margin
10	Distance from (9) to posterior apex of elytra
11	Height of abdomen, measured from (9)
Hind leg measurements	
12	Length of femur
13	Maximum width of femur
14	Inside length of tibia (curved)
15	Inside length of tibia (straight line)
16	Maximum distance from (14) to (15)
17	Width of tibia across apex
18	Area of tibia (mm square)
19	Length of tarsi (not including claws)

were then used together with the body size index in the PCA analysis, performed using CANOCO v. 4.0 (ter Braak & Šmilauer, 1998). This has the effect of confining body size to the first axis, whilst the subsequent axes describe only shape. An analysis was performed combining all Neotropical species to explore the assemblage-level differences at a local habitat level. A second analysis included all species from each of the four regions. The species scores for the resulting PCA ordination plot of global scarabaeine morphospace were then separated by region, allowing direct comparison between them.

Homogeneity of variances (Levene) tests were applied to the PCA species coordinates using STATISTICA, whereby the assumption was confirmed that each local assemblage of the Neotropics shares a consistent variance of species distribution along the first three PCA axes (Table S1 in Appendix S3). This justified the application of multivariate analysis of variance (MANOVA) to test for significant differences between the occupation of morphospace by the different assemblages and to compare the distribution of the functional nesting groups relative to each other and across the assemblages. Where a significant overall difference in morphospace was found, a *post-hoc* Tukey's honestly significant difference (HSD) test was performed to identify where the differences exist. A two-dimensional measurement of area of the morphospace occupied by individual functional groups and assemblages was calculated from the ordination diagrams. Digital images of the diagrams were produced and the perimeter was traced using AUTO-MONTAGE, calibrated using the scales of the axes, and a comparable measurement of area was produced that is equivalent to a convex hull volume measure. As a measure of species packing in ecomorphological

space, the mean nearest neighbour distances (NNDs) were calculated for each assemblage from the pairwise distances between the PCA coordinates of each species.

RESULTS

Functional morphology of the local Neotropical assemblages

In total, 11 species of Scarabaeinae were collected at Mountain Pine Ridge, Belize (MPR), 36 species at Las Cuevas, Belize, and 68 species at Tiputini Biodiversity Station, Ecuador (Appendix S2). Some 12,000 specimens were collected across these sites, with species abundances ranging from 1 to 3300 individuals. It is apparent that the species at MPR are fundamentally a subset of the species at Las Cuevas, whilst there is very little species overlap between Las Cuevas and Tiputini. Generic overlap, however, remains high between the three sites, with the Belizean genera largely consisting of a subset of those found at Tiputini. Biplots of the first three axes constructed by PCA for the Neotropical assemblages are presented in Figs 1 & 2. The first ordination axis was found to explain 39.8% of the total variance in the measurements, whilst axes 2 and 3 explained 20.6% and 14.8% (Table S2 in Appendix S3). Body size alone is represented by axis 1, and is excluded from axes 2 and 3 (Fig. 1). The species in each assemblage were separated along axis 2 according to functional behaviour: rolling and tunnelling. Axis 2 is most strongly positively correlated with measurements 14, 15 and 16 (Table S2 in Appendix S3), representing a greater relative length and degree of curvature of the hind tibiae. These can be considered as being 'roller characteristics'. This axis is strongly negatively correlated with measurements 4, 17 and 3 ('tunneller characteristics'), indicating that these species have a larger-proportioned pronotum and a greater width of the tibia at its apex.

In each assemblage, much of the morphospace occupied by the dwellers falls within that of the rollers on axes 1 and 2. The smaller rollers and tunnellers also exhibit a slight overlap, whilst these functional groups move apart on both axes, suggesting that their shapes diverge more as the species become larger. When considering shape alone (axes 2 and 3), the tunnellers are separated from the rollers by measurements 9, 5 and 3 in particular (tunnellers show relatively greater height and width of elytra, and greater pronotum width), and to a lesser extent by measurements 8 and 7 (greater width and length of head) (Fig. 2). The tunnellers are separated from the dwellers by measurements 14, 15 and 16, indicating that the tunnellers have relatively shorter and less curved hind tibiae. Finally, the dwellers occupied similar areas of the morphospace as the rollers on axes 1 and 2, but are in fact well separated along axis 3. Their division can be seen to correlate most closely with measurements 18 and 12, reflecting their longer hind femora and a greater area to the hind tibiae. MANOVA tests performed upon the species PCA coordinates, followed by Tukey's HSD tests, confirm that the three functional groups in
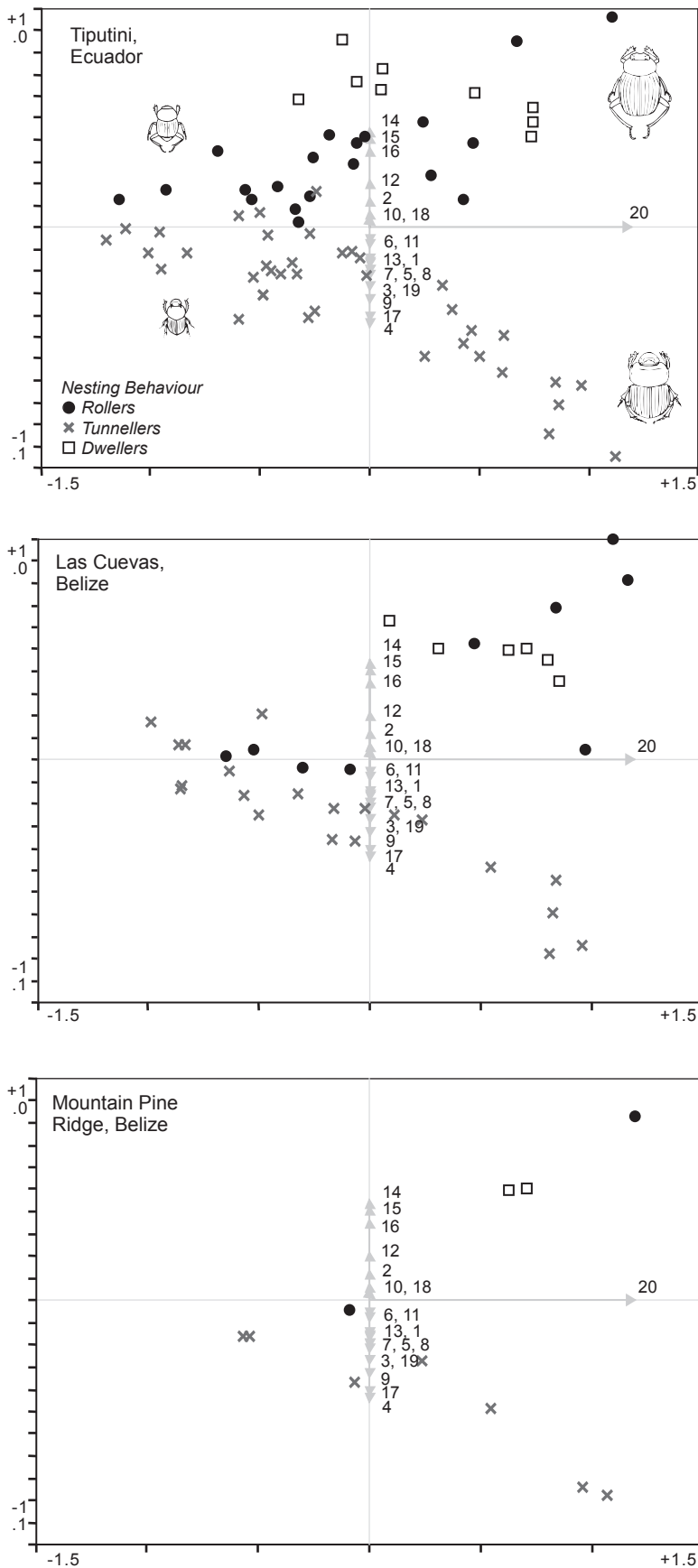
Figure 1 Principal components analysis (PCA) biplots illustrating the morphospace occupied by three Neotropical dung beetle assemblages (axes 1 and 2). Linear measurements of body shape (Table 1) are represented by numbered arrows, indicating the loading of each measurement on each PC axis, and pointing in the direction of increase of the measurement across the species analysed. Species are coded according to their nesting behaviour. The approximate distribution of large and small rollers and tunnellers in morphospace is illustrated.

Figure 2 Principal components analysis (PCA) biplots illustrating the morphospace occupied by three Neotropical dung beetle assemblages (axes 2 and 3). Linear measurements of body shape (Table 1) are represented by numbered arrows, indicating the loading of each measurement on each PC axis, and pointing in the direction of increase of the measurement across the species analysed. Species are coded according to their nesting behaviour.

the Neotropical forests occupy significantly different positions in morphospace along both axes 2 and 3 ($P < 0.001$; Table S1 in Appendix S3).

Local assemblage structure

The Levene test for homogeneity of variances showed no significant differences in the sampling of species variance among the three Neotropical assemblages as drawn from the combined species pool. MANOVA tests further revealed that within each functional group, compared among the three assemblages, there was no significant difference in the areas of morphospace occupied on any of the first three axes (Table S1 in Appendix S3). Measurements of the morphospace for the three assemblages indicate only a slight reduction in area with a decreasing number of species, particularly when the body size component is removed; Las Cuevas maintains 92% of the total area of Tiputini, and MPR has 88% of the area of Las Cuevas (Table 2), i.e. the total shape variation in local Neotropical assemblages is similar over a wide range of species numbers. This is supported by decreasing nearest neighbour distance from the species-poor assemblage at MPR to the species-rich Tiputini (Table 2), indicating increased species density, rather than expanding total morphospace.

Regional assemblage structure

The consistency of morphological variation identified in the local Neotropical assemblages justifies combining them into a single composite regional species pool for comparisons of assemblage structure at the continental scale. An examination of the morphospace areas occupied by the species-rich and species-poor habitats in the African data set (Kruger and West Coast National Parks, respectively) through homogeneity of variances tests, and subsequent MANOVA tests, similarly reveals that no significant differences existed between them in either the variance or mean position in morphospace distribution along each of the first three axes. Thus composites of several local dung beetle assemblages are likely to be a good representation of the total variation present on a continent.

In the analysis of the four major regional assemblages, the first three ordination axes were found to explain 39% of the total variance for axis 1 (representing size), with axis 2 explaining 18.5% and axis three 12.5% (Table S2 in Appendix S3). As with the local Neotropical analysis, the functional nesting groups in the regional analysis remain
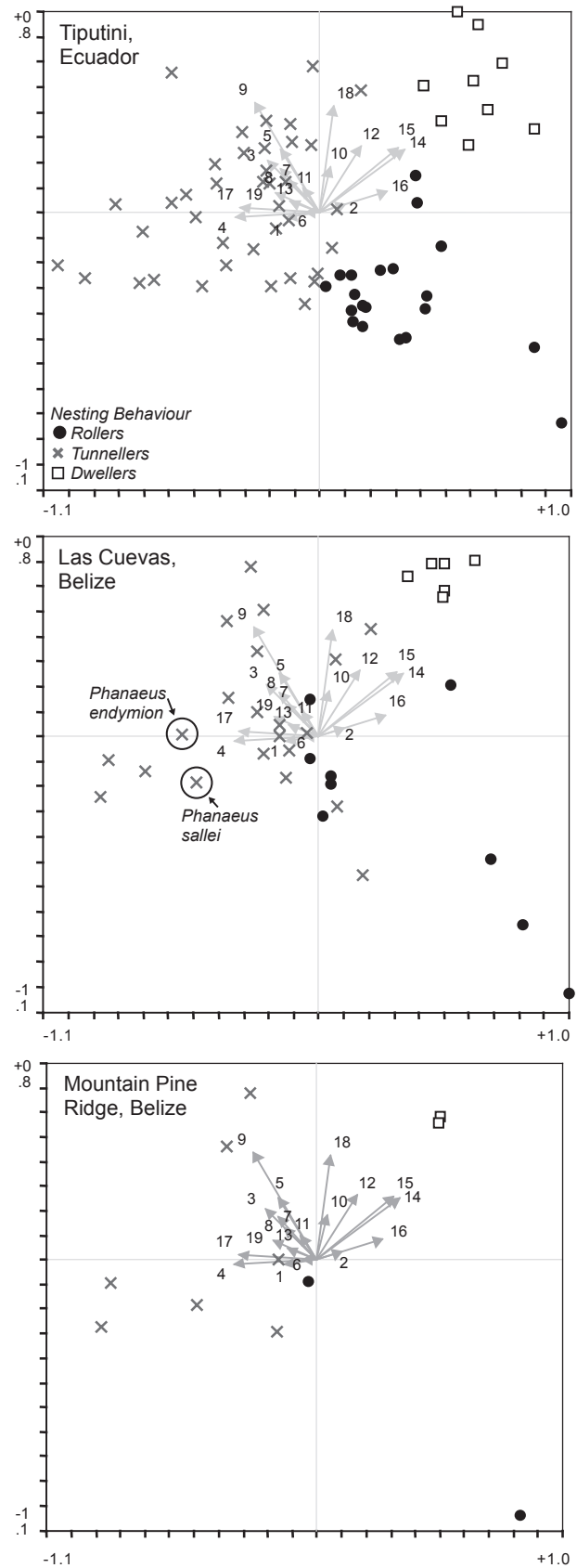
Table 2 Two-dimensional morphospace areas and nearest neighbour distances for principal components analysis (PCA) axes 1 and 2, and axes 2 and 3, for the Neotropical assemblages of dung beetles. Area values are given for the total regional species pool and for each functional nesting group. Mean nearest neighbour distances between species are also given for the whole assemblage in each case. (The required minimum three species were not available for rollers and dwellers at Mountain Pine Ridge, Belize.)

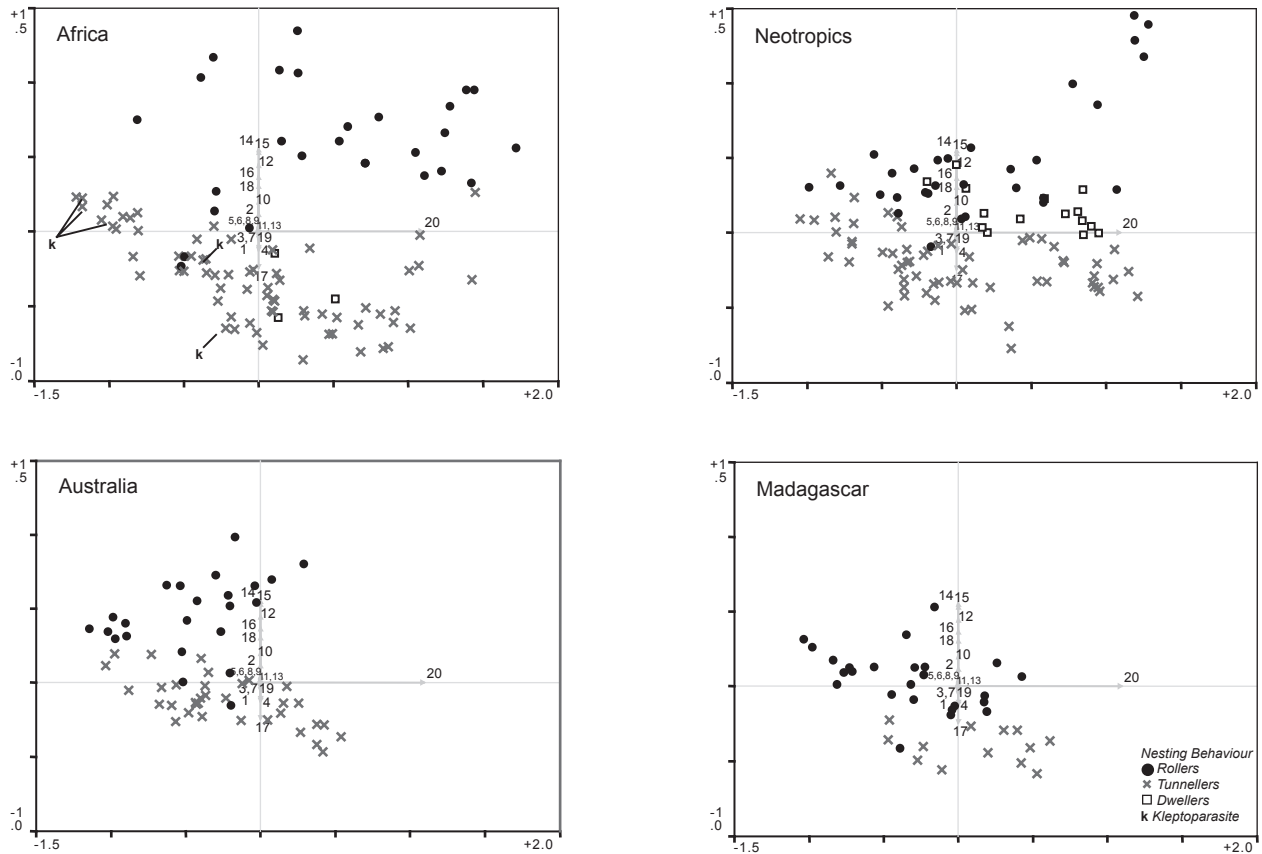|	Tiputini, Ecuador		Las Cuevas, Belize		Pine Ridge, Belize	
	Axes 1 & 2	Axes 2 & 3	Axes 1 & 2	Axes 2 & 3	Axes 1 & 2	Axes 2 & 3
Morphospace areas						
All species	3.039	2.083	2.28	1.91	1.454	1.679
Rollers	0.835	0.38	0.876	0.582		
Tunnellers	1.013	0.806	0.759	0.85	0.215	0.397
Dwellers	0.227	0.134	0.059	0.021		
Mean nearest neighbour distance	0.913	0.705	1.008	0.76	1.056	0.936

Figure 3 Principal components analysis (PCA) biplots illustrating the morphospace occupied by regional dung beetle assemblages (axes 1 and 2). Linear measurements of body shape (Table 1) are represented by numbered arrows, indicating the loading of each measurement on each PC axis, and pointing in the direction of increase of the measurement across the species analysed. Species are coded according to their nesting behaviour.

distinctly separated along axis 2 (Fig. 3). Strikingly, the same characteristics are shared between regions (longer and more curved tibia, and a longer femur in the rollers, and a wider, more spade-like tibia in the tunnellers; Table S2 in Appendix S3). These similarities in functional morphology underline the general consistency of morphospace usage by the rollers and tunnellers of each biogeographic region (Figs 3 & 4), and no significant differences were found between any

region along this key roller–tunneller axis (Table S1 in Appendix S3).

There are, however, some differences among the regional assemblages. Specifically, along axis 1, although there exists great similarity in body size distribution between the African and Neotropical regional assemblages, as there is between the Australian and Madagascan assemblages, these two groups were significantly different from each other, particularly in the

Table 3 Two-dimensional morphospace areas and nearest neighbour distances for principal components analysis (PCA) axes 1 and 2, and axes 2 and 3, for the regional assemblages of dung beetles. Area values are given for the total regional species pool and for each functional nesting group. Mean nearest neighbour distances between species are also given for the whole assemblage in each case.

	Africa		Neotropics		Australia		Madagascar	
	Axes 1 & 2	Axes 2 & 3	Axes 1 & 2	Axes 2 & 3	Axes 1 & 2	Axes 2 & 3	Axes 1 & 2	Axes 2 & 3
Morphospace areas								
All species	4.423	2.602	3.259	1.982	1.579	1.145	1.132	0.999
Rollers	2.476	1.203	1.691	0.913	0.831	0.523	0.786	0.322
Tunnellers	2.141	1.146	1.463	1.006	0.55	0.45	0.284	0.139
Dwellers	0.085	0.063	0.35	0.111				
Mean nearest neighbour distance	1.100	0.736	0.903	0.655	0.693	0.602	0.654	0.603

sizes of the rollers ($P < 0.01$ in each case, Table S3 in Appendix S3). There is an absence of large-bodied species, particularly rollers, in the Australian and Madagascan assemblages (Fig. 3), giving them total morphospace areas of one-third and one-quarter the area of the African assemblage,

respectively, across the first three axes (Table 3). Additionally the Madagascan rollers are identified as being significantly different from those of the other regions (Fig. 4; $P < 0.0001$ in each case on axes 2 and 3, Table S3 in Appendix S3), lacking the more extreme shaped rolling species with longer hind legs
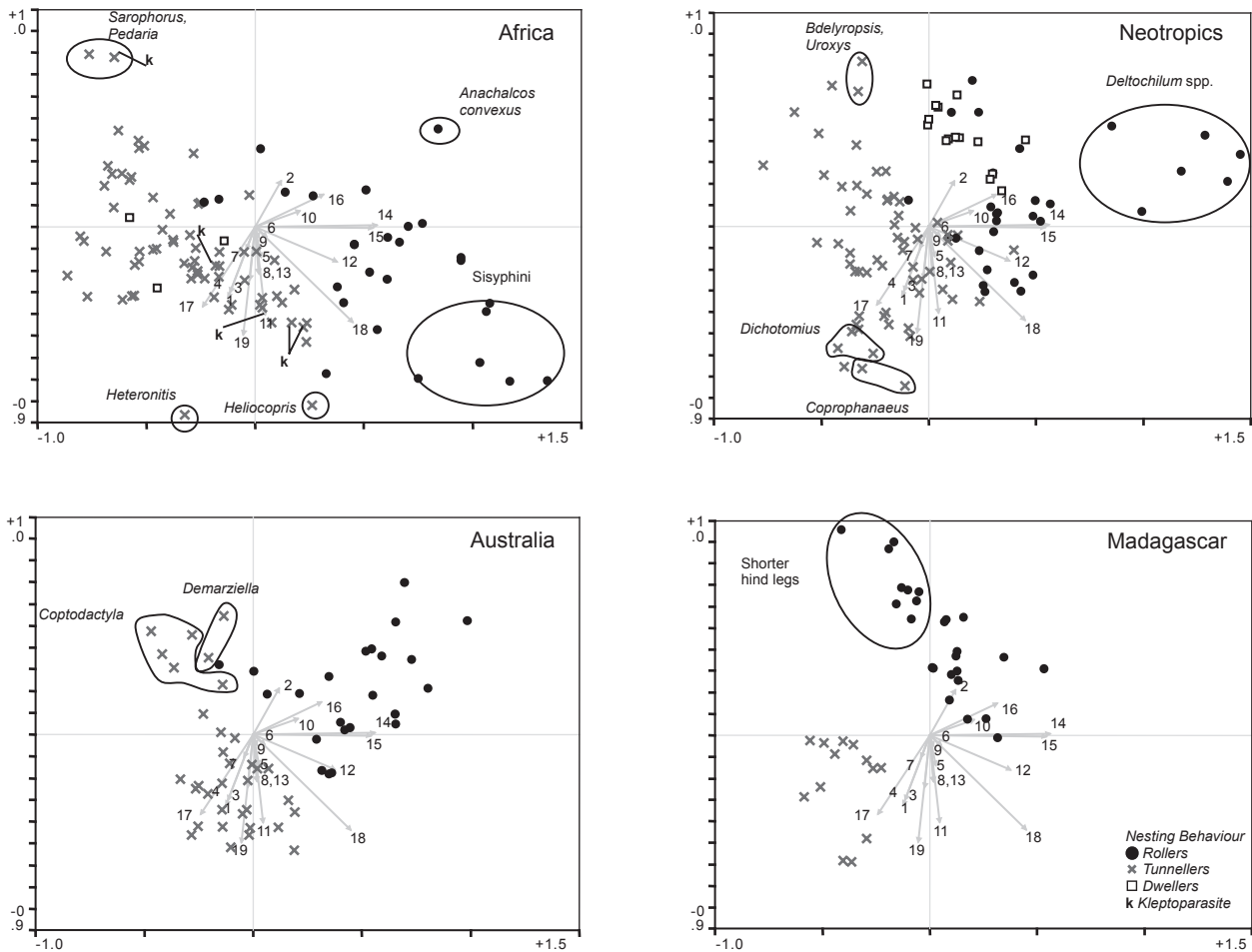

Figure 4 Principal components analysis (PCA) biplots illustrating the morphospace occupied by regional dung beetle assemblages (axes 2 and 3). Linear measurements of body shape (Table 1) are represented by numbered arrows, indicating the loading of each measurement on each PC axis, and pointing in the direction of increase of the measurement across the species analysed. Species are coded according to their nesting behaviour.

and strongly curved tibiae (as exemplified by the African Sisyphini and Neotropical *Deltochilum* in Fig. 4). Instead, they include a group of rollers with relatively shorter hind legs, placing them in an area of morphospace more closely allied to the tunnellers from the other regions.

The morphology of the African and Neotropical rollers diverges significantly on axis 3. This is primarily due to the morphology of the endemic groups *Deltochilum* and Sisyphini. Whilst these groups share the long roller-type tibiae, the African Sisyphini have relatively longer tarsi, deeper abdomens and shorter elytra than the Neotropical genus *Deltochilum* (Fig. 4). Thus there is a 'core' area of morphospace which is utilized by rollers in all regions, but each region also has an additional roller group which occupies an area distinct from the others.

The 'tunnelling morphospace' remains more consistent throughout, but a number of regional differences are apparent on axis 2 (Fig. 4; Table S3 in Appendix S3). These can be partially accounted for by the species richness of the tunnellers in each region; the species-rich African and Neotropical assemblages share a similar distribution of tunnelling morphospace. Australia has an intermediate level of species richness, and occupies a smaller morphospace area, but its tunnellers are distributed along a similar gradient to Africa and the Neotropics (Fig. 4). Madagascar is particularly species poor, having only one genus of endemic tunneller, *Helictopleurus*, in which all species cluster quite closely.

Kleptoparasites were only collected in the Kruger National Park, where five species (two of *Cleptocaccobius*, two of *Onthophagus* and one of *Pedaria*) are thought to demonstrate this behaviour (Appendix S2). Whilst three of the five species are small (Fig. 3), perhaps due to the limited resource provided by their hosts, there is no obvious tendency towards a particular morphology that distinguishes them from related tunnellers (Fig. 4). The dwellers, however, occupy distinctly different morphospace in the regions where they are found. The African dwellers (*Oniticellus*) are located within the 'tunneller morphospace' and the Neotropical dwellers (*Eurysternus*) located in the 'roller morphospace' (Fig. 3), indicating quite different morphologies.

DISCUSSION

Local assemblage structure

The most species-rich Neotropical and African sites supported around six times as many species as the most species-poor sites surveyed in these regions, and were correlated with greater differences in species packing (nearest neighbour distance) than in the total assemblage morphospace. Local-scale dung beetle assemblages appear to be drawn from the regional species pool under an assembly process that maintains ecomorphological structure specific to the biogeographic region, even when species poor. The fact that a local assemblage represents the overall ecomorphological diversity available in the regional pool permits the use of a rather limited sample (tens of species from a total of many hundreds or thousands of species in a biogeographical region) to represent the regional pool in inter-continental comparisons. This finding also supports a role of species interactions in structuring the assemblage composition via limiting similarity, and suggests that species richness is related to finer subdivision of resources. As assemblages become more species poor, taxa are progressively lost from all lineages in the regional pool until only those which are functionally distant from one another remain. The most species-rich Neotropical assemblage (Ecuador) exhibits the highest species packing, while this assemblage also occupies a structurally more complex habitat, benefiting from a greater variety of resources.

Studies on avian assemblages (e.g. Ricklefs & Travis, 1980; Travis & Ricklefs, 1983) found that with increasing diversity, species tended to be added to the periphery of the morphospace, i.e. additional taxa occupied new niche space, while NND remained relatively constant. A survey of 13 ecomorphological studies on birds, fish, bats and lizards also found that NND tended not to vary with species diversity in comparisons of similar communities (Ricklefs & Miles, 1994). This suggests that species interactions in these groups might set a general limit to the morphological and ecological similarity between species (Travis & Ricklefs, 1983; Ricklefs & Miles, 1994). In contrast, a study of Neotropical river fish found species density and levels of species packing to increase with greater habitat complexity (Willis *et al.*, 2005). In the dung beetles, community composition follows this latter type. Communities of dung beetles appear to be shaped by greater levels of competition than those of most other animals, given the large number of species often sharing a largely uniform resource (the dung pat). They hence might constitute an extreme case of a competition-mediated community structure in a spectrum that at the other end includes largely neutral communities. Given an apparent limitation to functional design preventing further expansion of the ecomorphological space, niche partitioning may result in more subtle differences in resource utilization such as diurnal and nocturnal life style, or endothermal ability (Verdú *et al.*, 2007; Scholtz *et al.*, 2009), which are reflected in morphological traits and shape variation, for example larger eyes in nocturnal dung beetle species (Emlen, 2001). In other cases, further resource segregation may be achieved by differences in diet choice, although this may not be evident in the morphology. For example *Phanaeus endymion* and *Phanaeus sallei* co-occur at Las Cuevas and occupy very similar positions in morphospace (Fig. 2), and might be expected to be competitors, but whereas *P. sallei* is strictly coprophagous, *P. endymion* is primarily necrophagous, with 85% of individuals attracted to carrion (Inward, 2002). They are an example of how greater niche overlap between species (as defined by morphometric divergence) may be achieved by finer subdivision of resources among species (MacArthur, 1972). This effect may be particularly relevant with the increasing complexity of ecosystems such

as those in the mammal-rich Neotropical forests or African savannas.

Regional assemblage structure

The most striking finding from the inter-continental comparisons is that the dung beetle faunas of Africa, the Neotropics, Australia and Madagascar show clear similarity in the morphospace occupied, despite being composed of distantly related lineages. This indicates convergence on different continents driven by similar evolutionary–ecological processes at the level of local assemblages. Specifically, the 'core' functional morphology of the rollers and tunnellers, as defined by a set of linear measurements dividing the major behavioural types, remains consistent across the regions. Hence, although dung beetles vary a lot in their shape there is a limit to this variation, and these constraints may be determined functionally. This in turn would add constraints to the diversity at the level of all Scarabaeinae and determine the degree to which local subsets, including the four regional groups studied here, may diverge from each other, even in the face of strong selection for divergence from competition.

While the functional types show great similarity, the overall morphological composition of the regional pool differs among regions. In particular, there is a dichotomy between the species-rich African and Neotropical dung beetle assemblages and the less species-rich Australian and Madagascan assemblages. The latter show a smaller total area of morphospace occupied, i.e. a smaller range of body size and shape, and presumably a narrower range of ecological roles. The reduced body sizes may be related to the availability and diversity of mammal dung with which dung beetle assemblages are so closely associated. The endemic Australian marsupials typically produce small pelleted dung, as do the native mammals of Madagascar, where lemurs provide the most abundant dung resources. There appears to be a metabolic constraint to body size in dung beetle assemblages (Chown & Steenkamp, 1996), and size affects the selection and mode of handling of food resources, with larger species requiring larger dung pellets (Hanski & Cambefort, 1991b). Increased body size correlates with greater morphological differentiation of functional types, although it is unclear whether this is a result of more intense inter-specific competition and greater resource segregation among large-bodied species or simply an expression of functional design and allometric differences that increase with body size (Peters, 1983). Certainly, local diversity of dung beetle assemblages would seem to be related to the richness and diversity of the regional mammal fauna. Sub-Saharan Africa has some 2000 of the 5000 Scarabaeinae species world-wide (Doube, 1991) and has a rich mammal fauna, including many large bovids and ungulates, providing an abundant and diverse dung resource. Conversely, many large mammals were lost from the Neotropics during the large-scale extinctions at the end of the Pleistocene (Owen-Smith, 1987),

leading to a reduction in the diversity of available dung types as well as dung size. However, a high scarabaeine species richness has been maintained, possibly through the increased utilization of small omnivore dung or a more widespread switch to generalist or necrophagous feeding behaviour evident in this region (Halffter & Matthews, 1966). For illustration, in Ecuador, only 14% of species collected for this study showed a strictly coprophagous diet preference, compared with 77% of species collected in Kruger National Park (Inward, 2002). Phylogenetic history may also have influenced the build up of present-day species richness and ecomorphological diversity in various continental areas. An evolutionary scenario for the Scarabaeinae (Monaghan et al., 2007) places the origin of dung scarabs in Africa, from which Neotropical lineages were derived repeatedly and early, while the Madagascan and Australian lineages are derived more recently and on fewer occasions. This suggests that phylogenetic diversity and lineage age of these continental faunas has influenced their overall diversity. These differences have modulated the precise composition of lineages in various continents, but nonetheless there remains great similarity due to the presence of (phylogenetically independent) major functional types and wide overlap in ecomorphological space within each of them.

Regional ecomorphology of the nesting groups

A brief examination of the core characteristics of the functional groups may help us to understand the regional variations. In the PCA analyses, the tunnellers had generally more robust bodies than the rollers, including a bigger pronotum and broader abdomen. These most likely reflect the greater musculature in the thorax required for digging the often extensive burrows made by this group. They also have wider, spade-like tibia, providing a larger surface area for soil movement, and a broader, deeper head used like a shovel to both loosen earth and remove it from the burrow (Halffter & Matthews, 1966). The rollers tend to have longer hind femora and tibiae than the tunnellers, with a greater degree of curvature. This is clearly required for the formation and rolling of dung balls, and is seen in independently derived rolling groups in all biogeographic regions.

While rollers and tunnellers each appear to converge in ecomorphological traits throughout the Scarabaeinae, the dwellers illustrate that independent lineages can attain the same functional role without convergence. The placement of the Neotropical Eurysternini within the roller morphospace, and the African Oniticellus within the tunnellers, seemingly reflects phylogenetic history, whereby each group retains its ancestral morphology whilst adopting a distinct lifestyle. Similarly, within the tunnellers, kleptoparasites also exhibit no clear grouping or convergence, and are instead distributed with closely related taxa. On a broader scale though, the tunnellers of all four regions, each representing a set of phylogenetically diverse taxa, in fact show great ecomorphological similarity (Fig. 4), perhaps reflecting a more generalized

body form for movement through soil. Species of tunnellers are partitioned by depth of burrows, preferred soil type and even the speed at which they dig (Doube, 1991), and a range of digging abilities seems to be reflected in the variation of the hind tibia (surface area for soil excavation), depth of abdomen (size of digging muscles) and relative length of femur (e.g. balancing efficiency of locomotion and digging). The tunnellers at one end of this gradient of variation are probably less efficient, and include primitive lineages (Monaghan *et al.*, 2007) such as *Sarophorus* and *Pedaria* from Africa, and *Bdelyropsis* and *Uroxys* from the Neotropics (Fig. 4). Amongst the more 'efficient' tunnellers are large species excavating deep burrows, such as the African *Heliocopris* and *Heteronitis*, and Neotropical *Coprophanaeus* and *Dichotomius*.

Distinct regional evolutionary histories of rolling

Some consistent morphological characteristics associated with the shaping and rolling of dung balls are shared by the rollers of all four regions, despite multiple originations of this behaviour (Monaghan *et al.*, 2007), indicating widespread convergence in form and function. Unlike the tunnellers, however, there are also distinct regional differences, with the occupation of unique areas of ecomorphological space requiring some interpretation. For example, the outlying position of the endemic Neotropical *Deltochilum* may be explained by the proximity of the unrelated African *Anachalcos* (Fig. 4). Both are large rollers with similar generalist tendencies, and their morphology may reflect an ability to process carrion, to which they are strongly attracted. The outlying Madagascan roller group, including species of *Arachnodes* and *Nanos*, have relatively short hind legs and occupy an area more similar to the tunnellers of other regions. A lack of large mammals on Madagascar has meant that the endemic dung beetles are adapted to utilize the pellets and small dung resources available, and some of the rollers may have become specialized pellet rollers, as seen in the Neotropical genus *Canthidium* (Gill, 1991), where pelleted dung is simply rolled away with no prior ball-shaping activity. Alternatively they may have abandoned rolling altogether, behaving more like tunnellers; they occupy a similar area of morphospace to two Australian tunnelling genera, *Coptodactyla* and *Demarziella* (Fig. 4), which were recently identified to have undergone a similar reversal (Monaghan *et al.*, 2007). Members of a clade of small rollers, these taxa apparently switched to tunnelling to exploit a vacant niche, as only one other tunnelling genus, *Onthophagus*, exists in Australia.

CONCLUSIONS

This study demonstrates that the ecomorphological diversity of coexisting species in local assemblages is a good reflection of the diversity of the much larger regional species pool, justifying the comparison of regional faunas based on the study of a small number of local assemblages. We also reveal remarkable similarities in the ecomorphology of the Scara-

baeinae among continental assemblages, despite the distant relationships of the participating lineages and the frequent evolutionary shifts between tunnelling and rolling. These findings suggest that local assemblage diversity is strongly influenced by resource segregation among species, and that such inter-specific interactions may scale up in their effects on the convergent patterns of total ecomorphological space occupied by different biogeographical regional species pools. Although species differ greatly in their abundance, the regularities in assemblage structure can be detected based on presence–absence data alone. Subtle differences identified among biogeographical regions may reveal differences in the selective regime exerted by the dung producers, local environmental and climatic conditions, and the evolutionary history of the specific lineages constituting the regional pool of dung beetles. However, these effects are minor compared with the overriding processes of intra-assemblage selection for resource segregation that are shaping the current composition at local sites, as well as the evolutionary diversity of the participating lineages at the continental scale.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Illustrations of the 19 linear morphometric measurements recorded from the body and hind leg of dung beetle specimens.

Appendix S2 Dung beetle species inventory of the local assemblages collected in each region (the Neotropics, Africa, Australia and Madagascar).

Appendix S3 Additional statistical test results (Tables S1–S3).

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