

Localised and regional patterns in ground-dwelling beetle assemblages in a semi-tropical arid zone environment

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Abstract – Ground-dwelling beetles were sampled by pitfall traps at 304 quadrats positioned to represent the geomorphic extent and profile of the Pilbara Region, a semi-tropical arid region in north-west Western Australia. For each quadrat, 47 climatic, soil, landform, geological and vegetation attributes were determined. A total of 429 taxa across the Bolboceratidae, Carabidae, Hybosoridae, Scarabaeidae and Tenebrionidae were identified, of which 68% could not be assigned to currently recognised species.

Species richness ranged from 1 to 36 species per quadrat, with an average of 11.6 ± 5.9 species ($n = 296$ quadrats). Species recorded at one quadrat only ('singletons') constituted 33% of the fauna and were collected mainly from areas near the edge of the region or were associated with the Fortescue subregion; they included 36% of the Bolboceratidae (8 species), 32% of the Carabidae (72 species), 33% of the Hybosoridae (2 species), 46% of the Scarabaeidae (45 species) and 22% of the Tenebrionidae (17 species). Those from the region's edge may have their distributions centred elsewhere, while singletons from the Fortescue subregion may be restricted to marsh habitats that are rare elsewhere in the region.

Locally, compositional patterns were correlated with landform and soil attributes (slope, soil depth, exchangeable calcium, exchangeable potassium and sandiness). Heavy cracking clays, and saline and riverine-associated muds, supported a distinctive suite of species, from which the more widespread or common species were generally absent. At the regional scale, patterns in composition reflected the region's physio-geographical subregions.

Localised evolutionary processes associated with and promoting low mobility have resulted in fauna with a high proportion of strongly-localised endemic forms. Detailed comparisons of the beetle fauna with neighbouring semi-arid areas such as the Great and Little Sandy Deserts, Ashburton and Northern Carnarvon Basin are required to determine phylogenetic relationships between taxa, distributions, and to explore further the correlation of species composition with various land attributes that have emerged from our analysis.

Key Words - Bolboceratidae, Carabidae, Hybosoridae, Scarabaeidae, Tenebrionidae, Pilbara, biogeography, biodiversity, pitfall traps, regional survey, species richness

INTRODUCTION

Attempts to estimate and document terrestrial beetle (and other insect) species richness in Australia have been affected by the state of taxonomic knowledge, in addition to difficulties in access to many habitats and environments (Austin *et al.* 2004). This biodiversity information has direct application in biogeographical surveys, environmental monitoring, conservation and diversity assessment studies (e.g. Solem and

McKenzie 1991; Margules 1992; Abensperg-Traun *et al.* 1996; Michaels 1999; Davies and Margules 2000; Harvey *et al.* 2004; Gibson and New 2007). However, the use of terrestrial invertebrates in contemporary Australian surveys is still constrained by problems associated with taxonomic resolution and a lack of ecological and faunistic information (New 1998).

The major causative agents driving the high beetle (and insect) diversity in the Pilbara, and across Australia as a whole, are, in combination, the large size of the continent, extremely long

geological isolation, and repeated retreat and expansion of rainforests with radiation of *Eucalyptus* and *Acacia* communities in response to Miocene aridification (also reflected in other Australian fauna and flora; Hopper *et al.* 1996; Main 1996, 2000; Cowling and Lamont 1998; Beard *et al.* 2000; Austin *et al.* 2004; Ślipiński 2007).

These agents have led to a tendency towards many localised species, with a high proportion being flightless, reflecting limited available habitat but within a generally stable environment (Matthews 1974; Howden 1981; Baehr 2005). An example of such an environment is the Pilbara, which experiences radical short-term substrate changes due to floods, but is very stable over decades and greater time spans, and it has not changed significantly in its structure through much of the Tertiary (Baehr 2005).

Earlier collecting of beetles in Australia has been sporadic, and opportunistic, with many very early collections consisting of single or few isolated specimens (e.g. Western Australian Museum records, Australian National Insect Collection records). This has inhibited assessment of species distributions and relationships between taxa. More recently, localised, isolated, opportunistic and restricted surveys have been carried out,

usually focusing on a taxon or habitat (e.g. Baehr 1990; Majer and Recher 1988 and others). These studies have indicated that, even in habitats such as beneath hanging tree bark in semi-arid and arid zones, there is high beetle diversity (Baehr 1990).

As these surveys and collections are isolated in time and context, their usefulness as baseline information for contemporary surveys and conservation and diversity assessment studies is limited. Therefore, as a component of a large study documenting the biodiversity patterns in the Pilbara biogeographic region of Western Australia, data on the ground-dwelling terrestrial beetle fauna were collected. This was the first opportunity to survey the region systematically for beetles. This has provided baseline information on distribution, taxonomy and morphological variability for future surveys and monitoring programs. Specifically, the Bolboceratidae, Carabidae, Hybosoridae, Scarabaeidae and Tenebrionidae were chosen as representatives of the ground-dwelling beetle fauna, for assessment of assemblage structure and species turnover across the Pilbara landscape in terms of geographic, climatic and substrate attributes. This decision was based on information from previous surveys, relatively stable taxonomy and representativeness of generalised feeding

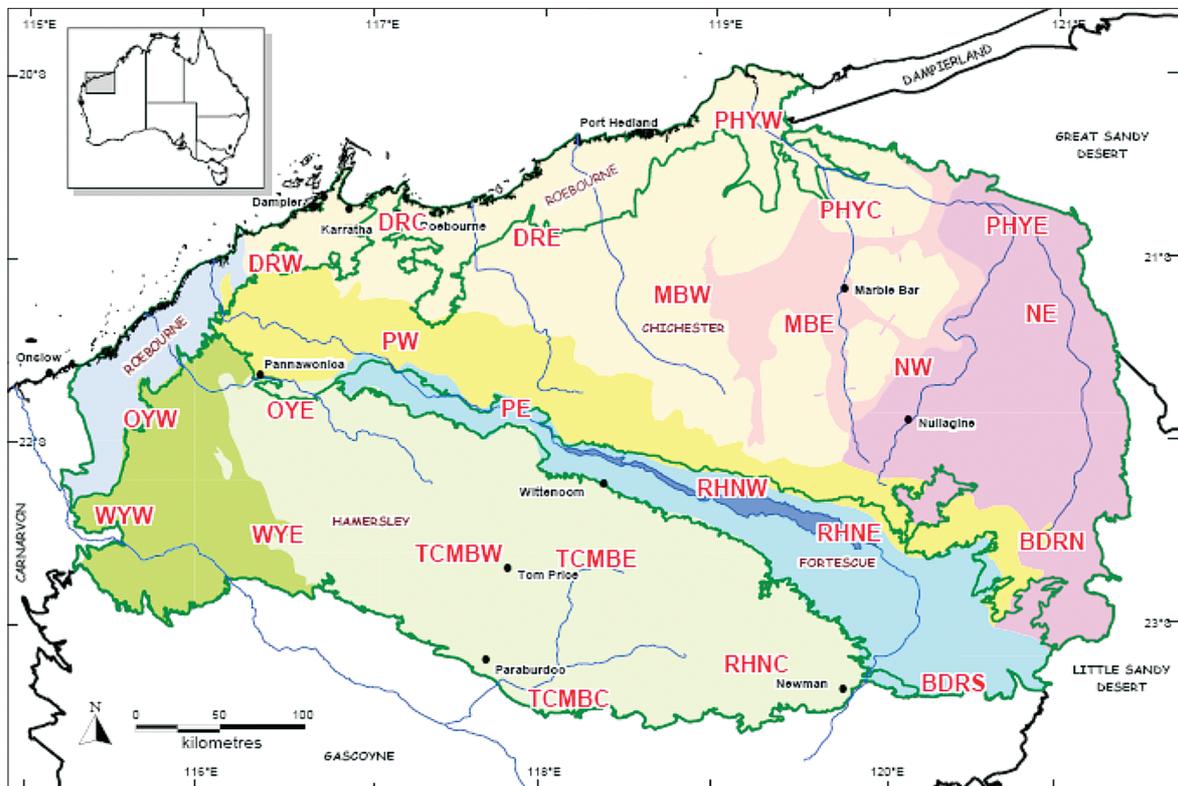


Figure 1 Map of the Pilbara showing a) locations of Survey Cells, b) boundaries of the four IBRA subregions outlined in green, c) the eight physio-geographical subregions recognised by Beard (1975): Oakover Valley – dark pink, central Gorge Range – pale pink, Abydos Plain – beige, Chichester Plateau – yellow; Fortescue – pale blue; Hamersley Range – pale green, Stuart Hills – green, Onslow Plain – mauve, d) major rivers – dark blue and towns.

niches (Naumann, Weir and Edwards 1991; Lawrence and Britton 1994; Bouchard and Yeates 2001; Cassis and Weir 2002; Matthews and Bouchard 2007).

METHODS

Survey region

Encompassing the Pilbara Craton, the Pilbara IBRA biogeographic region is situated in the north-west of Western Australia, and covers approximately 179,000 km² (Figure 1). It has a semi-desert tropical climate, becoming arid on the coast and towards the north-east interior. Rainfall is highly variable year to year and across the region, averaging circa 300 mm, provided mainly by summer cyclonic events (May and McKenzie 2003). Geology and vegetation communities differ across the four distinct subregions: Chichester, Fortescue, Hamersley and the Roebourne Plains (Figure 1; Beard 1990; Environment Australia 2008). McKenzie *et al.* (2009) describe the climatic, geophysical and vegetation characteristics of the Pilbara in detail so only a brief description is given below.

The Chichester subregion, occupying the northern Pilbara Craton, consists of undulating Archaean granite and basalt plains and ranges. Several rivers drain the northern Chichester (De Grey, Oakover, Nullagine, Shaw, Yule and Sherlock). Beard (1975) subdivided the subregion further into the Oakover Valley in the east; central Gorge Range; Abydos Plain in the western third plus the northern Roebourne Plain; and the Chichester Plateau as separate physiographic units (Figure 1). Broadly speaking, these physiographic units consist of *Acacia inaequilatera* shrub steppes over *Triodia wiseana* hummock grasslands on the plains, and snappy gum (*Eucalyptus leucophloia*) tree steppe in the ranges (May and McKenzie 2003).

Dissected by deep gorges in the west, the Fortescue subregion has drainage lines fringed with river red gum (*Eucalyptus camaldulensis*) woodlands, and salt marshes, mulga-bunch and short grass communities on the eastern alluvial plains. River red gum and cadjeput (*Melaleuca*) woodlands occur along permanent springs and wetlands in the central Fortescue (May and McKenzie 2003).

The Hamersley subregion overlies the southern Pilbara Craton and features Proterozoic sedimentary ranges and plateaux dissected by gorges. It is drained by the Fortescue River in the north, Ashburton in the south and the Robe River to the west. The Stuart Hills and remaining Hamersley Plateau were identified as separate physiographic units by Beard (1975). Both units have snappy gum over *Triodia brizoides* hummock grasslands dominating the ranges, with Mulga

(*Acacia aneura sens. lat.*) low woodland over bunch grasses on the plains.

The Roebourne subregion delineates the western coastal plain of the Pilbara. Linear basalt ranges with exposed granite dissect Quaternary alluvial and older colluvial coastal plains (May and McKenzie 2003). Beard (1975) identified the Onslow Central Plain as a distinct physiographic unit of the Roebourne Plain, with the northern section of this subregion as part of the Abydos Plain. *Triodia* hummock grasses occur on the ranges, with *Eucalyptus victrix* or *Corymbia hamersleyana* woodlands on ephemeral drainage lines. Bunch and hummock grass savannahs with *Acacia stellaticeps*, *A. pyrifolia* and *A. inaequilatera* dwarf shrub steppe characterise the plains, with samphire, *Sporobolus* and mangal communities present on the river deltas and surrounding flats (May and McKenzie 2003).

Sampling strategy

The region was divided into 24 survey cells that together encompassed the geographical and environmental variation of the Pilbara (Figure 1). In each survey cell, 11 to 13 quadrats were positioned to represent examples of the major habitats on the major landforms, choosing sites least disturbed by human use, stock or fire. The 304 quadrats across the region were positioned to sample the main components of the Pilbara's geomorphic profile. Where possible, quadrats were pseudo-replicated between survey cells and within individual areas for the more extensive geomorphic units. For each quadrat, climatic attributes were derived and physical attributes including landform, soil chemical and texture values and vegetation were assessed; these are provided in Appendices A–D of McKenzie *et al.* (2009).

To reduce bias associated with variations in climate and bushfire damage, quadrat establishment and sampling occurred in separate years in a chessboard pattern of the 24 survey cells (Figure 2). Twelve survey cells were established with pitfall traps opened mid-2003 and closed late-2004, while the second series of 12 survey cells was sampled between mid-2005 and late-2006. Thus, the average length of sampling across all quadrats was 395 days each ($n = 304$ quadrats; min = 309, max = 461; sampling dates are provided in Appendix 1). This reduced the bias associated with sampling for short periods (such as a few weeks in a single season).

Each 50 × 50 m quadrat consisted of five pitfall traps: one at each corner and one in the middle (Figure 3). Each pitfall trap consisted of a 2 litre, UV resistant plastic container (80 mm neck diameter) inserted into a PVC sleeve dug into the ground, flush with the ground surface. To form a continuous

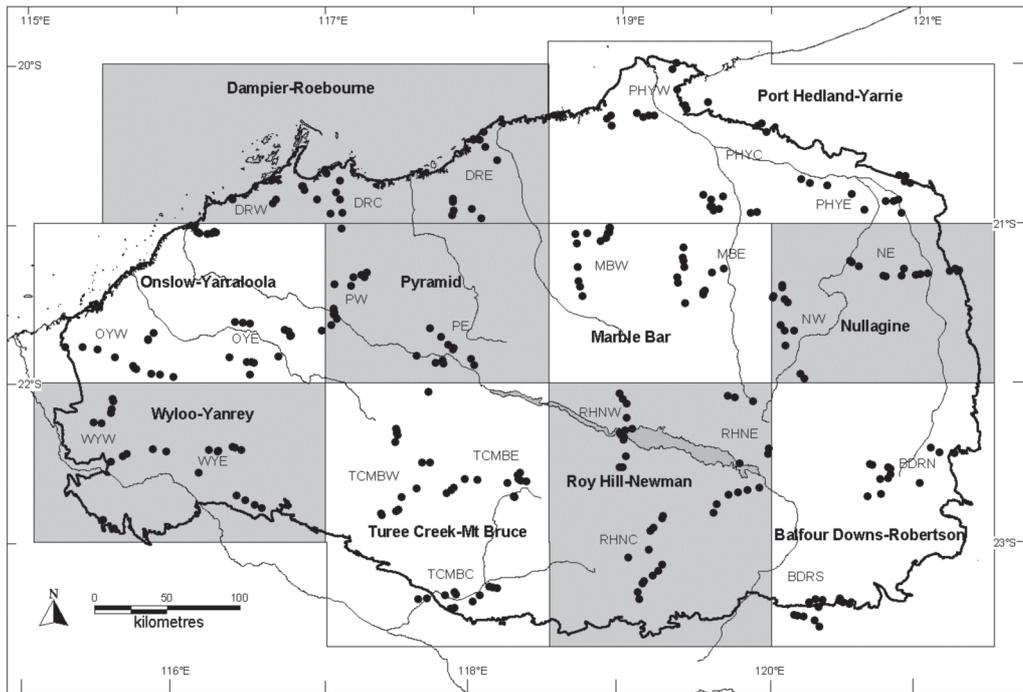


Figure 2 Map of the Pilbara showing a) locations of Survey Cells, b) 304 quadrats, and c) chessboard sampling of survey cells in two sets of 12 cells: cells sampled between mid-2003 and late-2004 highlighted in grey, and survey cells sampled between mid-2003 and late-2004 in white.

surface between the ground and jar lip, an acrylic ring covered in glued sand was attached between the PVC sleeve and jar lip. Two hoop iron stands fitted between the PVC sleeve and jar supported a 200 × 200 mm colourbond roof approximately 4 cm above the ground surface. One litre of ethylene glycol mixed with 4% formalin was used as the preserving fluid in each pitfall trap. Each pitfall trap was collected and reset at least once during

the surveying period (Appendix 1). Samples were returned to the laboratory, washed in water and stored in 75% ethanol until sorting, processing and identification.

Taxonomy

Adult specimens were identified using current taxonomic literature (Allsopp 1990; Baehr 1984, 1986a,b, 1992, 1993, 1994, 1997, 2004, 2005; Bänninger 1940; Britton 1957, 1980, 1986, 1987, 1988, 1990, 2000; Freitag 1979; Giachino 2003; Howden 1974, 1976, 1979, 1984, 1985, 1992, 1993; Howden and Cooper 1977; Hudson 2000; Matthews 1972, 1974, 1980, 1984, 1987, 1992, 1993, 1998; Matthews and Bouchard 2008; Matthews and Stebnicka 1986; Matthews and Weir 2002; Moore 1963, 1965; Paulian 1980; Roig-Juñent 2000; Stebnicka and Howden 1995, 1996, 1997; Storey 1991) and comparisons to accessible type specimens were made. Nomenclature and taxonomy follow Cassis and Weir (2002a,b,c,d, 2002e), Houston and Weir (2002), Matthews and Bouchard (2007) and Moore, Weir and Pyke (1987, 2007). A morphospecies approach was adopted where confidently assigning specimens to known described or undescribed taxa was difficult and available literature insufficient (Harvey *et al.* 2000). Taxa of Bolboceratidae, Carabidae, Hybosoridae, Scarabaeidae and Tenebrionidae identified in the survey are presented in Appendix 2. Representative series encompassing the distributional variation in the taxa (herein termed 'species') are lodged

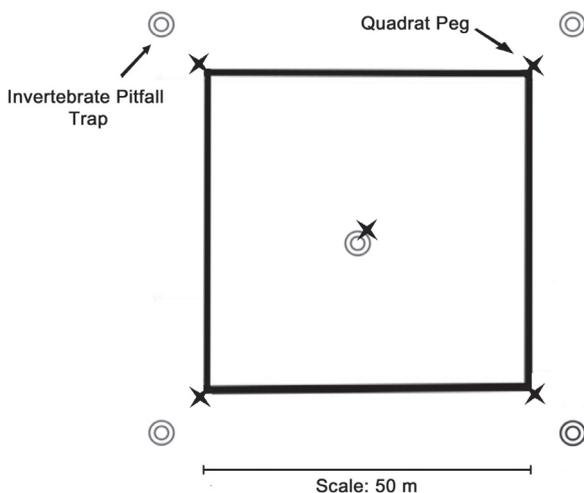


Figure 3 Design of quadrat, showing position of botanical quadrat, and invertebrate pitfall traps.

at the Western Australian Museum (WAM) and Australian National Insect Collection (ANIC). The remaining invertebrate material was sorted to order or family, lodged with the Western Australian Museum but not analysed due to time and personnel constraints.

Analysis

Patterns in the Pilbara beetle matrix (presence and absence of species at quadrats) were explored using the computer package PATN (Belbin 1995). To minimise distortions in the analysis from under-sampling due to major disturbances (cyclonic events, inundation, fire), affected quadrats were removed from the matrix. Likewise, species recorded at only one quadrat (irrespective of numerical abundance at that quadrat) and quadrats with beetle assemblages comprising one species (herein referred to as 'singletons') were also removed prior to quadrat-level analyses. Next, overall sampling effectiveness for beetle species was assessed using both the Chao2 and incidence-based (ICE) estimators in the EstimateS software (Colwell 2006).

The Czekanowski association measure was used to compare quadrats according to similarities in their species composition, and the Two-Step association measure was used to compare species on the basis of their co-occurrences at quadrats. Dendrograms were constructed from these association matrices using an unweighted pair group arithmetic averaging (UPGMA) hierarchical clustering strategy (Sneath and Sokal 1973; Belbin 1995), and the reordered data were displayed as a two-way table. Structure in the quadrat dendrogram was assessed in terms of the quadrat descriptions, and statistically in terms of the

substrate and climatic attributes measured for the quadrats using univariate Kruskal-Wallis tests.

The relationship between assemblage structure and substrate was investigated further by analysing the quadrat resemblance matrix using the ANOSIM routine in PRIMER v6 (Clarke and Gorley 2006). A single ('gestalt') substrate factor was used for this test, in which each quadrat was assigned to one of three states – predominantly rocky, sandy or clayey (see McKenzie *et al.* 2009).

Quadrats were pseudo-replicated between survey cells and within individual cells for the more extensive geomorphic units. This allowed each survey cell to be treated as a single landscape-scale relevé. Thus, broad biogeographical patterns could be assessed by classifying survey cells according to similarities in their overall species composition. Singleton species were restored to the matrix for this analysis, but not the under-sampled quadrats. The resulting classification structure was examined statistically in terms of the average environmental attributes of the survey cell's component quadrats using Kruskal-Wallis sample tests.

RESULTS

The Fauna

A total of 429 species representing 126 genera of ground-dwelling beetles from the Bolboceratidae, Carabidae, Hybosoridae, Scarabaeidae and Tenebrionidae were recorded from the quadrats sampled during the survey (Appendix 2; 427 species were used in the analyses, *Megacephala* nr. *intermedia* and *Megacephala* nr. *karratha* were collected only from excluded quadrat DRC12, and therefore not included). The Bolboceratidae were

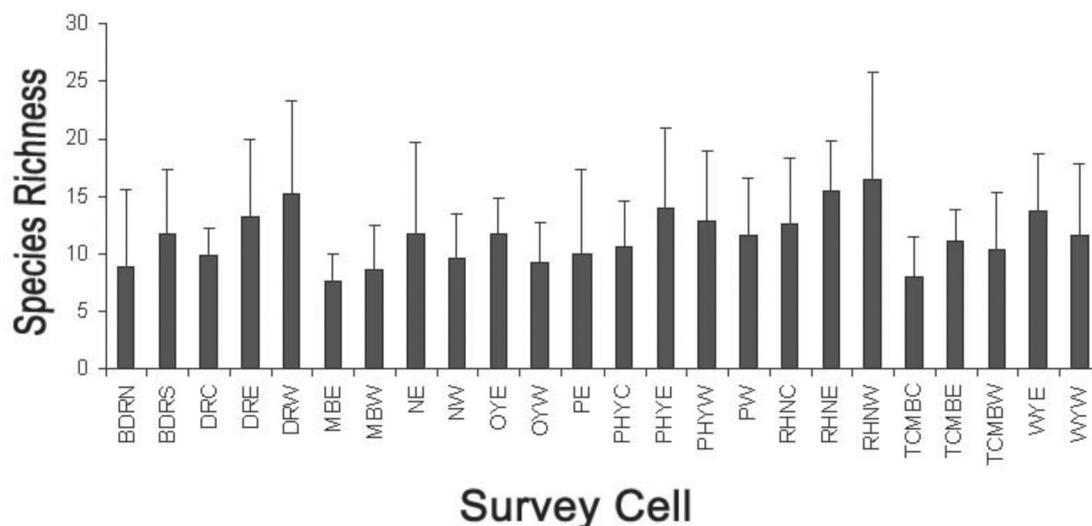


Figure 4 Average species richness for individual survey cells (cells listed in alphabetical order). Number of sampled quadrats within each cell: 9-NW; 11-DRC, MBE, OYE, PHYC; 12-PE, RHNE, TCMBC, WYW; 13-BDRN, BDRS, DRE, DRW, MBW, NE, OYW, PW, PHYE, PHYW, RHNC, RHNW, TCMBE, TCMBW, WYE.

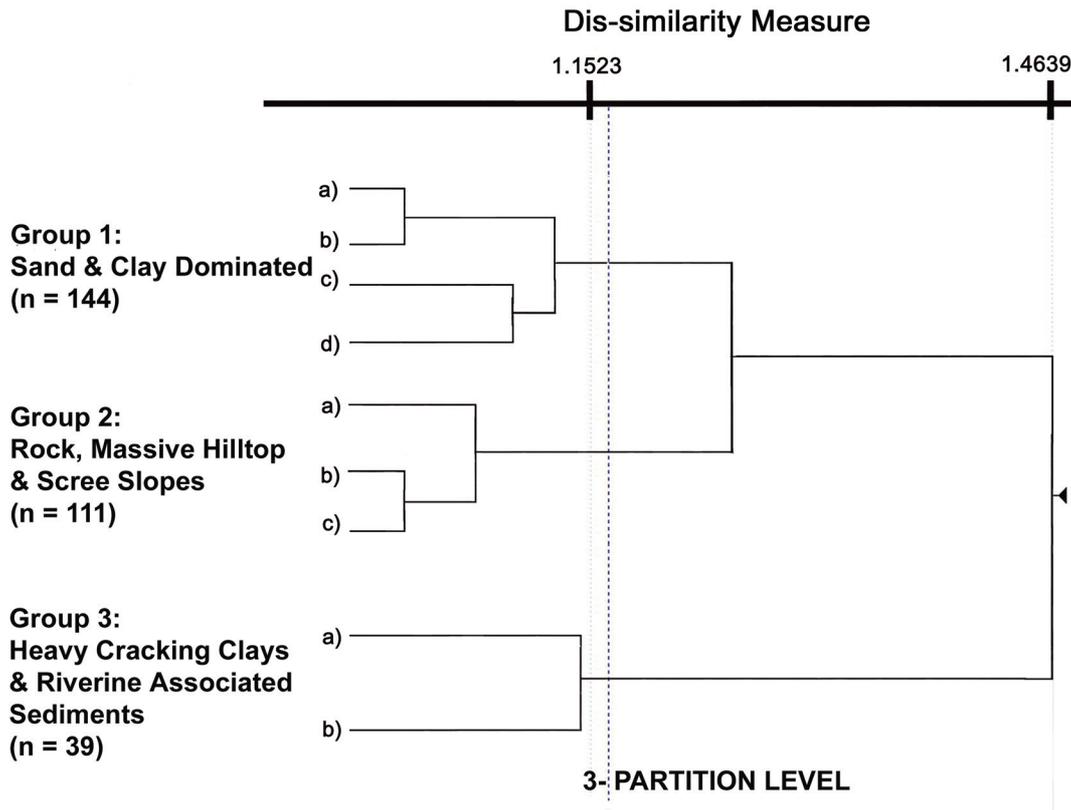


Figure 5 Quadrats classified according to similarities in species composition. Dendrogram structure displayed to the 3-group level. See text for detailed explanation of sub-groups.

represented by 22 species in six genera from the Bolboceratinae. The Carabidae were represented by 223 species in 61 genera within 21 subfamilies. Six species from three genera represented the Hybosoridae and 95 species in 25 genera represented four subfamilies of the Scarabaeidae. The six Tenebrionid subfamilies recorded were represented by 80 species in 32 genera.

Species richness ranged from 1 to 36 species per quadrat (TCMBC06, 1 Carabidae only; DRW02, 16 Carabidae, 10 Tenebrionidae, 10 Scarabaeidae respectively) with an average of 11.6 ± 5.9 species S.D. ($n = 294$ quadrats). Within individual survey cells, average species richness per quadrat ranged between 7.6 (MBE) and 16.4 (RHNW) respectively, with no significant difference between cells established in either year (Figure 4).

One hundred and forty-three species, or 33% of the fauna, were recorded at one quadrat only. All five families were represented by singletons in this study, and comprised: Bolboceratidae 36% (8 species), Carabidae 32% (72 species), Hybosoridae 33% (2 species), Scarabaeidae 46% (45 species) and Tenebrionidae 22% (17 species). Ninety-five quadrats were found to have at least one singleton species with the most singletons occurring at quadrat DRW02 (5 species). The majority of singletons were

recorded from cells DRE (13 species), DRW (13), NE (12), PHYE (10) and RHNE (10).

ICE and Chao2 procedures in EstimateS produced estimates of 585 and 596 species, respectively, for the 294 quadrats. Therefore, the trapping program revealed 72–73% of total estimated richness across the range of Pilbara environments sampled. The accumulation curves had flattening-off but were not yet asymptotic; over the final 20 quadrats sampled, 0.5 additional species were being added per quadrat.

Quadrat composition

Nine quadrats were under-sampled because they were inundated (DRC12 – tides, OYE12 – cyclonic flooding), burnt (MBE01; NW01, NW09, NW10) or inaccessible (MBE10, NW01, OYE08) during the sampling period, so were excluded from the analysis matrix along with species that occurred at only one quadrat. The final matrix comprised 321 species and 294 quadrats. When the quadrats were classified according to similarities in their species compositions, the resulting quadrat dendrogram structure reflected differences in soil and landform attributes (Figure 5).

Group 1 comprised sand- and clay-dominated quadrats. Four internal partitions were discerned:

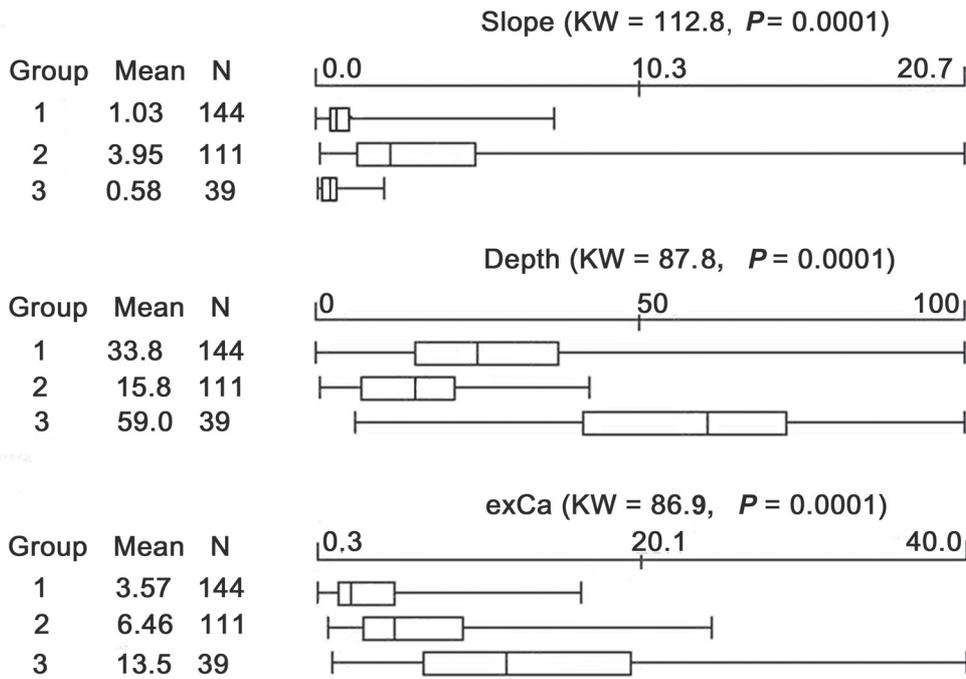


Figure 6 Statistical assessment of the three-group classification (Figure 5) according to the slope (° above the horizontal), depth (cm), exchangeable Calcium (exCa; me%), exchangeable Potassium (exK; me%), and sand (%) values for the quadrats. Bars indicate 95% confidence intervals around the mean; Group = classification group number in Figure 5; N = number of survey cells in each classification group.

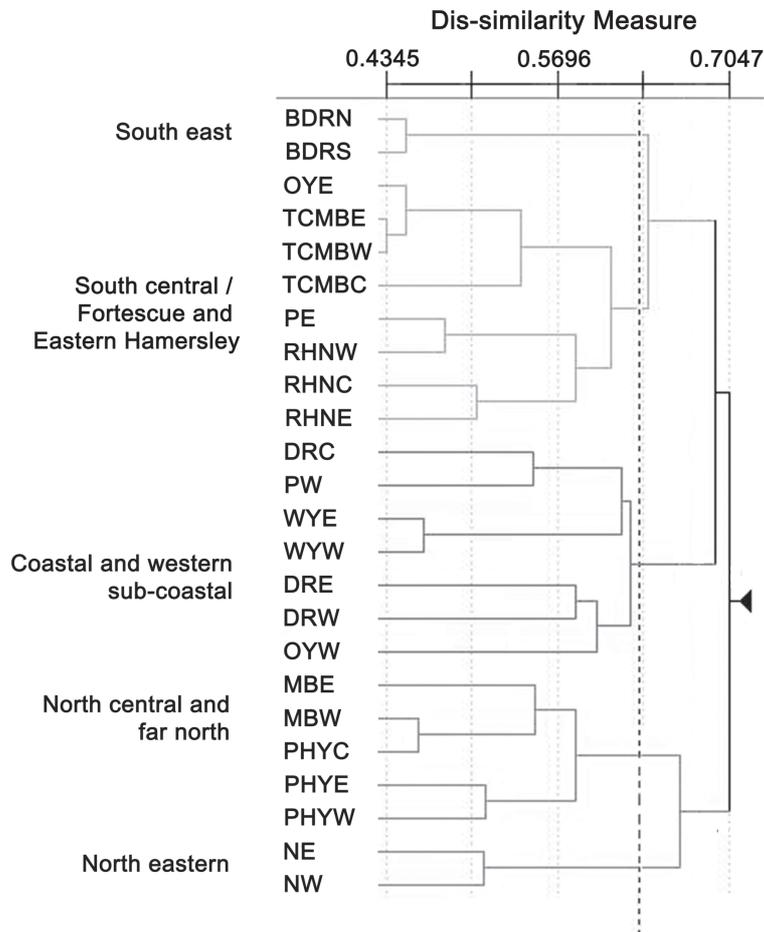


Figure 7 Survey cells classified according to similarities in species composition. Dendrogram structure displayed at the 5-group level.

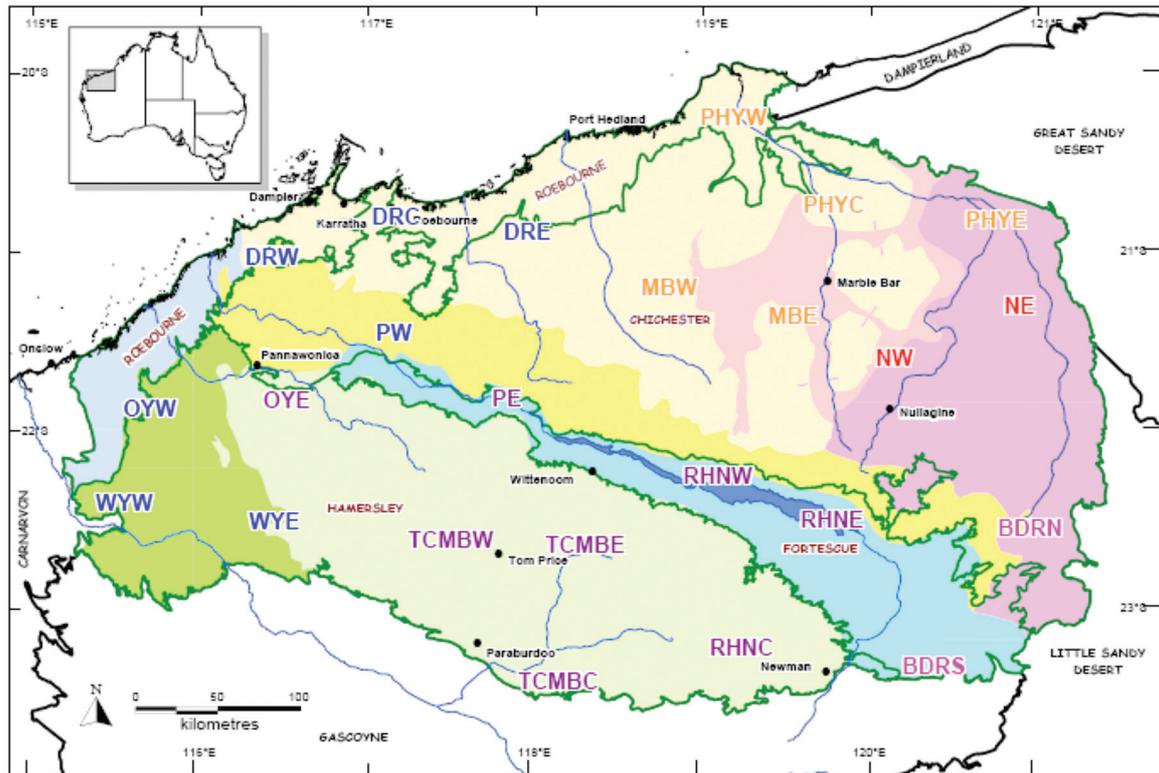


Figure 8 Map of the Pilbara showing a) survey cells colour coded to their clustering position in the survey cell dendrogram (Figure 7): Group 1 (South-east) – pink; Group 2 (South central & Fortescue/ Eastern Hamersley) – purple; Group 3 (Coastal & western sub-coastal) – blue; Group 4 (North central & far north) – orange; Group 5 (North eastern) – red. b) boundaries of the four IBRA subregions outlined in green, and c) Beard's (1975) eight subregions: Oakover Valley (dark pink), central Gorge Range (pale pink), Abydos Plain (beige), Chichester Plateau (yellow), Fortescue (pale blue), Hamersley Range (pale green), Stuart Hills (green), Onslow Plain (mauve), d) major rivers (dark blue) and towns.

a) beach and desert sand dunes; b) gritty sands, deep clays with stony profiles, clay pans and clay-silts; c) deep clays with stony profiles and surface strew of fragments and some stony uplands; and, d) sand dunes and deep clay profiles with outcropping of varying amounts rock or boulders. Group 2 comprised quadrats with massive rocks of hilltops and steep scree slopes, along with stony uplands and calcrete or opaline hills. Three internal partitions were identified: a) massive hilltop and scree slopes from the Chichester Range, Oakover valley and Stuart Hills; b) deep clayey profiles with surface strew and/or stony profiles, with Onslow Plains quadrats clustering together; c) massive hilltops and steep scree slopes primarily from coastal regions and the Stuart Hills. Group 3 comprised heavy cracking clays and riverine-associated muds and clays; its two internal partitions separated a) heavy cracking clays and saline muds from b) riverine levees with alluvial clay-silt, river sand beds or grit-sand river beds.

In combination, slope, soil profile and depth separated all three groups in the partition structure (Figure 6), although three other soil attributes showed a pattern of statistical differences similar

to exchangeable calcium (exCa): exchangeable potassium (KW = 65.4, $P = 0.0001$), sand (KW = 54.5, $P = 0.0001$) and exchangeable magnesium (exMg).

An ANOSIM test revealed significant differences in beetle assemblage composition when quadrats were assigned among three categories (predominantly rocky, sandy, or clayey; global $R = 0.20$, $P < 0.001$). All possible pairwise comparisons were significant at $P < 0.001$, with an R statistic of 0.27 for rocky *versus* sandy, 0.20 for rocky *versus* clayey and 0.12 for sandy *versus* clayey. Despite differences in the beetle assemblage composition, individual families were not restricted to any one quadrat category (i.e. rocky, sandy or clayey; Appendix 3).

Biogeographical regionalisation

The landscape-scale matrix comprised 24 survey cells and 427 species. The dendrogram derived from classifying the survey cells according to their total species composition (Figure 7) revealed strong geographically localised patterns down to the five partition level at least (Figure 8). The combination of two attributes statistically separated all five

partitions: longitude and elevation (Figure 9). Thirty-six percent of species were recorded in only one survey cell and 46% were restricted to a single dendrogram partition as mapped in Figure 8.

DISCUSSION

The fauna

The Pilbara assemblages of Bolboceratidae, Carabidae, Hybosoridae, Scarabaeidae and Tenebrionidae were species-rich, with a total of 429 species identified in the present survey. Across these families, 68% could not be assigned to currently recognised species. It is likely that many more species are yet to be discovered, particularly in habitats and substrates not sampled during the present survey. The proportion of unrecognised taxa differed considerably between families, reflecting the groups currently requiring taxonomic revisions. Of the Carabids, 140 taxa could not be assigned to recognised species. The majority of these were in the Scaritine genera *Carenum* and *Clivina* (28 of 33 and 14 of 16 species, respectively). The Melolonthine genus *Heteronyx* accounted for 20 of the 98 unassigned species within the Scarabaeidae, and only one Tenebrionid species could be attributed to a known species. At the generic level, however, assignment of taxa was extremely high with all Bolboceratidae, Hybosoridae and Scarabaeidae assigned to recognised genera, while three Carabidae and ten Tenebrionidae taxa could not be attributed to recognised genera. Of these Tenebrionidae, four

were within the Alleculinae, three in the Lagriinae, two representing the Palorinae and one taxon could not currently be assigned to a subfamily. We infer that the majority of the genera within these five beetle families present in the region have been described but it is expected that many more species remain to be discovered, particularly in habitats and substrates not sampled during the present survey.

Singleton species or those occurring at few quadrats might be rare, volant, 'tourist species' (passing through the area), only able to move short distances, or might have short adult reproductive phases so that opportunities to fall into pitfall traps are limited (Davies and Margules 2000). These species can provide an important percentage or portion of the total species richness of an area (Gaston 1996, cited in Lobo *et al.* 2004). If they are excluded from analyses such as predictive modelling, then differences between localities are reduced, limiting the model's predictive power (Lobo *et al.* 2004). However, to reduce type II errors in species composition analyses, singleton species must be removed. But the singleton species must be considered during interpretation of the results when reconstructing biogeographic histories of taxa and forming conservation decisions for areas and species (Lumaret and Lobo 1996). Singleton species constituted 33% of the fauna recorded during the Pilbara survey. The majority were either collected from areas near the edge of the region or were associated with the Fortescue subregion. The former may have their distributions centred elsewhere, while singletons from the Fortescue

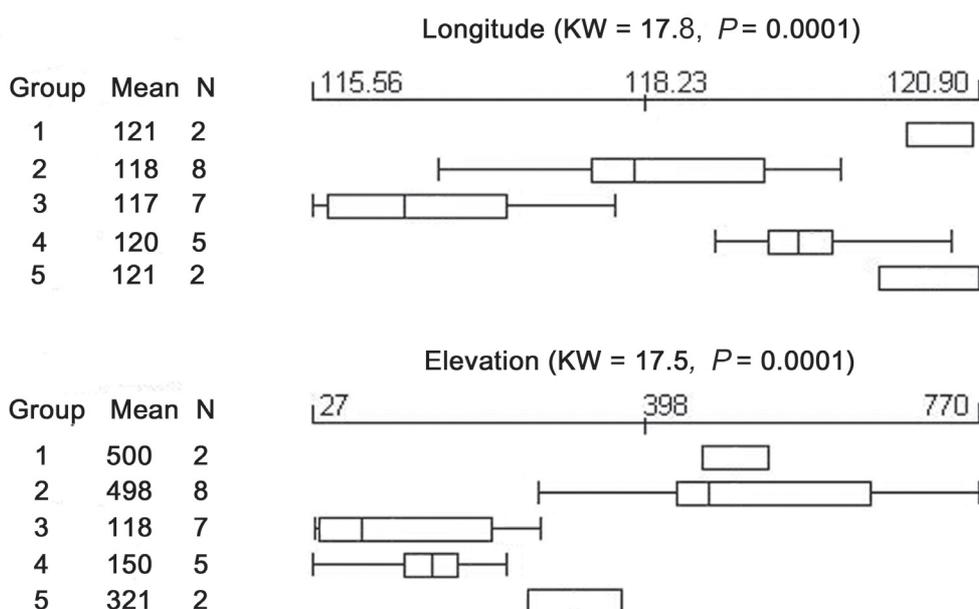


Figure 9 Environmental attributes that best separated the five survey cell groups defined in Figure 7. Bars indicate 95% confidence intervals around the mean; Group = classification group number in Figure 7; N = number of survey cells in each classification group.

subregion may be restricted to habitats that are rare elsewhere in the region.

There is no doubt that under-sampling influenced the analytical result. The 72% sampling effectiveness value (from EstimateS) may reflect the quick response of the highly mobile, volant beetle species to local fluctuations in environmental productivity. There were pronounced fluctuations in rainfall across the study area during the survey period (quadrat-to-quadrat, season-to-season and year-to-year; see McKenzie *et al.* 2009).

Australian Bolboceratidae exhibit high generic endemism and occur mainly along coastal regions and to a lesser extent in the dry interior (Howden 1981). There is little ecological information for Australian species but associations with sandy habitats for larger species have been recorded (Howden 1981). Twenty-two Bolboceratid species in six genera were collected during the survey. Six species of *Austrolobolbus* were usually found at either rocky or clay-based quadrats. *Austrolobolbus pseudobscurius*, *A. subretusus* and *A. impressicollis* were found in discrete populations across the survey region. Five of the 10 *Blackburnium* species were recorded only from sand dune quadrats of the region's eastern periphery and one on various landforms there, suggesting a wider range in the sandy deserts extending eastwards from the Pilbara. *Bolboleus truncatus* and *B. trifoveicollis* were distributed more widely, having several discrete populations on deep clay or rocky quadrats in most survey cells.

Twenty-one Carabid subfamilies were collected in the survey. The Amblystominae were represented by 13 specimens from three species. Three genera of Bembidinae were collected in the survey; the most diverse was *Tachys* with 11 species, including *Tachys convexicollis* present at 11 sites. Our collection of *Sarothrocrepis benefice* (Cyclosominae) was a minor range extension for this wide-ranging species. Range extensions were recorded for three species of *Gnathaphanus* (Harpalinae): *G. froggatti*, *G. melbournensis*, and *G. multipunctatus*. Two undesignated *Helluo* (Helluoninae) species were collected well outside the genus's known range in the Murray-Darling basin. *Nototarus* (Lebiinae) was represented by three described and 16 undescribed species. The related genus *Anomotarus* was represented by three dry-country species: *A. nitidior*, a little-known northern Australian 'forest litter' dwelling species (Baehr 2005) collected during the survey only from MBW07, *A. nubilis*, and *A. umbratus*, a halophile inhabiting sand flats (Baehr 2005). *Gestroania amplipennis* (Odacanthinae) was collected only from WYE13, and may be on the northern limits of its otherwise south-western distribution. *Renneria kamouni* (Odacanthinae) was recorded from 10 sites, representing a

significant range extension south-westward from far north Kimberley and adjacent Northern Territory. Undetermined species were recorded for the Pterostichinae genera *Cratogaster*, *Darodilia*, *Loxandrus*, *Platycoelus* and *Rhytisternus*. Significant range extensions were recorded for *Loxandrus laevigatus*, *L. micantior* and *Platycoelus melliei*. Nine genera (including one undesignated genus) represented the Scaritinae in the survey. Twenty-eight of the 33 *Carenum* species were unplaced, and *Clivina* was represented by 14 unplaced and 2 described species. Six species from four genera represented the Zuphinae: *Acrogenys* and *Zuphium* were each represented by two species. The record of *Acrogenys centralis* (Zuphinae) at NE13 represents a major range extension from the only known locality, Amata, Musgrave Range, South Australia. Likewise, the record of *Zuphium flavum* (Zuphinae) at TCMBW04 represents a range extension of 2000 km from the previously known distribution in the Lake Eyre Basin, South Australia.

The Hybosoridae have undergone extensive species-level radiation in Australia, with 40 species in 3 genera, compared to 183 species in 31 genera worldwide. Present across mainland Australia, the richest fauna is found in the tropical northern regions. Six species, representing all three Australian Hybosorid genera, were recorded during the Pilbara survey. They were often found on rocky quadrats, usually with massive boulders and steep scree slopes, or on calcrete or opaline hills and mesas, but were rarely collected from quadrats with predominantly sand or clay profiles. Three undesignated *Antiochrus* species were centred on (but not limited to) quadrats scattered around the periphery of the survey region. *Liparochnus carnei* and *L. rufus* were collected within their known ranges. *Phaeochrous australicus* exhibited several discrete populations occurring in adjacent quadrats across several survey cells.

Ninety-five species within 25 genera represented four subfamilies of the Scarabaeidae. Nine species within three genera of the Aphodiinae had distributions centred on (but not limited to) the survey cells RHNC, RHNE and RHNW in the south-eastern Pilbara. The Dynastinae were represented by six species in four genera; notably, *Cryptodus caviceps* was recorded at several coastal quadrats with deep clay profiles or rocky landforms, and *Teinogenys aurilegulus* was usually recorded at Fortescue Valley quadrats with deep clay profiles or rocky landforms. Fifty-six species across 11 genera represented the Melolonthinae. Six genera were represented by single species (one species at two quadrats, the rest at one quadrat). *Lepidiota squamulata* occurred in discrete populations at adjacent quadrats across several

survey cells. Twenty-nine species of *Heteromyx* were collected, most of which were recorded widely across the survey region. *Liparetrus* and *Gnaphalopoda*, with 11 and 6 species respectively, were also recorded at widely scattered quadrats across the region. The Scarabaeinae were represented by 26 species in seven genera; of these, four genera had single species. Fourteen *Onthophagus* species were recorded in the survey, seven of which were restricted to ten or fewer quadrats. The other seven were widely distributed across the region. Of the determined species of Scarabaeinae, records within the survey corresponded with generalised known or hypothesised distributions (Matthews 1972, 1974) with a few minor range extensions. The native Scarabaeinae recorded in the Pilbara prior to this survey were six *Onthophagus* species; of these, only *O. murchisoni* was not recorded in this survey.

The Tenebrionidae were represented by 80 species within 32 genera across seven subfamilies. Eleven species across five genera of the Alleculinae were recorded, including four undesignated species in two tentative genera. *Metiste* sp. 1 was the only widespread Alleculine recorded in the survey. The Coelometopinae was represented by *Hypaulax orcus*, widely distributed and absent only from PHYW and TCMBW, and *Oectosis* sp. 1, present only at DRW02. Five *Isopteron* species (Lagriinae) exhibited discrete distributions across adjacent survey cells. The three unplaced Lagriinae and two unplaced Palorinae taxa were widely distributed across several rocky habitat quadrats. The myrmecophilous genera *Thorictosoma* and *Wattiana* (Pimeliinae), represented by six and one species respectively, were recorded at scattered quadrats across the survey region. The most diverse subfamily represented in the survey was the Tenebrioninae, with 45 species in 14 genera across three tribes. The five species of *Chalcopteroides* (Amarygmini) were widely distributed, with three species each collected at one quadrat only. The Opatrini were represented by two widespread genera, *Gonocephalum*, *Mesomorplus*; and two genera previously collected on littoral sands (Matthews and Bouchard 2008), *Caedius* and *Sobas*; all were recorded in scattered quadrats across the survey region. Twenty-four species across eight genera represented the Heleini. Three species of the highly localised subterranean *Dysarchus* (Matthews and Bouchard 2008) were recorded at several coastal quadrats with either rocky, stony or granitoid profiles. The most commonly encountered genus was *Boreosaragus*, with three undetermined species, with *Boreosaragus* sp. 1 present at 200 quadrats.

All five families sampled, therefore, have significant species richness in the Pilbara, and all include a range of taxa that appear to have restricted distributions.

Compositional patterns

At the quadrat or local-scale, beetle composition was correlated with the land substrate attributes slope, soil depth, and exchangeable calcium (along with exchangeable potassium and sand). Heavy cracking clays, saline muds and riverine-associated muds formed a distinct group in the quadrat analysis. A distinctive suite of species was recorded but was not necessarily limited to these quadrats. Most of the common or widely distributed species were absent from this quadrat group.

At the biogeographic regional scale, strongly localised geographical patterns emerged from the survey cell analysis. Longitude and elevation showed strong correlations with compositional turnover, and the 5-group level dendrogram partitions reflected the physio-geographical subregions described by Beard (1975) (Figure 7).

It is difficult to place our findings into a wider context; an extensive literature search has failed to find comparable studies examining environmental attributes and beetle assemblage turnover. However, when the gross morphology and general ecology of the various families are taken into account, our findings are logical. All five families are ground-dwelling terrestrial beetles, and within each family there exist varying fossorial abilities and adaptations to different soil and terrain types.

Therefore, to preserve the diversity of these families in the Pilbara region, reserves encompassing a range of land and soil substrate attributes (at the localised micro-scale) are required in each of the subregions as part of a comprehensive conservation reserve system.

Little is known about regions of endemism for Australian beetles. Matthews and Bouchard (2008) described 10 areas of endemism for Tenebrionids, with the closest to the Pilbara being the 'Murchison'. These regions may have acted as historical refugial areas, with fauna repeatedly retreating to them during times of aridity or marine incursions. Whether or not the Pilbara has acted in the same manner is unknown, but the relatively high number of local endemics (33%) found in this survey suggests that the Pilbara may be an important and previously unrecognised refugial area with high endemism.

CONCLUSIONS

We noted that the resident Pilbara assemblages of Bolboceratids, Carabids, Hybosorids, Scarabaeids and Tenebrionids are species-rich, but dominated by few highly abundant species. Assemblages comprise a component of common or widely distributed species (often with large numbers of individuals appearing to exhibit wide morphological variability within and between

quadrats), and components of species that occur at relatively few quadrats (each represented by a few specimens at any one quadrat). This could reflect actual species distributions, or be an artefact of highly variable multiple year-to-year population fluctuations influencing trapping success and/or deficiencies in the current taxonomic resolution.

Assemblage composition varied at the local and regional scales, reflecting landform (slope) and soil characteristics at the local scale and the physiogeographical subregions regionally.

It appears that localised evolutionary processes associated with limited mobility have resulted in a beetle fauna with a high proportion of strongly-localised endemic forms. Detailed comparisons with neighbouring semi-arid areas such as the Great and Little Sandy Deserts, Ashburton and Northern Carnarvon Basin are required to clarify phylogenetic relationships between beetle taxa, their distributions, and to explore further the correlation of species composition with various land surface attributes that have emerged from our analysis.

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APPENDIX 1

Sampling dates for invertebrates in wet pitfall traps in all survey quadrats.

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APPENDIX 2

Frequency of occurrence across quadrats of all species in the families Bolboceratidae, Carabidae, Hybosoridae, Scarabaeidae and Tenebrionidae, collected in wet pitfall traps in each of the 24 survey cells. Number of sampled quadrats in each cell: NW-9; DRC, MBE, OYE, PHYC-11; PE, RHNE, TCMBC, WYW-12; BDRN, BDRS, DRE, DRW, MBW, NE, OYW, PW, PHYE, PHYW, RHNC, RHNW, TCMBE, TCMBW, WYE-13.

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APPENDIX 3

Data matrix re-ordered according to quadrat compositional similarities and species co-occurrences. Classification partition boundaries are shown at the 3-group level for the quadrats plus sub-groups; and at the 6-group level for species (for illustrative purposes only).

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Huntsman spiders (Sparassidae) live under bark and in rocky areas (Lochman).