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Environmental associations of small ground-dwelling mammals in the Pilbara region, Western Australia

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Abstract – Small (< 50 g) ground-dwelling mammals were sampled as a part of a larger survey of the Pilbara biogeographic region in Western Australia. Environmental attributes influencing the probability of occurrence of individual small mammal species were identified using the multivariate adaptive regression splines (MARS) modelling approach. Interpretation of co-occurrence patterns, based on known habitat associations throughout wider ranges in the Pilbara and/or elsewhere in Australia, was used to facilitate comparisons of sub-sets of the species models. Eighteen species were recorded during this study (mean of 3.4 per survey site [range: 0–7]), but only 14 had sufficient survey records to construct models with reasonable certainty. Complex, non-linear responses were observed for most of the MARS species models, with model performance higher for species with a restricted distribution than the more widely ranging species. Species co-occurrence patterns appeared to be best explained by substrate with three alignments linking species that tend to occur on increasingly sandy, clayey and rocky substrates. Similarly, variables describing the substrate were consistently and strongly represented in the models, indicating that these mammals partition their habitat on substrate type at the local scale in the Pilbara. Climate attributes added little information to the models, although distance to the coast, a surrogate for a range of climatic influences, was important for some species. That all species previously known to occur in this region were recorded in the current study suggests that this fauna is still intact, despite a variety of factors (e.g. pastoralism, weed invasion, inappropriate fire regimes and mining) that have been transforming the region's ecology for more than a century.

INTRODUCTION

Data on the occurrence of small (< 50 g) ground-dwelling mammal species were collected as a part of a larger study documenting biodiversity patterns in the Pilbara biogeographic region of Western Australia (Figure 1). Beside opportunistic records, mainly held by the Western Australian Museum, previous ground mammal surveys from the Pilbara have been either localised or species-specific (e.g. Dunlop and Sawle 1983; How *et al.* 1991; How and Cooper 2002; Biota Environmental Sciences 2005; Bamford Consulting Ecologists 2005), including searches for deposits of recent sub-fossils (A. Baynes, pers. comm.).

At the outset of this study, 41 species of non-volant mammal had been recorded from the region during the period of European settlement (Table 1). Three biogeographical components were recognisable in this fauna: Torresian, Eyrean (Spencer 1896) and endemic, although at least three of the six 'endemics' extend into adjacent regions such as the Little Sandy Desert (e.g. Start *et al.* 2000; Western Australian Museum records). This fauna has collapsed during the last 150 years (McKenzie and Burbidge 2002), and the remainder is dominated by species with mean adult body weights of less than 35 g. Twelve species are now extinct in the region, two persist only on its coastal islands (*Pseudomys nanus* and *Rattus tunneyi*) and one (*Hydromys chrysogaster*) has contracted to the coast (Burbidge *et al.* 2009). Although known losses of Australian mammals have been confined to species with a mean adult body weight greater than 25 g, the magnitude of this loss far exceeds that reported for any other component of the biota. This points to the particular sensitivity of mammals to the changes that have accompanied European settlement in Australia (e.g. McKenzie *et al.* 2006) and the consequent need to pay particular attention to the conservation of the remaining species.

Regional conservation planning requires knowledge of biogeographic patterning of biodiversity across the region, as well as an understanding of the factors that define those patterns (Ferrier 2002; Ferrier *et al.* 2007), including the habitat requirements of each species (Bennett *et al.* 1991). Patterns in the species composition of small ground-dwelling mammals have been investigated in other Australian regions (e.g. Friend and Taylor 1984; Braithwaite *et al*. 1985; Bradley *et al*. 1987; McKenzie and Hall 1992; Woinarski *et al*. 1992; 1994; McKenzie *et al.* 2000). By relating those patterns to environmental attributes, these studies implicate annual average temperature, substrate type and environmental disturbance as important influences on mammal composition. Temperature has a direct effect on the ecophysiology and consequently habitat selection of many homeotherms (e.g. McNab 1980). Functional adaptations to sandy, fine-textured or rocky substrates are evident in the foot pads of the dasyurids recorded during these surveys, implying 'stationarity' in habitat use (*sensu* Hengeveld 1994) over evolutionary timeframes. For example, the sand specialist *Sminthopsis youngsoni* has bristly foot pads, while the rock specialist *S. longicaudata* has rubbery, striated foot pads (McKenzie *et al*. 2000). A study by How and Cooper (2002), documenting the occurrence of terrestrial small mammals of Adybos/Woodstock Reserve in the Pilbara, found that assemblages differed across three main habitat types: areas adjacent to rocky breakaways, deep alluvial soils adjacent to a creek and *Triodia*-dominated habitats on a sandplain.

In interpreting these relationships, better resolution can be achieved by associating environmental attributes with the presence (or abundance) of individual species. The derived statistical models can be used to predict the potential distribution (Ferrier *et al*. 2002; Araújo and Guisan 2006; Elith and Leathwick 2007; Ferrier *et al*. 2007) and assist in delineating the specific habitat requirements of each species (e.g. Gibson *et al*. 2007). Over the past decade, this approach has become increasingly popular and the statistical modelling procedures progressively more sophisticated (e.g. Elith *et al*. 2006). Emphasis is now being placed on selecting methods that relate the responses of species to environmental predictors more realistically (Austin 2007). For example, generalised linear models (GLM) have been criticised for their limited ability to fit non-linear relationships between species and environmental variables (Austin 2007), and there are now a number of alternative procedures that allow more flexible model-fitting (e.g. Muñoz and Felicísimo 2004; Moisen *et al.* 2006). Indeed, techniques to model species' distributions are now so numerous (e.g. Guisan and Thuiller 2005; Elith *et al.* 2006) that the decision on which method to use requires careful consideration (Guisan and Thuiller 2005; Austin 2007).

Generalised additive models (GAM; Hastie and Tibshirani 1990) are one technique commonly used to model complex ecological relationships, using non-parametric smoothing functions to fit non-linear responses. Another, relatively new approach to modelling species distributions that has been shown to perform comparatively well (Moisen and Frescino 2002; Muñoz and Felicísimo 2004; Elith *et al.* 2006; Leathwick *et al.* 2006) is the application of multivariate adaptive regression splines (MARS; Friedman 1991). MARS uses piecewise linear fits rather than the smooth functions of a GAM, and is computationally much simpler (Elith *et al.* 2006). An important consideration with all methods that fit complex functions is the interpretability of the resulting response curves, i.e. are they ecologically meaningful (Austin 2007)?

Here, we use the MARS technique to identify the environmental attributes influencing the occurrence of individual species of small ground-dwelling mammals in the Pilbara.

METHODS

Study area

The Pilbara biogeographic region encompasses an area of approximately 179,000 km^2 (Figure 1). Monthly average maximum temperatures range from 25.3°C in July to 37.8°C in January, and average minimum temperatures range from 11.8°C in July to 25.2°C in January (Leighton 2004). The broad near-coastal band has a hot, humid summer with a warm winter while inland areas experience a hot, dry summer and a mild winter. Most rainfall occurs in summer, with occasional cyclonic activity. Average annual rainfall is 290 mm, ranging from a monthly average of 1.7 mm in September to 66.1 mm in February. There is substantial year-to-year variation in rainfall, both locally and regionally.

The Pilbara straddles two bioclimatic regions (Beard 1990). The higher rainfall areas inland (the Hamersley Range) and the cooler areas near the coast have a semi-desert tropical climate with 9 to 11 months of dry weather when precipitation is insufficient to sustain growth, but receiving rainfall in summer (Leighton 2004). The rest of the region has a desert climate with summer rain (characterised by up to 12 months without rain) and higher temperatures.

The region corresponds closely to the Pilbara Craton (see McKenzie *et al.* 2009) and is divided into four geomorphically distinctive subregions. Its northern part, the Chichester subregion, is characterised by undulating Archaean granite and basalt plains that include significant areas of basaltic ranges. Plains support a shrub steppe characterised by *Acacia inaequilatera* over *Triodia wiseana* hummock grassland, while *Eucalyptus leucophloia* tree steppes occur on ranges. It is drained to the north by numerous river systems including the De Grey, Oakover, Nullagine, Shaw,

Table 1 List of the ground-dwelling mammals recorded in the Pilbara biogeographic region (adapted from McKenzie *et al*. 2006). EX: extinct in Pilbara; SD-Is: substantial decline in range, now persists only on the region's islands; MABW: mean adult body weight, g; n: endemic; t: Torresian; e: Eyrean; b: Bassian.

Species	Common Names	Status	MABW	Range
Monotremes				
Tachyglossus aculeatus (Shaw, 1792)	Echidna		4000	e,t,b
Dasyurids				
Dasycercus cristicauda (Krefft, 1867)	Mulgara		115	e
Dasycercus blythi (Waite, 1904)	Ampurta	EX	148	e
Dasykaluta rosamondae (Ride, 1964)	Little Red Kaluta		25	n
Dasyurus geoffroii Gould, 1841	Chuditch	EX	1075	e,b
Dasyurus hallucatus Gould, 1842	Northern Quoll		525	t
Pseudantechinus woolleyae Kitchener and Caputi, 1988	Woolley's Antechinus		40	e
Pseudantechinus roryi Cooper, Aplin and Adams, 2000	Tan Antechinus		25	e
Phascogale calura Gould, 1844	Red-tailed Phascogale	EX	53	e
Planigale 'species 1' (Pilbara WA)			7	n
Planigale 'species 2' (Pilbara WA)			10	n
Ningaui timealeyi Archer, 1975	Pilbara Ningaui		8	n
Sminthopsis longicaudata Spencer, 1909	Long-tailed Dunnart		18	e
Sminthopsis macroura (Gould, 1845)	Stripe-faced Dunnart		20	e
Sminthopsis ooldea Troughton, 1965	Ooldea Dunnart		11	e
Sminthopsis youngsoni McKenzie and Archer, 1982	Lesser Hairy-footed Dunnart		10	e
Bandicoots/Bilbies				
Isoodon auratus (Ramsay, 1887)	Golden Bandicoot	EX	450	t,e
Macrotis lagotis (Reid, 1837)	Greater Bilby		1500	e
Possums				
Trichosurus vulpecula (Kerr, 1792)	Common Brushtail Possum		3000	e,b,t
Macropods				
Bettongia lesueur (Quoy and Gaimard, 1824)	Boodie	EX	1500	e
Bettongia penicillata Gray, 1837	Woylie	EX	1300	e,b
Lagorchestes conspicillatus Gould, 1842	Spectacled Hare-wallaby		3000	e
Lagorchestes hirsutus Gould, 1844	Rufous Hare-wallaby	EX	1660	e
Macropus robustus Gould, 1841	Euro		23500	t,e
Macropus rufus (Desmarest, 1822)	Red Kangaroo		33500	e
Petrogale lateralis Gould, 1842	Black-footed Rock-wallaby	EX	3700	e
Petrogale rothschildi Thomas, 1904	Rothschild's Rock-wallaby		5250	n
Rodents				
Leggadina lakedownensis Watts, 1976	Lakeland Downs Mouse		18	t
Leporillus apicalis (Gould, 1853)	Lesser Stick-nest Rat	EX	125	e
Mesembriomys macrurus (Peters, 1876)	Golden-backed Tree-rat	EX	205	t
Notomys alexis Thomas, 1922	Spinifex Hopping-mouse		32	e
Notomys longicaudatus (Gould, 1844)	Long-tailed Hopping-mouse	EX	80	e
Pseudomys chapmani Kitchener, 1980	Western Pebble-mound Mouse		10	n
Pseudomys delicatulus (Gould, 1842)	Delicate Mouse		12	t,e
Pseudomys desertor Troughton, 1932	Desert Mouse		25	e
Pseudomys hermannsburgensis (Waite, 1896)	Sandy Inland Mouse		12	e
Pseudomys nanus (Gould, 1858)	Western Chestnut Mouse	SD-Is	35	t,e
Zyzomys argurus (Thomas, 1889)	Common Rock-rat		45	e,t
Zyzomys pedunculatus (Waite, 1896)	Central Rock-rat	EX	60	e
Hydromys chrysogaster Geoffroy, 1804	Water-rat	SD	700	t,b
Rattus tunneyi (Thomas, 1904)	Pale Field-rat	SD-Is	90	t,e*

*originally 'b' also

Yule and Sherlock. The Fortescue subregion comprises alluvial plains and frontages of the Fortescue River. Salt marsh, mulga low woodland over bunch grass, and short grass communities occur on the alluvial plains, while River Gum woodlands fringe the drainage lines. Scrub steppe occurs on sandstone ranges. Drainage is oriented west-north-west. The Hamersley subregion occupies the southern part of the Pilbara Craton. It is a mountainous area of Proterozoic sedimentary ranges and plateaus dissected by gorges (banded ironstone, basalt, shale and dolerite). Mulga low woodland over bunch grasses occur on fine-textured soils, and *Eucalyptus leucophloia* over *Triodia brizoides* and *T. wiseana* hummock grassland characterises skeletal sandy soils of the ranges. It is drained southward into the Ashburton River, westward to the coast via the Robe River and northward into the Fortescue River. The Roebourne subregion comprises the Quaternary alluvial coastal and sub-coastal plains of the region. These support a grass savanna of mixed bunch and hummock grasses, and dwarf shrub steppe of *Acacia stellaticeps* over soft spinifex of *Triodia pungens* and *T. epactia*. Samphire dwarf shrublands, *Sporobolus* grasslands and low mangrove forests occur on marine alluvial flats and river deltas.

Land-use history

European activities, including pastoralism, the introduction of exotic plants and feral animals together with mining and associated infrastructure developments, have modified Pilbara vegetation and landscapes, although their effect has been mitigated by the large areas of rugged upland with low pastoral value (Hennig 2004). More than 100 years of over-grazing and frequent wildfires have changed vegetation cover and stripped soils of their organic and mineral-A layers, thereby reducing their water-holding capacities (Van Vreeswyk 2004). Consequently, most of the region's major river systems now carry heavy bed loads of sand, a direct consequence of excessive run-off

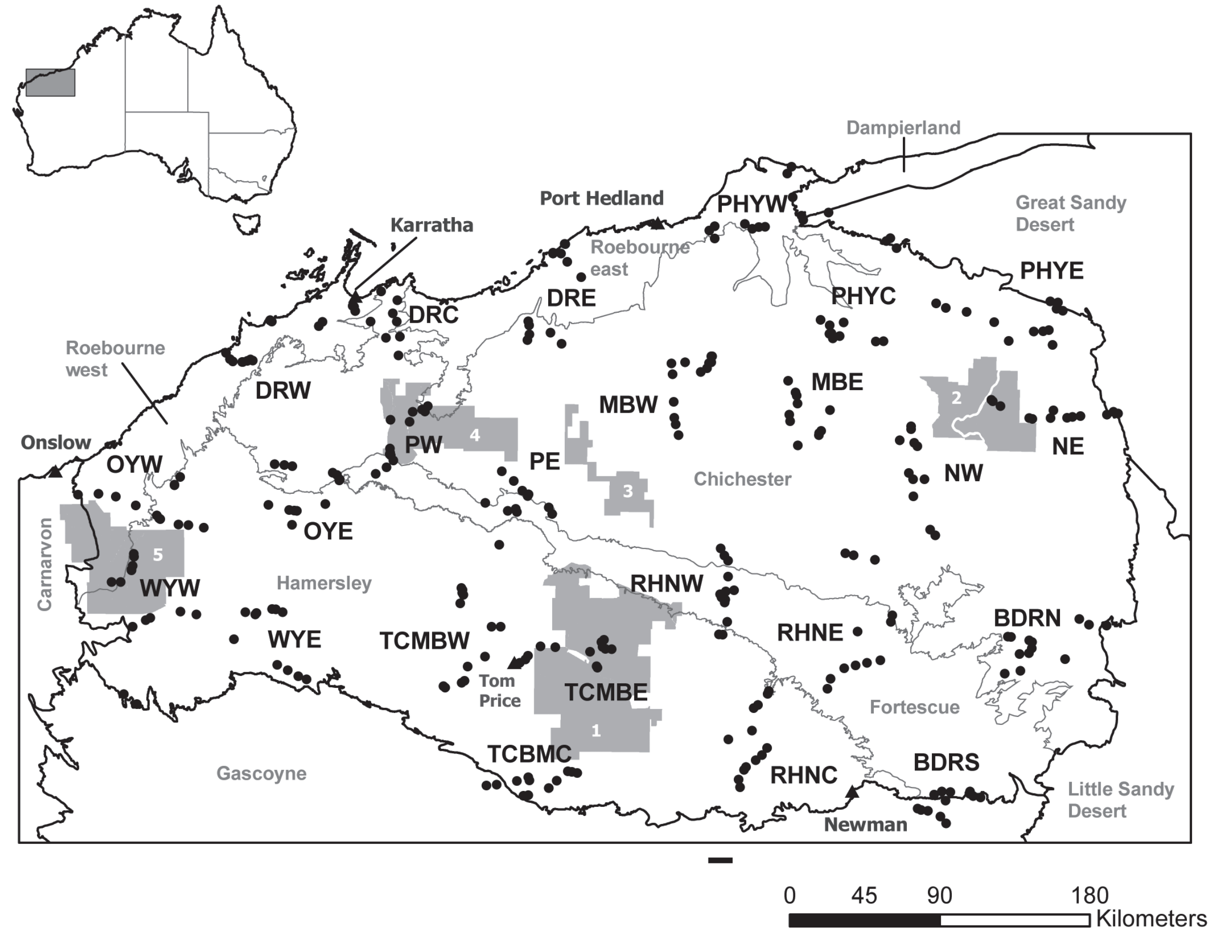

Figure 1 Pilbara biogeographic region. The relative positions of the 24 survey areas are indicated by their labels (e.g. PE, MBW etc.), and the 301 survey sites are marked as circles. Biogeographic region boundaries are shown as bold lines, and boundaries of the four Pilbara sub-regions are grey. Surrounding biogeographic regions and conservation reserves are also shown (1 – Karijini National Park, 2 – Meentheena Conservation Park, 3 – Mungaroona Range Nature Reserve, 4 – Millstream-Chichester National Park and 5 - Cane River Conservation Park).

Table 2 Environmental variable codes used in the modelling process and their descriptions. Inter-correlated variables removed from the analysis are indicated in **bold**.

Variable code	Description
MTEMP	Mean temperature of the coldest period
RAIN	Mean annual rainfall
SILT	Percent silt
NITGN	Total nitrogen (ppm)
XCAL	Exchangeable calcium
CLAY	Percent clay
GCOV	Ground vegetation cover (≤ 1 m)
ELE	Elevation (m above sea level)
SLP	Slope (degrees from horizontal)
RUG500	Topographic ruggedness
CST	Distance to the coast (km)
RIV	Distance to major drainage line (km)
FMAX	Maximum coarse fragment size (1–7)
OUTCRP	Abundance of rock outcrop (0–5)

volumes and velocities in substantial areas of their catchments (Van Vreeswyk 2004). Degradation caused by increased fire frequencies, buffel grass and/or over-grazing is overt throughout the region, with tussock grasslands and chenopod shrublands among the most obviously affected (Van Vreeswyk 2004).

Sampling design

The Pilbara region was divided into 24 survey areas, positioned so that the geographic extent of the region and likely environmental gradients were sampled (Figure 1). In each survey area there were 11–13 sites, positioned to represent the geomorphic profile (i.e. combination of geology and topographic position), although placement was restricted to habitat examples that were the least disturbed. As far as possible, sites were pseudo-replicated across geomorphic categories among survey areas. To allow for heterogeneity of the stratification units, two sites were positioned in the most extensive geomorphic units of each survey area. In total, 301 sites were sampled for small ground-dwelling mammals (Figure 1).

Each site consisted of 2 lines of 5 pitfall traps, with traps being 10 m apart and each line of 5 connected by a flywire drift fence 250 mm high. Pits consisted of PVC pipe (internal diameter of 125 mm and 600 mm in length) with a 2 L plastic jar inserted and a cone-shaped baffle hindering escape. Due to the large area to be sampled, site establishment and sampling occurred in two phases to reduce any loss of sites to wildfire damage, or biases from year-to-year variations in climate. The 24 survey areas (Figure 1) were arrayed in a roughly checker-board pattern (see Mckenzie et al. 2009, figure 6). Sites in the first 12 areas (white squares of the checker-board) were established in mid-2004, sampled in October 2004 then re-sampled in May 2005. Sites in the other 12 survey areas (black squares of the checker-board) were established in mid-2005, sampled in September/October 2005 then re-sampled in May 2006. Each sampling session consisted of 7 nights, a total of 140 trap-nights at each site. Accidental captures in the five invertebrate pitfall traps set for one year at each site were also included in the data set.

Selection of variables

The selection of variables was based on previous studies that examined the influence of environmental attributes on variation in small mammal species composition in Western Australia (e.g. McKenzie and Hall 1992; 1994; McKenzie *et al.* 2000; Start *et al.* 2000; How and Cooper 2002), as well as what was known of the habitat requirements of the same species elsewhere in Australia (e.g. Van Dyck and Strahan 2008). A list of the candidate variable set for inclusion in the modelling is shown in Table 2. Climate variables (MTEMP, RAIN) were derived using the BIOCLIM module of ANUCLIM (Houlder *et al*. 2000). Site-based soil geochemical variables (SILT, CLAY, NITGN and XCAL) were determined from bulked sub-samples collected from the floristic quadrat (50 m^2) at each site. The topographical variables (ELE, SLP and RUG500) were derived from the STRM (Shuttle Radar Topography Mission) 90 m resolution Digital Elevation Model (DEM) using Spatial Analyst tools in ArcGIS 9.1 (ESRI Inc., Redlands, California, USA), resampled at 100 m pixel resolution. Topographic ruggedness (RUG500) was determined by performing a neighbourhood function in ArcGIS (i.e. standard deviation in elevation in a 500 m radius). Raster layers of distance to the coast (CST) and distance to major drainage lines (RIV) were generated in the GIS from digitised hydrology information supplied by the Department of Environment and Conservation, Perth, Western Australia. The vegetation variable (GCOV) is an index of total ground cover at each site. The cover of each vegetation stratum (i.e. shrubs < 2 m, grasses and sedges) was estimated visually, scored (1: < 2%, 2: 2–10%, 3: 10–30%, 4: 30–70% and 5: > 70%) and tallied. As an indicator of the 'rockiness' of a site, the variables maximum coarse fragment size (FMAX) and abundance of rock outcrop (OUTCRP) were estimated visually and categorised following that of McDonald *et al*. (1984).

Model building

Only species with a prevalence of at least 0.05 were chosen for inclusion in the modelling process (see Table 3). Initially, pairwise Pearson correlations between all the candidate predictor variables were examined and the set reduced to those with Pearson correlations less than 0.8. A high ratio of candidate variables to the number of species observations can lead to over-fitting of the model, i.e. inclusion of spurious variables (Harrell 2001; Burnham and Anderson 2002). As a general rule, no more than *n*/10 predictors should be included in the final model, where *n* is the total sample size or, in the case of a binary response, the sample size of the least represented category (Harrell 2001). In this case, expert opinion helped to further reduce the variable set for the species where the limited number of occurrences required it (see Table 4).

The modelling approach used here to fit MARS models to the species presence/absence data set is detailed in Leathwick *et al*. (2005, 2006), and Elith and Leathwick (2007). Briefly, MARS describes the relationship between a response variable and predictors by fitting piecewise linear basis functions of differing slope, and the inflection point along the range of the predictor where the slope changes is termed a knot. Knots are initially selected in a forward stepwise procedure to produce an overfit model, then a backward pruning routine simplifies the model by removing those that contribute least to the model fit. Additions and deletions are assessed according to changes in the residual squared errors using generalised cross-validation. All analyses were run in the R statistical package (R Development Core Team 2004) using the *mda* library and additional customised code made

Table 3 Small (< 50 g) ground-dwelling mammal species recorded during the study, their code name captured. Species included in the analyses are indicated in **bold type**. D = dasyurid marsupial, R= rodent, N = number of occurrences.

Species	Code	Prevalence (N)
***Ningaui timealeyi* (D)**	NTIM	0.59 (179)
***Planigale* sp. 1 (D)**	PLA1	0.50 (149)
***Sminthopsis macroura* (D)**	SMAC	0.44 (131)
***Pseudomys hermannsburgensis* (R)**	PHER	0.42 (125)
***Dasykaluta rosamondae* (D)**	DROS	0.39 (118)
***Pseudomys desertor* (R)**	PDES	0.27 (80)
***Mus musculus* (R)**	MMUS	0.26 (77)
***Sminthopsis youngsoni* (D)**	SYOU	0.11 (33)
***Planigale* sp. 2 (D)**	PLA2	0.11 (33)
***Pseudomys chapmani* (R)**	PCHA	0.10 (29)
***Pseudomys delicatulus* (R)**	PDEL	0.06 (19)
***Leggadina lakedownensis* (R)**	LLAK	0.06 (18)
***Pseudantechinus woolleyae* (D)**	PWOO	0.05 (16)
***Zyzomys argurus* (R)**	ZARG	0.05 (14)
Notomys alexis (R)	NALE	0.03 (9)
Sminthopsis longicaudata (D)	SLON	0.03 (8)
Pseudantechinus roryi (D)	PROR	0.02 (5)
Sminthopsis ooldea (D)	SOOL	0.02 (5)

Table 4 Marginal contributions of each predictor variable to the MARS single-species models. Evaluation statistics are also shown – cross validated area under the curve (AUC) and standard error (se) of the ROC analysis and percentage of total deviance explained (% Dev exp).

Variable	SYOU	PHER	DROS	PDEL	PDES	NTIM	PCHA	MMUS	SMAC	PLA2	LLAK	PLA1	PWOO	ZARG
RAIN	18.7	0.0	14.2	–	15.0	23.2	–	10.6	14.6	5.3	6.1	0.0	–	–
SILT	57.7	17.3	33.5	24.0	0.0	0.0	–	0.0	0.0	–	–	9.0	–	–
NITGN	–	8.1	0.0	7.3	9.6	9.7	20.8	5.5	7.5	–	–	0.0	–	–
XCAL	–	0.0	0.0	–	15.6	0.0	–	0.0	17.0	10.6	3.3	10.1	–	–
CLAY	28.0	10.6	21.6	–	9.5	32.0	11.6	0.0	15.7	21.7	10.3	20.1	–	–
GCOV	–	0.0	0.0	–	4.7	0.0	–	5.7	0.0	–	–	0.0	–	–
RUG500	–	0.0	32.4	–	0.0	23.9	0.0	4.2	10.4	–	–	21.7	3.5	32.3
CST	–	8.5	0.0	14.9	29.3	6.8	16.7	29.9	34.7	–	–	21.0	5.5	–
RIV	–	8.7	12.9	8.9	0.0	0.0	–	8.0	0.0	–	–	8.1	–	–
FMAX	14.1	0.0	0.0	–	0.0	0.0	–	9.5	0.0	–	–	0.0	0.0	0.0
OUTCRP	–	31.3	0.0	–	0.0	0.0	–	0.0	0.0	23.6	0.0	51.2	14.7	0.0
AUC	0.94	0.79	0.71	0.85	0.68	0.76	0.64	0.74	0.74	0.95	0.83	0.89	0.79	0.86
AUC se	0.01	0.02	0.03	0.04	0.02	0.03	0.05	0.03	0.03	0.02	0.05	0.02	0.07	0.04
% Dev exp	60.4	31.1	20.3	30.3	18.0	24.9	20.8	29.2	24.8	62.8	42.9	50.7	24.7	28.5

A dash (–) denotes the *a priori* removal of a variable from the candidate set. A value of 0.0 indicates variables not retained in the models by the MARS analysis.

available online (see Elith and Leathwick 2007).

The predictive performance of all models was evaluated using the area under the receiver operating characteristic (ROC) curve. A ROC curve is a plot of true positive cases (or sensitivity) against corresponding false positive cases (or 1 – specificity) across a range of threshold values (Fielding and Bell 1997). The area under the curve (AUC) provides a measure of discrimination ability, and varies from 0.5 for a model with discrimination ability no better than random, to 1.0 for a model with perfect discriminatory ability (Pearce and Ferrier 2000). As an independent data set was unavailable, estimates of AUC were obtained using *k*-fold cross validation (CV, see Hastie *et al*. 2001), dividing the data into 10 subsets for those species occurring on at least 75 sites (25% prevalence). For species with a prevalence of less than 25%, the data were divided into 5 subsets, the CV repeated and averaged. AUC values of 0.5–0.7 are indicative of low accuracy, values of 0.7–0.9 moderate accuracy, while values of > 0.9 are considered highly accurate (Manel *et al*. 2001).

As a framework for comparing MARS response curves, the analysis package PATN (Belbin 1995) was used to cluster species according to their co-occurrences at the 301 sample sites (presence–absence data). First, the association measure 'Two-step' (Belbin 1980) was used to determine the quantitative relationship between each pair of species, then the dimensionality of the resulting matrix was reduced using Semi-strong Hybrid scaling (Belbin 1991). Finally, a Minimum Spanning Tree was superimposed on the three dimensional scatterplot derived from the ordination. Patterns overt in the scatterplot were assessed extrinsically, in terms of the known habitat associations of component species throughout their wider geographical ranges in Australia (e.g. McKenzie *et al*. 2000; How and Cooper 2002; Van Dyck and Strahan 2008).

RESULTS

Eighteen species of small, ground-dwelling mammals were recorded during the study: 10 dasyurid marsupials, 7 native rodents and an introduced rodent (*Mus musculus*) (Table 3). A revision of the genus *Planigale* in Western Australia has identified two species in the Pilbara which have yet to be formally described (Norah Cooper, pers. comm.); in Table 3 they are referred to as *Planigale* sp. 1 and *Planigale* sp. 2. All but three of the species small enough to be considered 'trappable' (even as sub-adults) by the pitfall method used here were recorded—*Zyzomys pedunculatus*, *Pseudomys nanus* and *Rattus tunneyi*. The first is thought to be extinct in the Pilbara, and the other two now persist in the region on coastal islands. Additionally, a single *Dasyurus hallucatus* (sub-adult) and *Dasycercus*

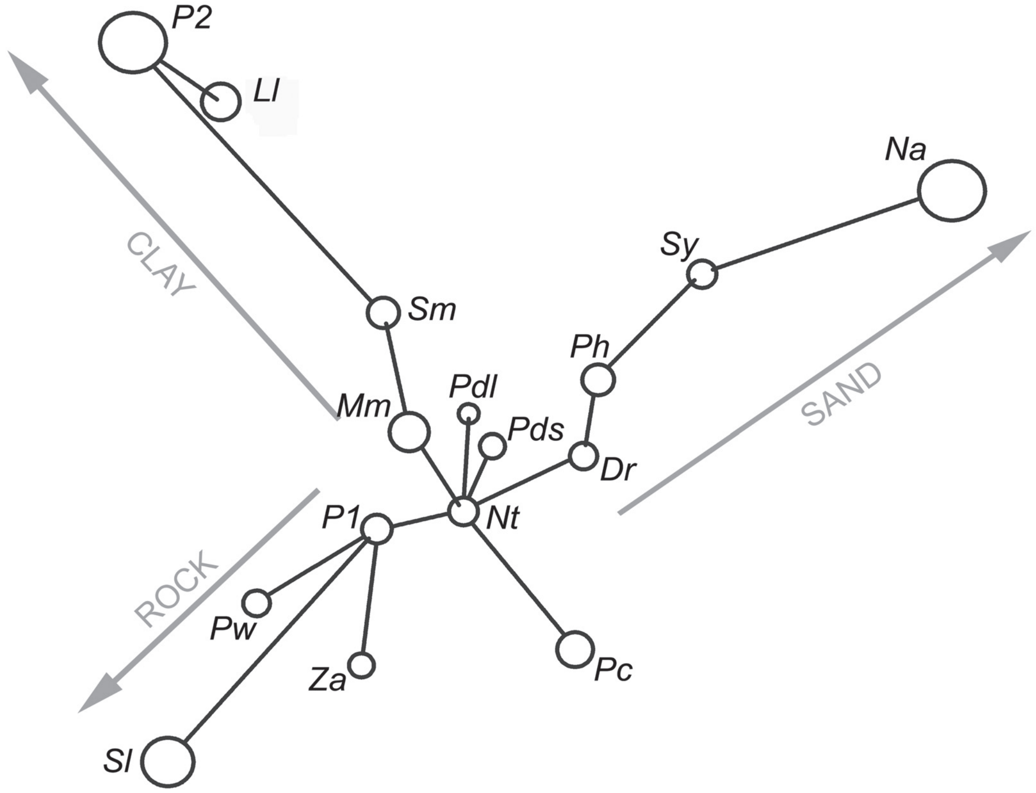

Figure 2 Three-dimensional ordination of the small ground-dwelling mammals according to their co-occurrences at the survey sites (stress = 0.097), with a Minimum Spanning Tree superimposed. The third dimension is indicated by circle diameters. Clay/sand/rock alignments are also shown (extrinsic evidence). Point labels comprise the first letter of the genus name and the first letter of the species name, as listed in Table 3, except P1 and P2 represent *Planigale* sp. 1 and sp. 2 (respectively), and Pdl: *Pseudomys delicatulus*; Pds: *P. desertor*.

cristicaudata were caught incidentally in the invertebrate traps, but these larger (> 50 g) species were not targeted in the current survey and were unlikely to be captured by the vertebrate traps (given the design). An average of 3.4±0.1 small mammal species were recorded from a total of 140 trap-nights per site (range: 0–7 species/site).

Figure 2 summarises the species co-occurrence patterns. Three distinct alignments extend outwards from the loose central cluster of species with peculiar (*P. chapmani*) or catholic habitat associations throughout their wider ranges in the Pilbara and/or elsewhere in Australia (*P. desertor*, *P. delicatulus* and *Ningaui timealeyi*). Substrate provides a consistent explanation for the patterns overt in this scatterplot, so the alignments are labelled according to substrate-associations of their component species, Australia-wide. Two of the four species forming the loose central cluster, *P. desertor* and *P. delicatulus*, are known to occur on clay, sand and, less frequently, even on rocky surfaces (Braithwaite and Covacevich 1995; Kerle *et al*. 2008); another, *P. chapmani*, occupies a peculiarly specific category of rocky substrates (gentle pebbly hill-slopes; Ford and Johnson 2007), while *N. timealeyi* (a Pilbara near-endemic) has been reported to occur equally on all three surface-types (Dunlop *et al.* 2008) which probably explains its central position in the co-occurrence network (Figure 2). The three protruding alignments link species that are faithful to increasingly sandy (*Dasykaluta rosamondae*, *P. hermannsburgensis*, *Sminthopsis youngsoni* then *Notomys alexis* – McKenzie *et al*. 2000), clayey (*M. musculus*, *S. macroura*, *Planigale* sp. 2 then *Leggadina lakedownensis* – McKenzie *et al*. 2000; Moro and Kutt 2008), and rocky substrates (*Planigale* sp. 1, then *S. longicaudata*, *Pseudantechinus woolleyae* and *Zyzomys argurus* diverging outwards – Burbidge *et al*. 2008; Woolley 2008; Fleming 2008). Because *Planigale* sp. 1 and *Planigale* sp. 2 are undescribed species and appear to be restricted to the Pilbara, we base these habitat interpretations on observations made during another (localised) survey in the region (Biota Environmental Sciences 2005).

MARS modelling

'Mean temperature of the coldest period', 'elevation' and 'distance to the coast' were all highly inter-correlated, as were slope and 'topographic ruggedness'. Distance to the coast was considered the most informative variable of the first three as it is likely to influence a number of climatic factors along with temperature (e.g. humidity), and therefore was retained in preference to the others. Topographic ruggedness (instead of slope) was also selected, as it was considered a better descriptor of the topographic position of the sites, leaving 11 variables in total (Table 2).

For each individual species model, the relative importance of the predictor variables in explaining variation in the probability of occurrence of each species can be determined by an examination of the marginal changes in deviance when dropping each individual variable from the final models (Leathwick *et al*. 2005). Additionally, inspection of the fitted functions helps to interpret the relationship between the predictors and the dependent variable. Table 4 summarises the contributions of predictor variables to each MARS single-species model. Table 5 describes the plots of the response functions for each species by indicating the knot value (i.e. the inflection point along the range of the predictor where the slope changes) and the sign of the association (positive/negative or nil) either side of each knot for each predictor. An example of how the values in this table relate to response functions is shown in Figure 3. In addition to the fitted functions, plots of the fitted values in relation to each of the predictors selected for modelling for each species are shown in Appendix 1.

Most of the MARS model response curves showed complex, non-linear responses (Table 5). Using the extrinsic interpretation of co-occurrence patterns above as a basis for comparing subsets of the species' models, the three species from the sand alignment that were modelled (*D. rosamondae*, *P. hermannsburgensis* and *S. youngsoni*) all showed an initial positive association with increasing clay content, but only up to a low percentage (≤ 10%), after which there was either no association or a negative association (*P. hermannsburgensis*). Percent sand in the soil was not included in the candidate variable set as it was assumed to be negatively correlated with percent clay. Subsequent analysis showed this to be the case (Pearson correlation: -0.93). While percent clay was highly ranked in terms of explanatory power (i.e. marginal contribution) for *D. rosamondae* and *S. youngsoni*, percent silt ranked highest for these two species and was also clearly important for *P. hermannsburgensis*, with occurrences declining with increasing silt content. The abundance of rock outcrop at a site had the highest explanatory power for *P. hermannsburgensis* with a linear negative relationship. Topographic ruggedness was also an important predictor for *D. rosamondae*, with occurrences decreasing with increasing ruggedness, while *S. youngsoni* showed a negative linear relationship with increasing rock fragment size.

For those species along the clay alignment, *L. lakedownensis* and *S. macroura* displayed similar responses to percent clay in the soil, with occurrences tending to increase with increasing clay content once a relatively low threshold was reached (8–11%). *Planigale* sp. 2 showed a more complex response, with an initial positive followed by a negative association at 17.5% and positive again beyond 24% clay. This dip in the response curve is likely to be an anomaly in the data, given the small number of sites where this species occurred and perhaps under-sampling within this range (i.e. 17–24% clay). Clay had the highest explanatory

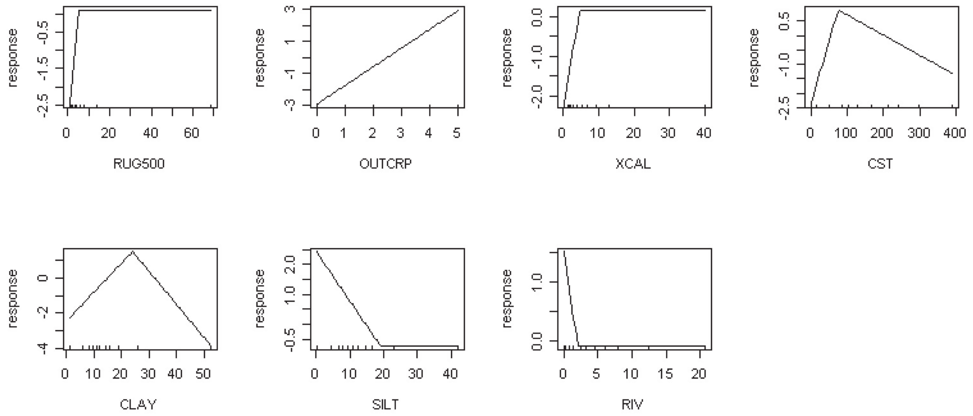

Figure 3 Response functions fitted for *Planigale* sp. 1 (PLA1) in relation to each environmental variable as listed in Table 5. Equates to the coding in Table 5: RUG500 +[5]; OUTCRP +; XCAL +[5]; CST +[76]-; CLAY +[24]-; SILT –[19]; and, RIV –[2].

Table 5 Descriptions of the plots of the response functions for each individual species by indicating knot values (the inflection point along the range of the predictor where the slope changes) and the sign of the association (positive/negative/nil) either side of each knot. Knot values are the attribute values at which the association changes.

	SYOU	PHER	DROS	PDEL	PDES	NTIM	PCHA	MMUS	SMAC	PLA2	LLAK	PLA1	PWOO	ZARG
RAIN	-[263]+ [295]-	0	+[295]	N/A	+[295]	+[276]	N/A	+[295]-	[342]+	[348]-	[309]+	0	N/A	N/A
SILT	-[12]	-[15]	-[24]	-[12]	0	0	N/A	0	0	N/A	0	-[19]	N/A	N/A
NITGN	N/A	-[0.06]+	0	+[0.03]	-[0.03]	[0.09]-	+[0.04]- [0.09]+	+[0.03]	-[0.07]	N/A	0	0	N/A	N/A
XCAL	N/A	0	0	N/A	+	0	N/A	0	+[9]	[4]+	[12]+	+[5]	N/A	N/A
CLAY	+[8]	+[10]-	+[8]	N/A	[14]-	+[14] [24]-	14[-]	0	[11]+	[11]+ -[24]+	[8]+	+[24]-	N/A	N/A
GCOV	N/A	0	0	N/A	[6]+	0	N/A	[6]+	0	N/A	N/A	0	N/A	N/A
RUG500	N/A	0	-[10]	N/A	0	+[4]	N/A	[4]+	-[4]	N/A	N/A	+[5]	[5]+	[8]+
CST	N/A	[168]+	0	[241]-	+[241]-	+[95]	[168]+ [240]-	[134]+	-[107]+	N/A	N/A	+[76]-	[285]+	N/A
RIV	N/A	+[2]	+[2]-[7]+	-[2]	0	0	N/A	-[4]+	0	N/A	N/A	-[2]	N/A	N/A
FMAX	-	0	0	N/A	0	0	0	-	0	N/A	N/A	0	0	0
OUTCRP	N/A	-	0	N/A	0	0	N/A	0	0	-	0	+	+	0

± = positive or negative linear association; ±[] = either a positive (+) or negative (-) association up to a threshold value in the brackets (knot) and nil association thereafter; []± = nil association up to knot, then a positive/negative association thereafter; ±[]± = positive/negative association up to a knot, followed by a negative/positive association; ±[]±[]± = positive/negative association up to a knot, followed by a negative/positive association to another knot then another positive/negative association; ±[][]± = nil association between knots. 'N/A' denotes the *a priori* removal of a variable from the candidate set. A value of '0' indicates variables not retained in the model.

power for *L. lakedownensis*, and close-to-highest for *Planigale* sp. 2. The highest ranked variable for the latter was abundance of rock outcrop with occurrences decreasing as more outcrop was exposed. Distance to the coast explained much of the variance for *M. musculus* and *S. macroura*, occurrences of both tending to increase with distance to the coast, but only after distances of 134 km (*M. musculus*) and 107 km (*S. macroura*) had been reached.

For those species extrinsically linked to rocky areas (Figure 2), the abundance of rock outcrop was the main contributor to both *Planigale* sp. 1 and *P. woolleyae* models, where occurrences increased with greater exposure of rock outcrop. Topographic ruggedness was retained in all three of the rocky species' models and was the sole contributor to the *Z. argurus* model, with positive relationships between occurrence and increasing ruggedness (although thresholds applied – see Table 5).

For the species that occurred in the central cluster of Figure 2, trends across the species were difficult to detect. This is not surprising, however, given the diversity of habitat types that at least three of these species (*P. desertor*, *P. delicatulus* and *N. timealeyi*) tend to occupy. *Pseudomys delicatulus* responded positively to decreasing levels of silt in the soil, but only within a range of 0 to 11.5%. Percent clay was an important predictor of *N. timealeyi* occurrence and distance to the coast for *P. desertor*, but these responses were complex. Percent nitrogen in the soil was the highest ranked variable for *P. chapmani*, with a generally positive response (greater occurrences) to increasing levels.

Other variables not yet mentioned, such as average annual rainfall, exchangeable calcium in the soil, ground cover of vegetation, distance to major drainage lines and maximum fragment abundance, had varying influences in the species models and, for those where these variables were retained, their marginal contributions were generally small.

AUC values obtained from cross-validation ranged from 0.658 for the *P. chapmani* model to 0.950 for *Planigale* sp. 2, with values tending to be highest for those species with relatively low prevalence such as *Planigale* sp. 2, *S. youngsoni* (0.943), *Z. argurus* (0.860), *P. delicatulus* (0.853) and *L. lakedownensis* (0.829) (Table 4). With the exception of *Planigale* sp. 1 which also had a relatively high AUC of 0.890, the values of species occurring at a high proportion of sites generally fell within the range of 0.7–0.8. Models with the worst performance were those for *P. chapmani* and *P. desertor*, with AUC values of less than 0.7. The percentage of deviance explained by the models largely followed the pattern of the AUC values, and ranged from 18.0% to 62.8% (Table 4). Models explaining at least half the deviance were those of the two *Planigale* species and *S. youngsoni*, with most species' models falling within the range of 20–30%.

DISCUSSION

That all small (< 50 g) ground-dwelling mammals previously known to occur in the Pilbara biogeographic region were captured in the current study suggests that this fauna is relatively intact. Of the 18 recorded, the most widely caught species were the near-endemic dasyurids, *N. timealeyi* and *Planigale* sp. 1. Both these species have distributions centred on the Pilbara, but also extend into the margins of the adjacent regions (Western Australian Museum records). Other frequently recorded species include *S. macroura* and *P. hermannsburgensis*, with distributions that extend across Australia's arid zone (Van Dyck and Strahan 2008), and *D. rosamondae*, another species virtually endemic to the region. Rarely caught, the two false antechinus species (*P. woolleyae* and *P. roryi*) and the hopping mouse (*N. alexis*) were likely escapees, given our pit trap dimensions, although Western Australian Museum records reveal that the latter has a patchy distribution in the Pilbara. Records of the long-tailed dunnart (*S. longicaudata*) were few but this is probably a reflection of their specific habitat preferences rather than rarity as such (A.A. Burbidge, pers. comm.). Little is known of the life history of long-tailed dunnarts, but available evidence suggests that this widely scattered species is restricted to rugged, rocky areas (Burbidge *et al*. 2008) and, once located, is present in reasonable numbers (M. Cowan, pers. comm.). For instance, eight individuals were trapped over a 5-night period from a 1 ha quadrat on the slopes of the Kennedy Range in May 1995 (McKenzie *et al*. 2000). In 1981, nine were trapped on a scree slope of the Young Range in the Gibson Desert over a 7-day period (Burbidge *et al*. 2008). Although there were insufficient Pilbara survey records of *S. longicaudata* to generate a distributional model with any confidence, sites where they were detected are consistent with the rocky habitat described elsewhere. Another dasyurid, *S. ooldea*, was detected at only five sites, all in the south-eastern periphery of the Pilbara biogeographic region, which is consistent with their 'southern arid' distribution (Foulkes 2008).

The average species richness per site reported herein (3.4±0.1) is comparable to values reported from sites of similar size using equivalent trapping regimes in the Carnarvon and southern Murchison regions, elsewhere in arid Western Australia (2.8 ± 0.1 and 3.8 ± 0.3, respectively; McKenzie *et al*. 2000).

Habitat associations

Disturbance heterogeneity is known to significantly influence small mammal site-occupancy models (e.g. Woinarski *et al*. 1992; Catling *et al*. 2000), so we intentionally reduced its influence on our data by avoiding overtly disturbed examples of habitat types. Also, the analysis presented here presumes a habitat paradigm (see Armstrong 2005), in which species' distributions are determined primarily by habitat characteristics. Under this paradigm we assumed that presences occur in suitable habitat, whereas absences do not. Microhabitat selection and resource availability hypotheses (see Hernández *et al*. 2005) were treated as second-order effects at regional scales, and not considered. Although this is the first study to define habitat associations influencing the occurrence of small ground-dwelling mammals in the Pilbara quantitatively, the results here generally concur with qualitative descriptions of preferred habitat, both within this region (Dunlop and Sawle 1983; How and Cooper 2002; Biota Environmental Sciences 2005; Bamford Consulting Ecologists 2005) and elsewhere in Australia where the species are distributed more widely (McKenzie *et al*. 2000; Van Dyck and Strahan 2008). Variables describing the substrate were represented consistently and with a high degree of confidence in the MARS models. Such descriptors included percent clay and silt in the soil, and estimates of rockiness and/or ruggedness. Species co-occurrence patterns were also linked extrinsically to substrate, with clay/sand/rock alignments evident. As such, it appears that the small ground-dwelling mammals in the Pilbara partition largely on substrate type at the local scale. McKenzie *et al*. (2000) reported a similar result for ground-dwelling mammals in the Carnarvon Basin of Western Australia whereby patterns in species composition of mammal assemblages were related to a soil texture gradient. Woinarski *et al*. (1992) likewise found that a single gradient of substrate and disturbance described the distributions of ground-dwelling mammals in Kakadu National Park in the Northern Territory, with rockiness being the key environmental attribute that most clearly associated with variation in mammal species composition. In the current study, however, as sites were purposely positioned in habitat types that were least disturbed, a disturbance gradient could not be quantified. The species extrinsically associated with the more sandy habitat types (*D. rosamondae*, *P. hermannsburgensis* and *S. youngsoni*) all appear to avoid areas of fine-textured soils (i.e. high silt content), but prefer a small percentage of clay as shown by the initial positive relationship with this variable. The typical appearance of these sandy sites in the Pilbara is illustrated in Plates 1 and 2. Only *P. hermannsburgensis* demonstrated a negative association as the percentage of clay increased to beyond 10% but, as the marginal contribution of this variable was not ranked highly, this suggests that this species is not restricted to sandy substrates, which is also supported by other studies both within and outside the Pilbara (McKenzie *et al*. 2000 ; Breed 2008). That *D. rosamondae* and *S. youngsoni* showed no association above 8% clay was somewhat surprising (a negative association was expected) although it seems that silt was a more important attribute in terms of defining occurrence anyway. These three species also tend to avoid rugged, massive rocky habitats, as indicated by their negative associations with topographic ruggedness (*D. rosamondae*), abundance of rock outcrop (*P. hermannsburgensis*) or maximum rock fragment size (*S. youngsoni*).

Core habitat for both *L. lakedownensis* and *Planigale* sp. 2 in the Pilbara has been identified as cracking and gilgaied clays (Biota Environmental Sciences 2005). Both species, as well as *S. macroura,* were commonly caught on these substrates during the current survey, and this is reflected by the positive associations with percent clay and exchangeable calcium in the relevant MARS models. A high level of exchangeable calcium is a characteristic of cracking clays (Barzegar *et al*. 1994). Here, the cracking clays averaged 19.5 (me%) exchangeable calcium compared to an overall average of 5.9. Clearly, these species prefer areas of high clay content, but the relative importance of percent clay in the *S. macroura* model was much lower (by approximately one third) than the other two species, indicating a broader habitat preference for this species. Examples of clayey sites where these three species were usually captured in the Pilbara are illustrated in Plates 3 and 4.

While *M. musculus* is distributed Australia-wide, this species tends to prefer the more fertile habitats in arid regions such as the fine-textured surfaces of alluvial loams and clays, but its distribution expands to occupy other habitats following good seasons when numbers are high (Dunlop and Sawle 1980; Masters 1993; How and Cooper 2002). The MARS model here does not suggest that this species is strongly associated with any particular substrate, with the variation between the marginal contributions of the variables in the MARS model being relatively small (with the exception of distance to the coast).

Observations that the two undescribed *Planigale* species in the Pilbara separate on habitat type (Biota Environmental Sciences 2005) are confirmed by this study. While *Planigale* sp. 2 appears to prefer clay substrates and avoids massive rocky habitats, *Planigale* sp. 1 prefers the rugged substrates dominated by exposed bedrock. These same habitat associations were recognised during a survey in 1979 (see Dunlop and Sawle 1980), although the two species were incorrectly assigned as *P. ingrami* (cracking clay habitat) and *P. maculata* (rocky habitat). While *Planigale* sp. 1 was associated positively with topographic ruggedness, this relationship was not continuous, i.e. there was no association after a threshold was reached. The other two species associated with rocky habitats, *P. woolleyae* and *Z. argurus*, did show a continuous positive relationship between occurrence and increasing ruggedness, once this same threshold (or close to it) had been achieved. This is probably a reflection of their more selective preference for the more rugged regions within the Pilbara than *Planigale* sp. 1, which was more widespread, occurring at almost half the sites. Some of the common rocky habitats in which *Z. argurus*, *P. woolleyae*, *Planigale* sp. 1 and *S. longicaudata* were recorded are illustrated in Plates 5 and 6.

In terms of substrate type, the remaining four species showed variable responses. Typical habitat associations in the Pilbara of *P. delicatulus*, *P. desertor* and *N. timealeyi* are depicted in Plates 7 and 8. Although these species occur across a diversity of habitat types, the Plates illustrate sites where all three were captured most often. Consistent with previous studies, *N. timealeyi*, the most commonly caught species, did not appear to associate with any particular substrate type (How and Cooper 2002; Dunlop *et al*. 2008). Although percent clay was ranked highly in its MARS model, the response was complex with an initial positive, then negative association with increasing clay content, indicating a preference for some clay, but avoidance of heavy clay substrates such as the cracking clays. Like *Planigale* sp. 1, *N. timealeyi* also has a preference for variable topography, but only up to a threshold value. The negative response of *P. delicatulus* to increasing silt content indicates that this species tends to avoid areas high in silt, probably because it prefers more friable soils suitable for burrowing (Ford 2008). The occurrence of *P. desertor* increases with increasing exchangeable calcium content but, unlike the other species associating with exchangeable calcium ('clayey' species), this species responds negatively to increasing clay content. Outside the Pilbara, *P. desertor* has been recorded on a variety of substrate types, from sand plains to limestone and conglomerate scree slopes (Kerle *et al*. 2008). A common feature of these habitat types is a dense ground cover of vegetation (Kerle *et al*. 2008), which is consistent with the positive association with ground cover observed in the MARS model here. The last of these four species, *P. chapmani*, associates positively with soils high in nitrogen but the reason for this is not clear.

According to the bioclimatic modelling, rainfall gradients across the region are weak, with values ranging between 289 and 386 mm (range: 157 mm). Consequently, the regional influence of annual average rainfall did not emerge as an important

Table 6 Small ground mammals extant in Pilbara conservation reserves. X: this study; M: Western Australian Museum specimens collected since 1985.

Species	Cane River Conservation Park	Karijini National Park	Millstream-Chichester National Park	Meentheena Conservation Park
Dasykaluta rosamondae	X	X	X	X
Leggadina lakedownensis			X	M
Mus musculus		X		X
Ningaui timealeyi	X	X	X	X
Notomys alexis	X			M
Planigale sp. 1	X	X	X	X
Planigale sp. 2	M		X	
Pseudomys chapmani	M	X	X	X
Pseudomys delicatulus	M		M	
Pseudomys desertor		X	X	X
Pseudomys hermannsburgensis	X	X		X
Pseudantechinus roryi				M
Pseudantechinus woolleyae			M	M
Sminthopsis macroura	X	X	X	M
Sminthopsis youngsoni	X			M
Zyzomys argurus	M	M	M	M

variable in the models (except for *N. timealeyi)*. However, 'distance to the coast', a distal variable representing a range of climatic influences and highly correlated with 'mean temperature of the coldest period', had high explanatory power for species such as *S. macroura*, *M. musculus*, *P. desertor* and *Planigale* sp. 1. The climate of the Pilbara's coastal band differs from the inland areas in terms of higher humidity and a warmer winter. The two species that show a predominantly positive response with increasing distance to the coast, namely *S. macroura* and *P. desertor*, have distributions centred largely on Australia's arid interior. The initial positive, then negative response of *Planigale* sp. 1 to increasing distance to coast reflects the distribution of this endemic species; it is most common in the central Pilbara. It is not clear why this variable was important for *M. musculus* as this introduced species is generally thought to be widely spread across the landscape (Singleton 2008).

Model performance

Models of those species with a restricted distribution in the Pilbara tended to perform better than those of the more widely ranging species. For example, the models of *Planigale* sp. 2 and *S. youngsoni*, both with a prevalence of 0.11, had AUC values greater than 0.9. At greater than 60%, the deviance explained by both these models was also highest. As discussed above, *Planigale* sp. 2 tends to occur in the heavy clay habitats such as cracking clays and *S. youngsoni* appears to be restricted to sandy substrates. The more prevalent species (> 0.4) fell within the AUC range of 0.7–0.8, with the exception of *Planigale* sp. 1 which had a higher AUC of 0.89. Leathwick *et al*. (2005) reported a similar result for MARS models of fish species, and suggested that the superior performance of the restricted species was a result of the ability of the models to identify correctly the extensive areas where species were absent. Intuitively, the ability of a model to discriminate between 'good' and 'bad' habitat for a 'specialist' species is likely to be better than for a 'generalist' species that occurs in a variety of habitat types.

Poor performing models were observed for two of the native rodents (*P. desertor* and *P. chapmani*) with AUC values less than 0.7. Elsewhere in Australia, *P. desertor* occupies a diverse range of habitat types (Kerle *et al*. 2008), suggesting that this species is a habitat generalist and probably explains the poor model performance observed here. On the other hand, *P. chapmani* has specific habitat requirements, mainly relating to their shelter of pebble mounds (Start *et al*. 2000; Ford and Johnson 2007). Broadly, the occurrence of this species is associated with hilly areas dominated by erosional processes to produce the pebbly substrates they prefer, and avoidance of sand and clay plains (Ford and Johnson 2007). More specifically, as indicated by the presence of pebble mounds, this species tends to occur on the gentle slopes of hills (slope angles of between 2° and 6°), and substrates with pebbles of a specific range size (Start *et al*. 2000). The poor performance of the *P. chapmani* model in the current study indicates that variables approximating the specific habitat requirements of this species were missing.

Conservation implications

An intact small ground-dwelling mammal fauna persists across the Pilbara's landscapes despite the variety of factors that have been transforming the region's ecology for more than 100 years, including pastoralism, mining, inappropriate fire regimes, weed invasion and feral mammal colonisation. This component of the region's fauna shows coherent relationships with environmental attributes, especially soil texture and geomorphology. These habitat associations provide the best available basis for conservation planning. Encompassing substantial areas in three of the Pilbara's four sub-regions, the existing conservation reserve system includes examples of a wide variety of the sandy, clayey and rocky substrates and geomorphic units that characterise the Pilbara (McKenzie *et al*. 2003) and, consequently, populations of virtually its entire small ground-dwelling mammal species. Sixteen of the 18 small ground mammals recorded during this study are known to be extant in Pilbara conservation reserves (see Table 6). The only exceptions are *Sminthopsis longicaudata* and *S. ooldea*. However, apparently suitable habitat for *S. longicaudata* is present in one of the reserves, Karijini National Park (Thorne and Tyler 1997), and it is known from several locations near the town of Tom Price on the Park's western periphery (this survey). Also, the geographical range of *S. ooldea* is centred on regions east and south of the Pilbara, only overlapping the Pilbara in the south-eastern corner (Foulkes 2008). If the reserves are managed to maintain the integrity of the plant and invertebrate communities associated with the above surfaces, they should be adequate to allow the relevant species to persist in the region. If, however, populations of *S. longicaudata* are not found in Karijini National Park, one option may be to extend the Park westwards to encompass known populations near Tom Price.

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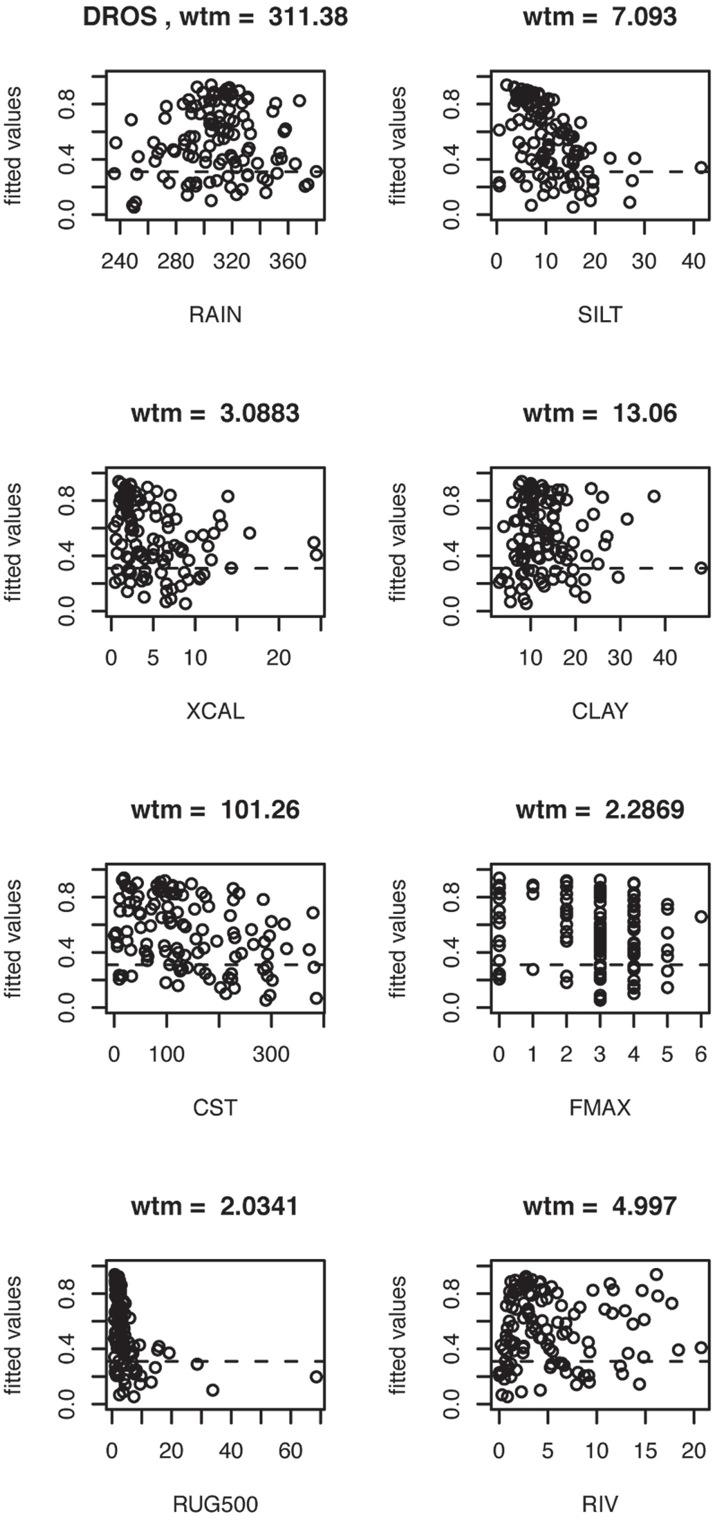
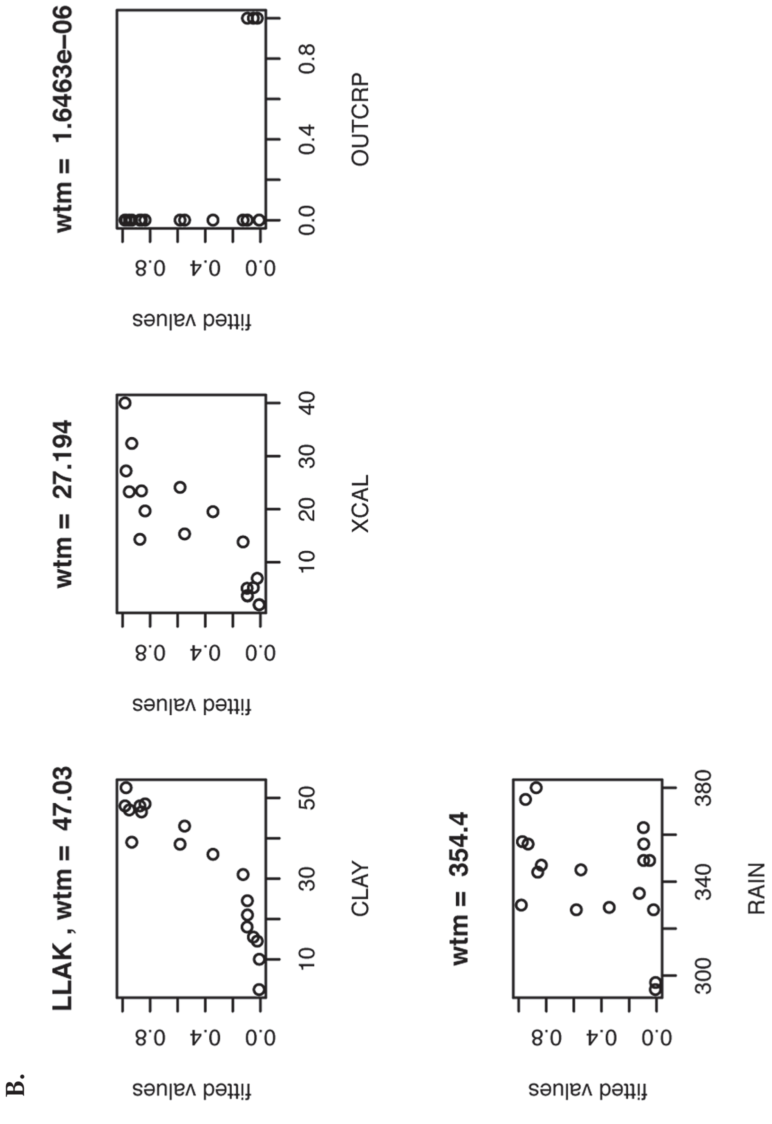
APPENDIX 1

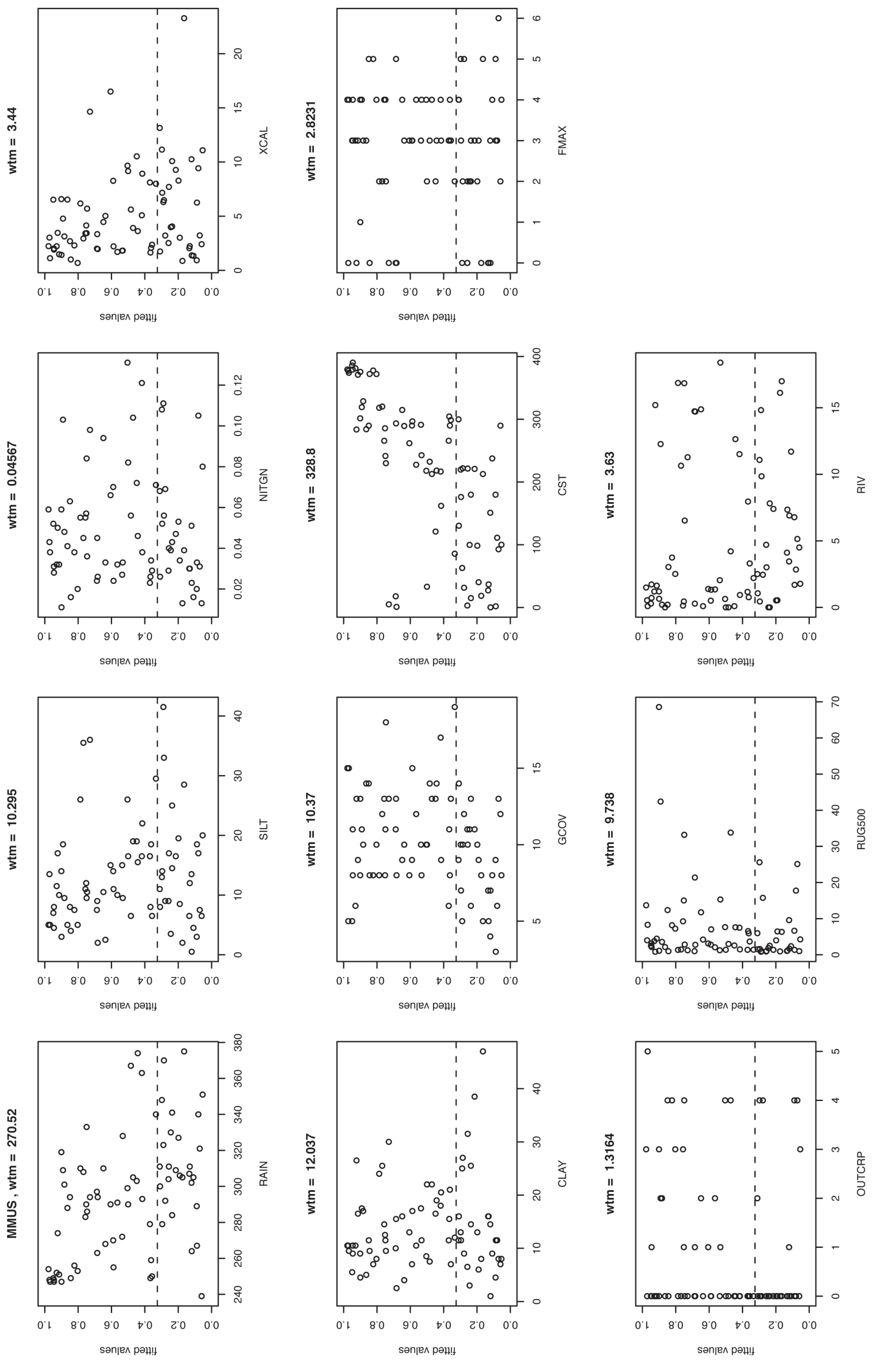
Plots of fitted values in relation to each predictor for each species: A) DROS - *Dasykaluta rosamondae*; B) LLAK - *Leggadina lakedownsensis*; C) MMUS - *Mus musculus*; D) NTIM - *Ningaui timealeyi*; E) PCHA - *Pseudomys chapmani*; F) PDEL - *Pseudomys delicatulus*; G) PDES - *Pseudomys desertor*; H) PHER - *Pseudomys hermannsburgensis*; I) PLA1 - *Planigale* sp. 1; J) PLA2 - *Planigale* sp. 2; K) PWOO - *Pseudantechinus woolleyae*; L) SMAC - *Sminthopsis macroura*; M) SYOU - *Sminthopsis youngsoni*; and N) ZARG - *Zyzomys argurus*. Values for positive observations only are shown. wtm = weighted mean of fitted values.

A.

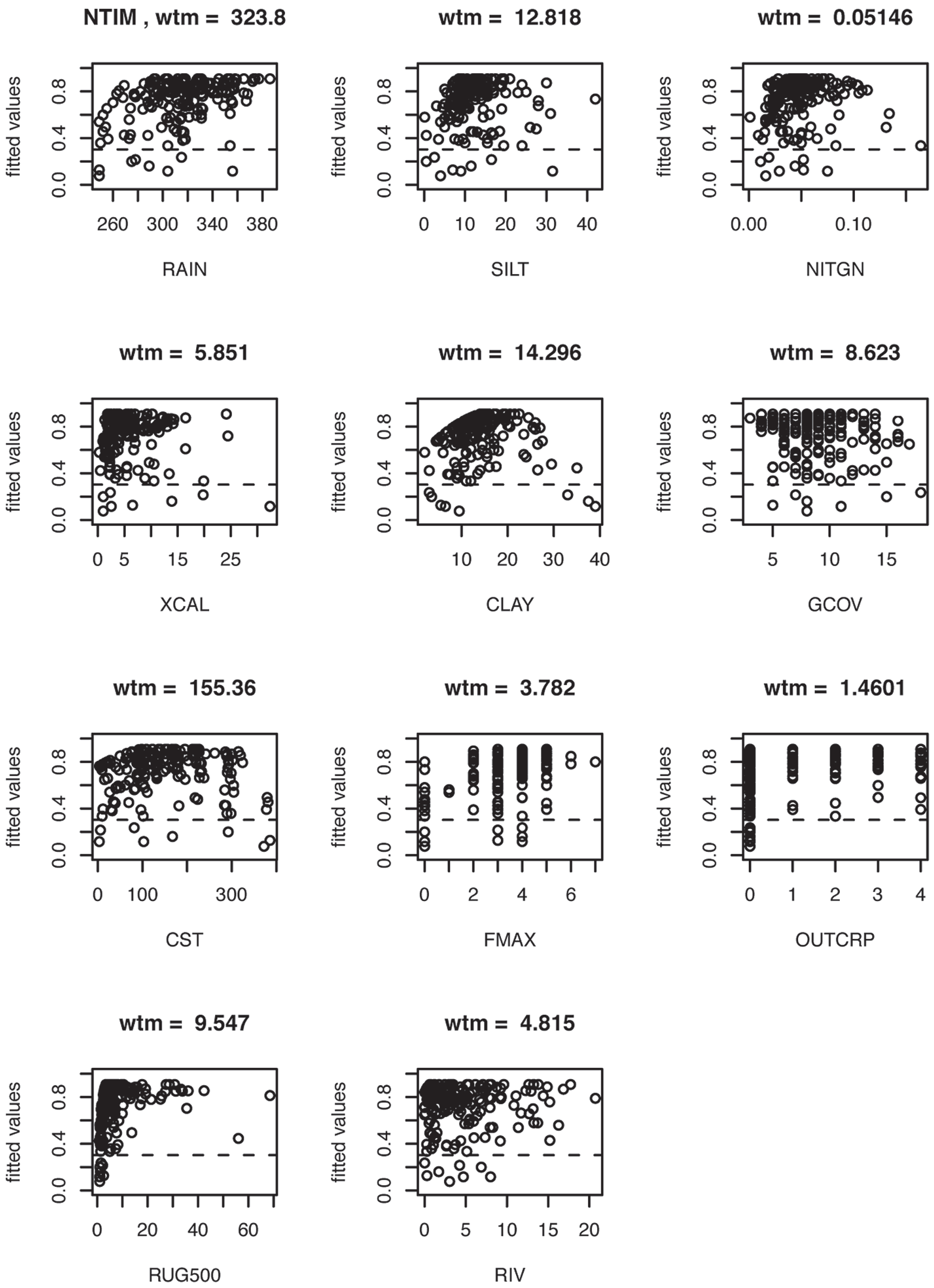



B.
LLAK , wtm = 47.03
wtm = 27.194
wtm = 1.6463e−06
wtm = 354.4
fitted values
0.0
0.4
0.8
CLAY
10
30
50
XCAL
10
20
30
40
OUTCRP
0.0
0.4
0.8
RAIN
300
340
380

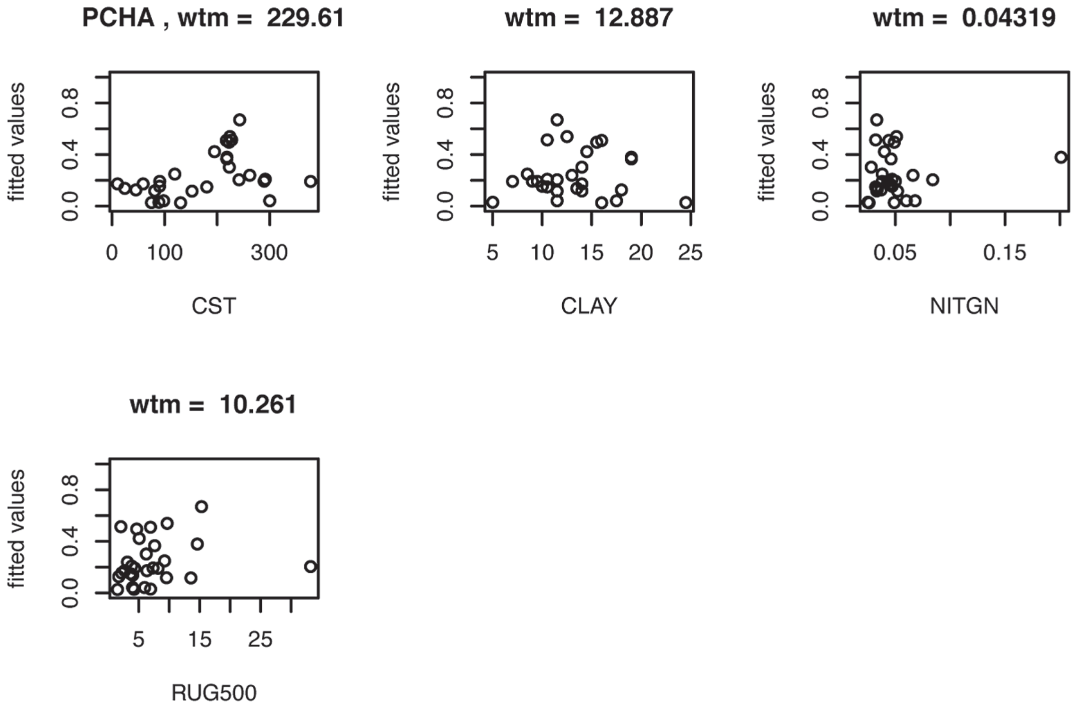
C.


MMUS , wtm = 270.52
fitted values
RAIN
wtm = 10.295
SILT
wtm = 0.04567
NITGN
wtm = 3.44
XCAL
wtm = 12.037
CLAY
wtm = 10.37
GCOV
wtm = 328.8
CST
wtm = 2.8231
FMAX
wtm = 1.3164
OUTCRP
wtm = 9.738
RUG500
wtm = 3.63
RIV

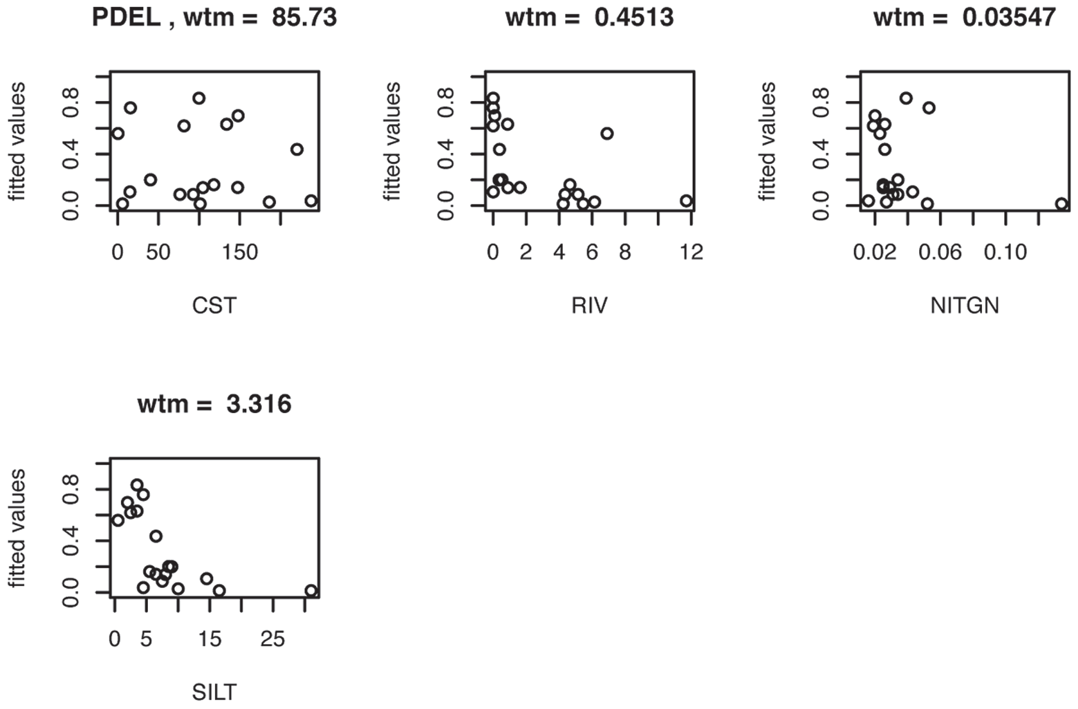
D.


NTIM , wtm = 323.8
fitted values
0.0
0.4
0.8
260
300
340
380
RAIN
wtm = 12.818
0
10
20
30
40
SILT
wtm = 0.05146
0.00
0.10
NITGN
wtm = 5.851
0
5
15
25
XCAL
wtm = 14.296
10
20
30
40
CLAY
wtm = 8.623
5
10
15
GCOV
wtm = 155.36
0
100
300
CST
wtm = 3.782
0
2
4
6
FMAX
wtm = 1.4601
0
1
2
3
4
OUTCRP
wtm = 9.547
0
20
40
60
RUG500
wtm = 4.815
0
5
10
15
20
RIV

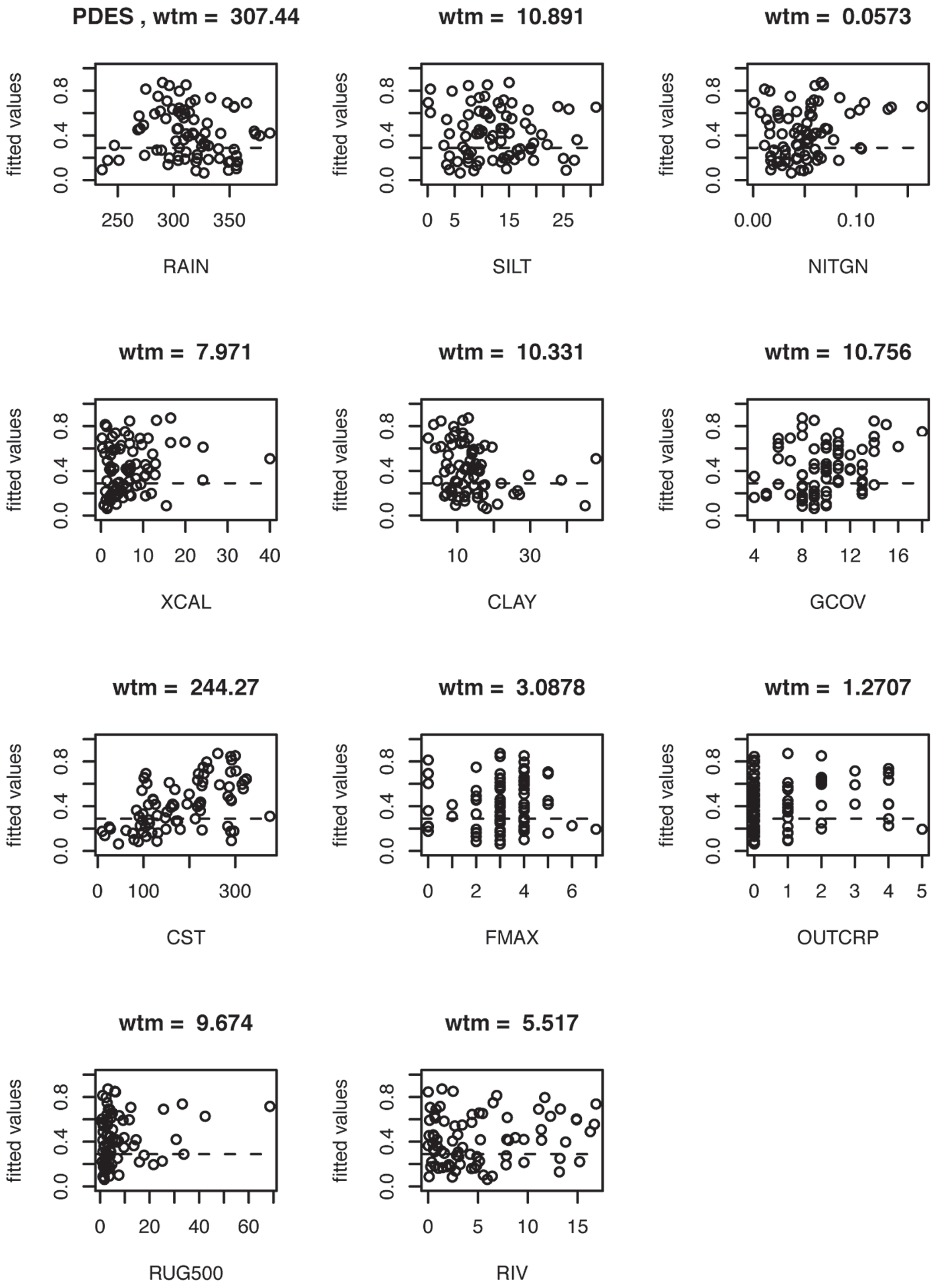
E.


PCHA , wtm = 229.61
fitted values
0.0 0.4 0.8
0 100 300
CST
wtm = 12.887
fitted values
0.0 0.4 0.8
5 10 15 20 25
CLAY
wtm = 0.04319
fitted values
0.0 0.4 0.8
0.05 0.15
NITGN
wtm = 10.261
fitted values
0.0 0.4 0.8
5 15 25
RUG500

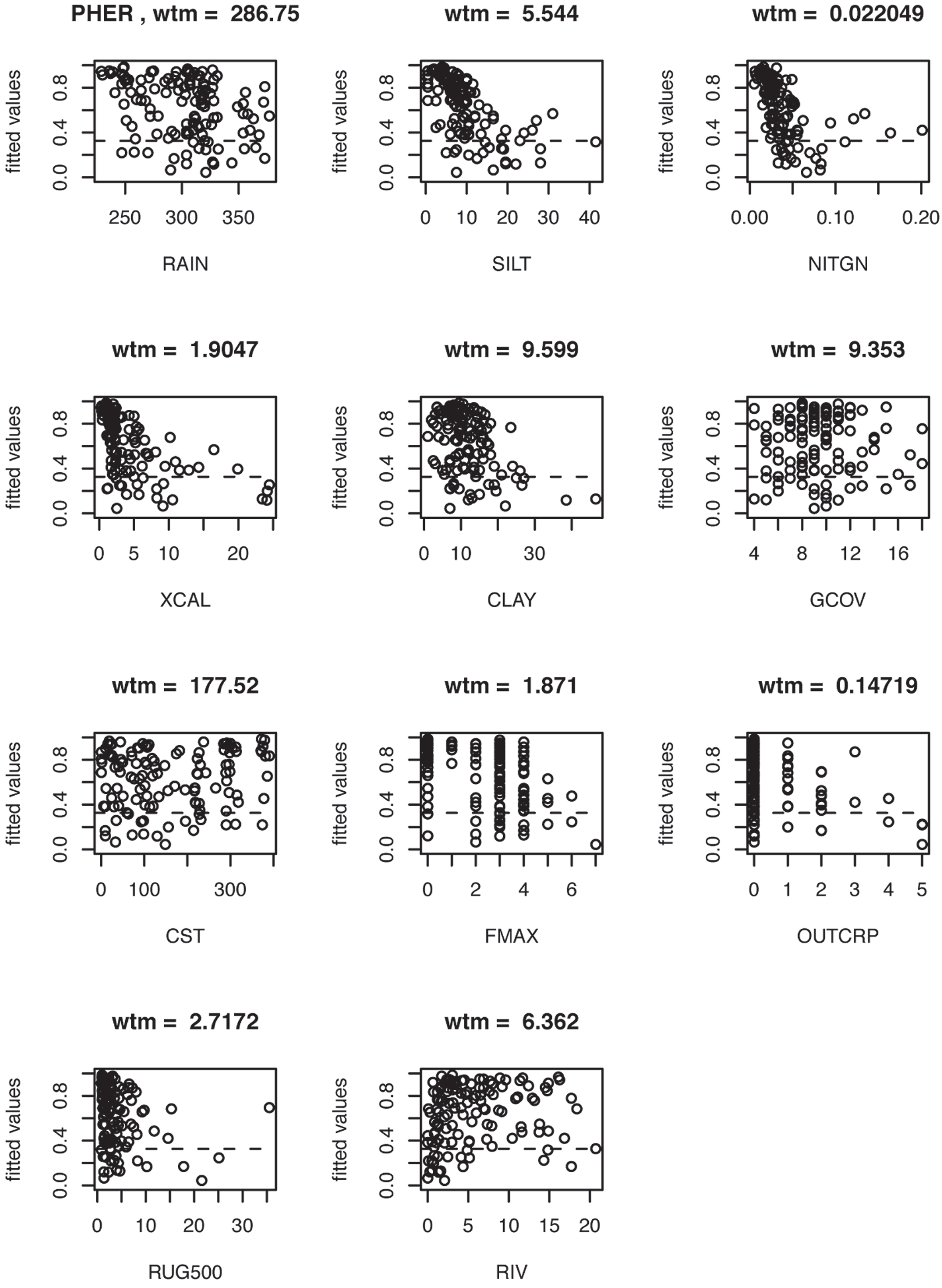
F.


PDEL , wtm = 85.73
fitted values
0.0 0.4 0.8
0 50 150
CST
wtm = 0.4513
fitted values
0.0 0.4 0.8
0 2 4 6 8 12
RIV
wtm = 0.03547
fitted values
0.0 0.4 0.8
0.02 0.06 0.10
NITGN
wtm = 3.316
fitted values
0.0 0.4 0.8
0 5 15 25
SILT

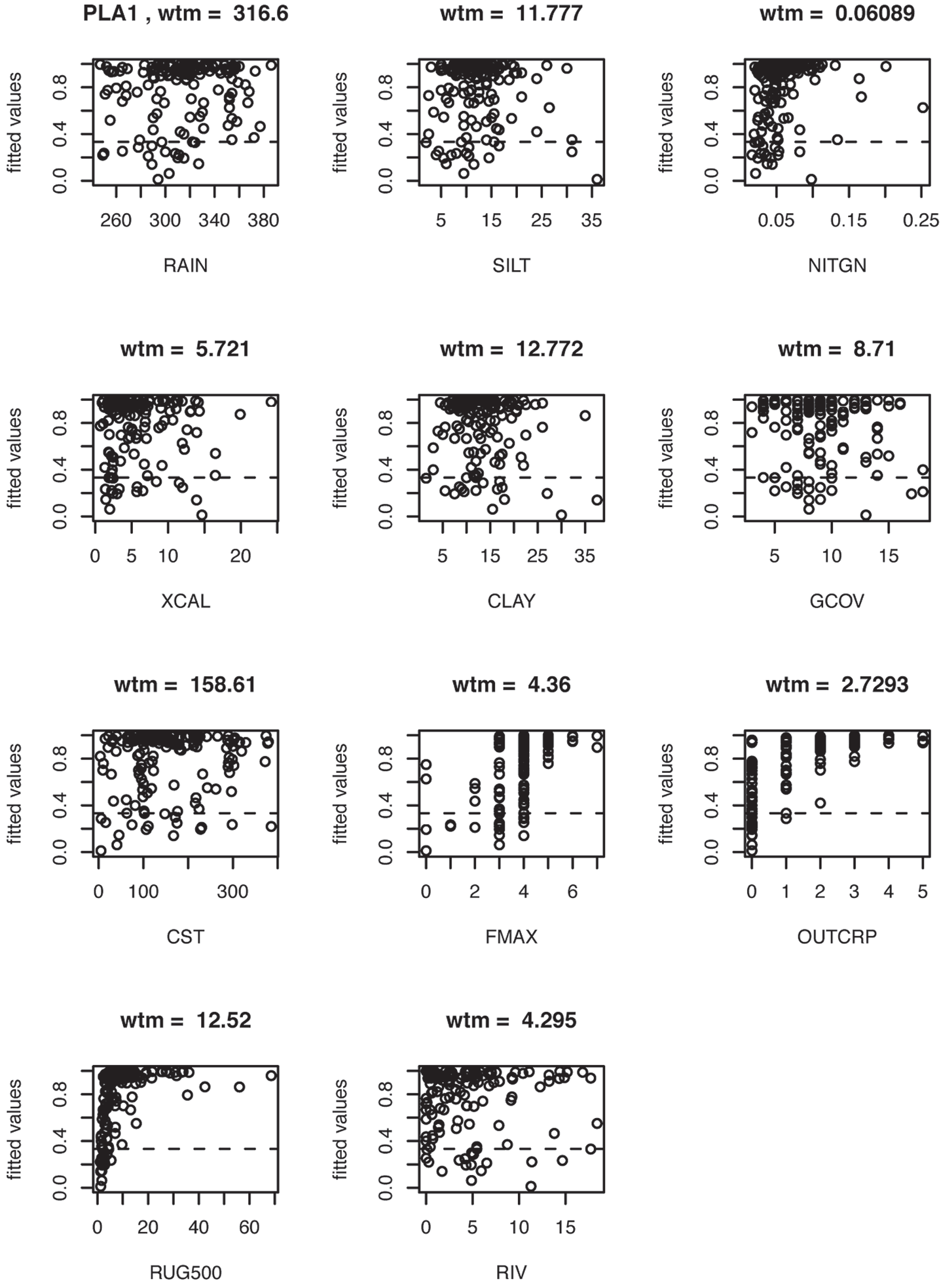
G.


PDES , wtm = 307.44
fitted values
0.0 0.4 0.8
250 300 350
RAIN
wtm = 10.891
0 5 15 25
SILT
wtm = 0.0573
0.00 0.10
NITGN
wtm = 7.971
0 10 20 30 40
XCAL
wtm = 10.331
10 30
CLAY
wtm = 10.756
4 8 12 16
GCOV
wtm = 244.27
0 100 300
CST
wtm = 3.0878
0 2 4 6
FMAX
wtm = 1.2707
0 1 2 3 4 5
OUTCRP
wtm = 9.674
0 20 40 60
RUG500
wtm = 5.517
0 5 10 15
RIV

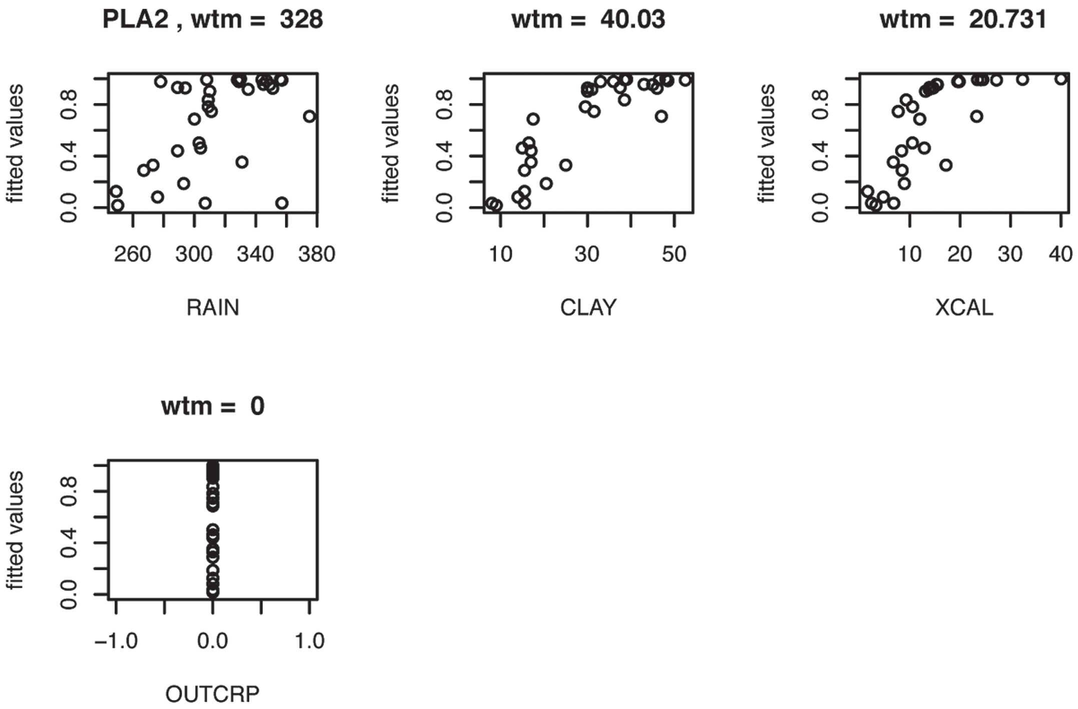
H.


PHER , wtm = 286.75
fitted values
0.0 0.4 0.8
250 300 350
RAIN
wtm = 5.544
0 10 20 30 40
SILT
wtm = 0.022049
0.00 0.10 0.20
NITGN
wtm = 1.9047
0 5 10 20
XCAL
wtm = 9.599
0 10 30
CLAY
wtm = 9.353
4 8 12 16
GCOV
wtm = 177.52
0 100 300
CST
wtm = 1.871
0 2 4 6
FMAX
wtm = 0.14719
0 1 2 3 4 5
OUTCRP
wtm = 2.7172
0 10 20 30
RUG500
wtm = 6.362
0 5 10 15 20
RIV

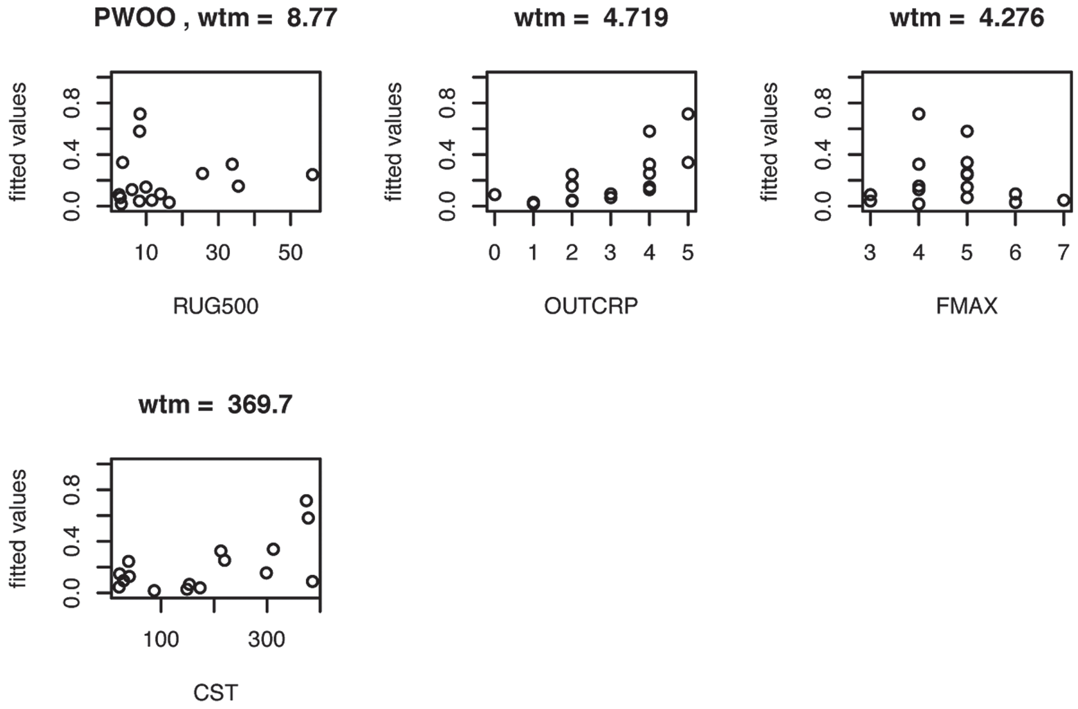
I.


PLA1 , wtm = 316.6
fitted values
0.0
0.4
0.8
260
300
340
380
RAIN
wtm = 11.777
5
15
25
35
SILT
wtm = 0.06089
0.05
0.15
0.25
NITGN
wtm = 5.721
0
5
10
20
XCAL
wtm = 12.772
5
15
25
35
CLAY
wtm = 8.71
5
10
15
GCOV
wtm = 158.61
0
100
300
CST
wtm = 4.36
0
2
4
6
FMAX
wtm = 2.7293
0
1
2
3
4
5
OUTCRP
wtm = 12.52
0
20
40
60
RUG500
wtm = 4.295
0
5
10
15
RIV

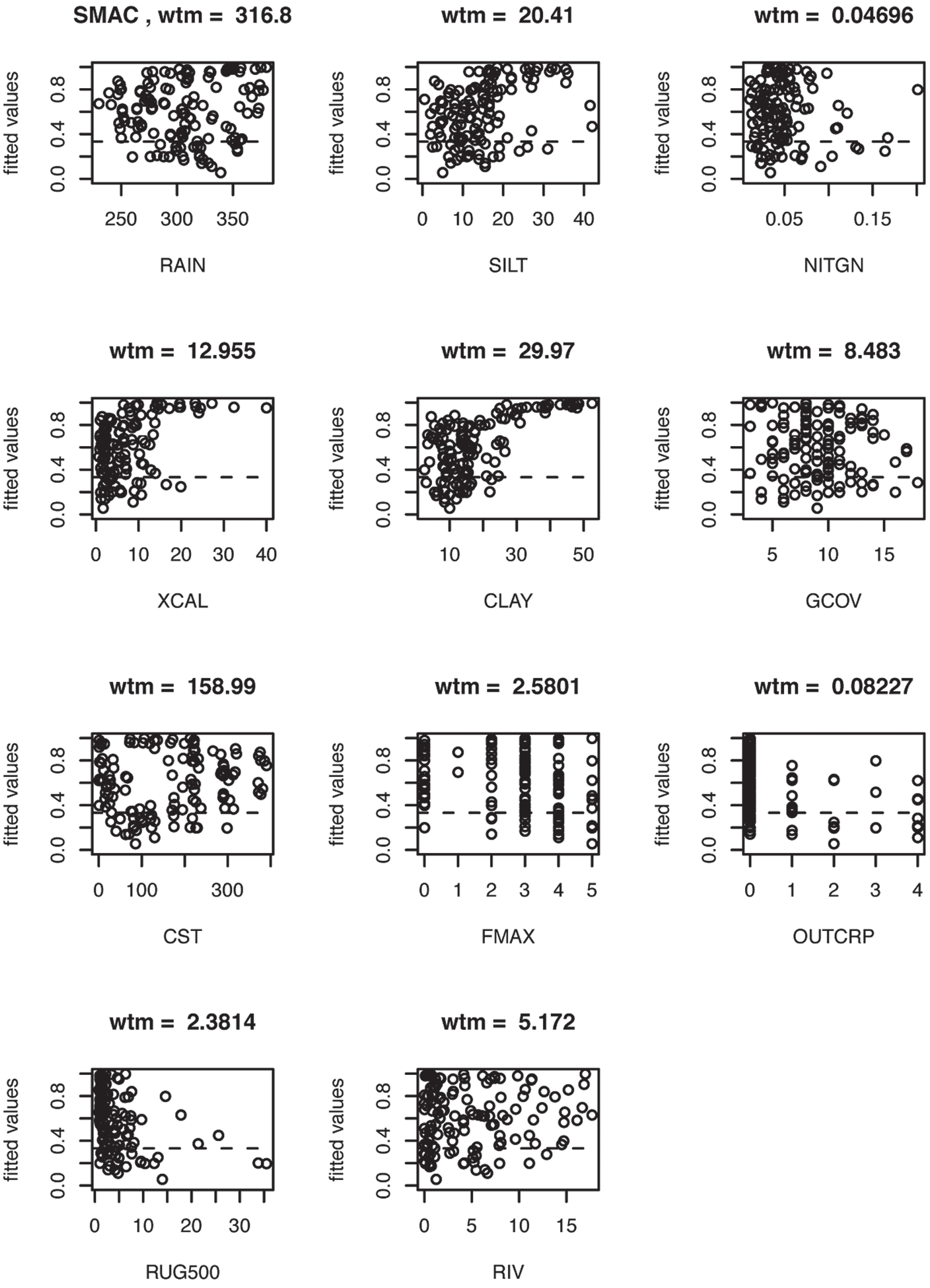
J.


PLA2 , wtm = 328
fitted values
RAIN
260 300 340 380
wtm = 40.03
CLAY
10 30 50
wtm = 20.731
XCAL
10 20 30 40
wtm = 0
OUTCRP
–1.0 0.0 1.0
0.0 0.4 0.8

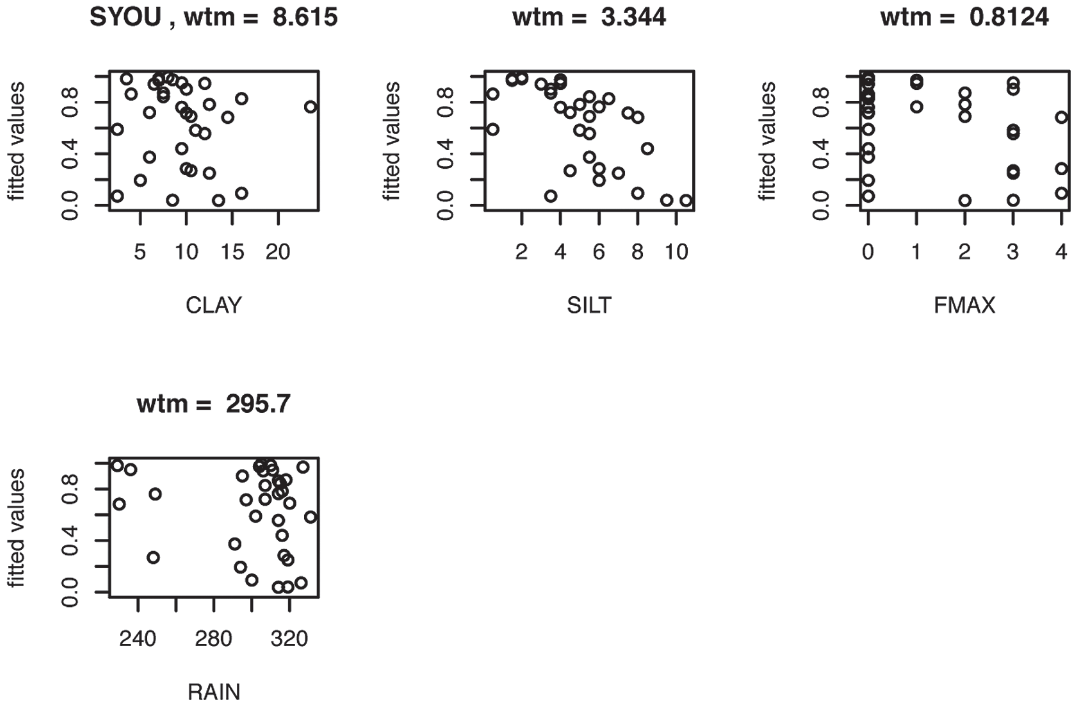
K.


PWOO , wtm = 8.77
fitted values
RUG500
10 30 50
wtm = 4.719
OUTCRP
0 1 2 3 4 5
wtm = 4.276
FMAX
3 4 5 6 7
wtm = 369.7
CST
100 300
0.0 0.4 0.8

L.


SMAC , wtm = 316.8
fitted values
0.0 0.4 0.8
250 300 350
RAIN
wtm = 20.41
0 10 20 30 40
SILT
wtm = 0.04696
0.05 0.15
NITGN
wtm = 12.955
0 10 20 30 40
XCAL
wtm = 29.97
10 30 50
CLAY
wtm = 8.483
5 10 15
GCOV
wtm = 158.99
0 100 300
CST
wtm = 2.5801
0 1 2 3 4 5
FMAX
wtm = 0.08227
0 1 2 3 4
OUTCRP
wtm = 2.3814
0 10 20 30
RUG500
wtm = 5.172
0 5 10 15
RIV

M.


SYOU , wtm = 8.615
wtm = 3.344
wtm = 0.8124
wtm = 295.7
fitted values
0.0
0.4
0.8
5
10
15
20
CLAY
2
4
6
8
10
SILT
0
1
2
3
4
FMAX
240
280
320
RAIN

N.

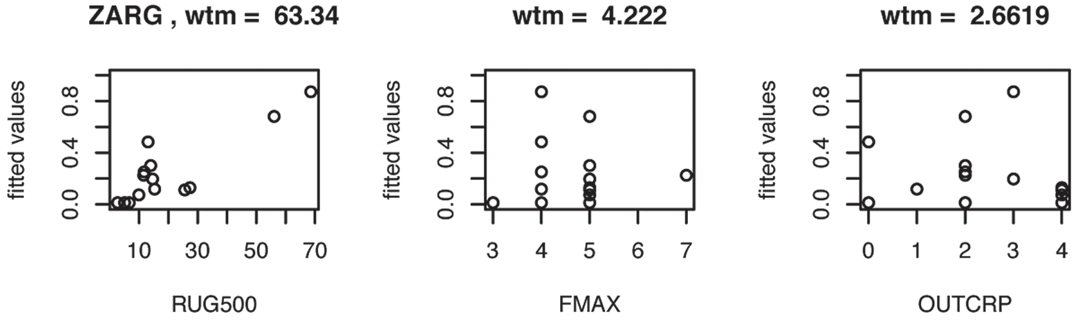

ZARG , wtm = 63.34
wtm = 4.222
wtm = 2.6619
fitted values
0.0
0.4
0.8
10
30
50
70
RUG500
3
4
5
6
7
FMAX
0
1
2
3
4
OUTCRP

Plate 1 Sandplains in the Pilbara are usually firm because the red sand is slightly clayey. Site MBW8 (21°04'16"S, 118°40'55"E), a typical example, supported mallee (*Corymbia hamersleyana*) and shrubs (*Acacia ancistrocarpa* and *A. inaequilatera*) over hummock grass (*Triodia* sp.) *(N.L. McKenzie).*

Plate 2 Large areas of the northern Pilbara are covered by plains of red sand and granitoid grit, containing gravel and quartzite pebbles that mantle massive sheet granite. For example, site MBW12 (21°24'03"S, 118°42'36"E) supported shrubs (*Acacia bivenosa* and *A. stellaticeps*) over hummock and bunch grass (*Triodia pungens*, *T. wiseana*, *Yakirra* sp. and *Eriachne* sp.) and sedges *(N.L. McKenzie).*

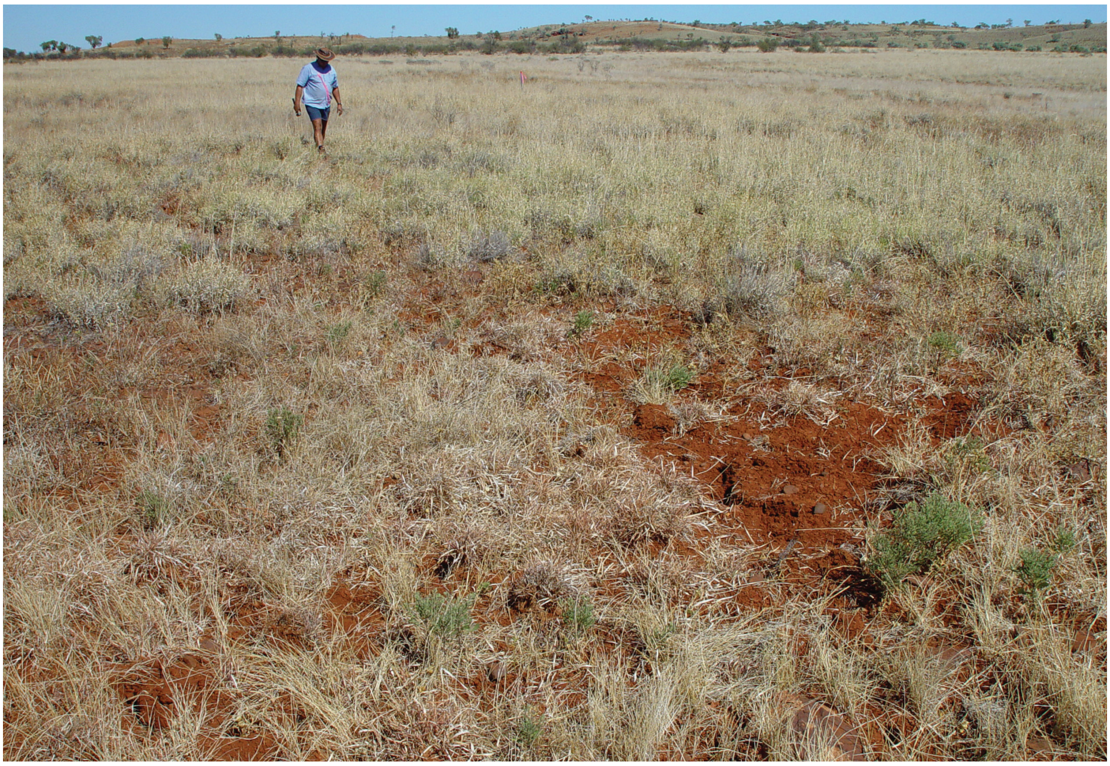


Plate 3 Flat and gently sloping plains of cracking and heaving clay occur in many parts of the Pilbara and are characterised by tussock grassland (*Astrebla* sp., *Eragrostis* spp. and *Aristida* sp.) and herbs (RHNW08: 22°06'24"S, 119°00'04"E) *(N.L. McKenzie).*

Plate 4 Flat alluvial plains and very gentle slopes of cracking and mulching gilgai clay often have a surface strew of rocks and gravel. Typical vegetation comprises the shrub (*Acacia xiphophylla*) over tussock, bunch and hummock grass (*Aristida* sp., *Sporobolus* sp., *Dichanthium* sp., *Yakirra* sp. and *Triodia pungens*) (TCMBW08: 22°30'13"S, 117°42'14"E) *(A.H. Burbidge).*

Plate 5 Steep boulder slopes of Archaean rock, with patches of soil on foot-slopes and in crevices and depressions, are common in the Pilbara. They support scattered *Terminalia canescens* and *Brachychiton acuminatus* trees, shrubs such as *Acacia bivenosa* and *A. arida*, hummock grass (*Triodia* sp.), tussock grass (*Cenchrus ciliaris*) and herbs (DRC08: 20°51'09"S, 117°05'46"E) *(S. van Leeuwen).*

Plate 6 Example of a massive basalt scree slope in the Pilbara. Areas of decomposing basalt occur in a shallow clay matrix, and support scattered trees (*Corymbia hamersleyana*), mallee (*Eucalyptus gamophylla*) and shrubs (*Acacia maitlandii*) over hummock and bunch grasses (*Triodia pungens*, *T. wiseana* and *Cymbopogon* sp.) (TCMBE13: 22°41'57"S, 117°48'58"E) *(N.L. McKenzie).*

Plate 7 Flat and undulating alluvial plains of sandy clay with rock fragments in the soil profile are common in the Pilbara. Site RHNW03 (22°27'59"S 119°01'22"E), a typical example, supported scattered *Corymbia hamersleyana*, *C. deserticola* and *Eucalyptus gamophylla* trees and mallees over *Acacia* spp. and *Corchorus* sp. shrubs, and *Triodia basedowii* hummock grass *(N.L. McKenzie).*

Plate 8 Undulating plains and valley floors of Cenozoic and Quaternary colluvium, comprising rock fragments and fine gravel in a red sandy clay matrix, are widespread in the southern Pilbara. For example, site TCMBE01 (22°34'17"S, 118°18'25"E) supported scattered trees and mallee (*Eucalyptus leucophloia*, *E. gamophylla*, *Corymbia deserticola* and *C. hamersleyana*) over shrubs (*Acacia* spp. and *Indigofera monophylla*), hummock grass (*Triodia wiseana*, *T. basedowii*), tussock grass (*Themeda triandra*), bunch grass (*Paraneurachne muelleri*) and sedges *(N.L. McKenzie).*