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Testing common habitat-based surrogates of invertebrate diversity in a semi-arid rangeland

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Abstract

Habitat-based surrogates are a low cost alternative to intensive biodiversity surveys, though they have been poorly investigated in semi-arid ecosystem compared to others such as temperate woodlands. In this study we tested potential habitat-based surrogates of invertebrate richness in a semi-arid rangeland in northwest Australia. Potential surrogates were: distance from artificial watering-point; soil hardness; habitat complexity; and individual complexity components. Generalised additive models (GAMs) were used to relate abundance and richness of selected invertebrates with environmental factors and cluster analysis was used to examine similarity in species composition. The most frequently selected factor was soil hardness, but taxa varied as to whether biodiversity was higher in soft or hard soils. Where distance from watering-point was an important predictor, there were generally higher abundances and richness closer to watering-points than further away. Abundance and species richness could be partially explained using individual complexity components, but relationships were weak and there were no consistent trends among taxa. Therefore, although habitat complexity has been correlated with species richness under some circumstances, our results cast doubt on the generality of this relationship. There are also dangers in assuming that all taxa respond in a manner similar to indicator taxa, as we observed that different taxa had higher richness at opposite extremes of some environmental gradients. Grazing may have a negative impact on biodiversity in some environments, but in regions where water is limiting, the net effect may be positive due to the creation of waterholes.

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21 **Abstract**

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23 though they have been poorly investigated in semi-arid ecosystem compared to others

24 such as temperate woodlands. In this study we tested potential habitat-based surrogates

25 of invertebrate richness in a semi-arid rangeland in northwest Australia. Potential

26 surrogates were: distance from artificial watering-point; soil hardness; habitat

27 complexity; and individual complexity components. Generalised Additive Models were

28 used to relate abundance and richness of selected invertebrates with environmental

29 factors and cluster analysis was used to examine similarity in species composition. The

30 most frequently selected factor was soil hardness, but taxa varied as to whether

31 biodiversity was higher in soft or hard soils. Where distance from watering-point was an

32 important predictor, there were generally higher abundances and richness closer to

33 watering-points than further away. Abundance and species richness could be partially

34 explained using individual complexity components, but relationships were weak and

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36 been correlated with species richness under some circumstances, our results cast doubt

37 on the generality of this relationship. There are also dangers in assuming that all taxa

38 respond in a manner similar to indicator taxa, as we observed that different taxa had

39 higher richness at opposite extremes of some environmental gradients. Grazing may

40 have a negative impact on biodiversity in some environments, but in regions where

41 water is limiting, the net effect may be positive due to the creation of waterholes.

42 **Keywords:** arthropods, complexity, GAM, grazing, indicators, watering-point

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Introduction

Developing conservation strategies for every component of biodiversity are far beyond our reach because of the mammoth task of collecting all the relevant data on every component (Stoms et al. 2005). Using surrogates to predict biodiversity (typically expressed in terms of species richness) in areas for which biodiversity information is not available is one way of addressing this problem (Gaston and Blackburn 1995).

Habitat-based surrogates are environmental variables that act as indirect measures of diversity (Hughes et al. 2000) and are a cheaper alternative to intensive biodiversity surveys. Vegetation condition scores, individual vegetation features (e.g., amounts of dead wood or tree basal area), habitat classification (e.g. aspen, meadow, and spruce) and climatic variables have all been used to predict faunal diversity (Catling and Burt 1995; Hughes et al. 2000; Ferrier and Guisan 2006; Grove 2002; Gillison et al. 2003; Fraser et al. 2007). Some habitat-based surrogates are commonly used, and justification for their use stems from long-standing ecological theory. For example, habitat complexity is positively correlated with faunal species richness (Hansen 2000; Lassau and Hochuli 2005; Lassau et al. 2005; Jiménez-Valverde and Lobo 2007), which supports the hypothesis that structurally diverse habitats support more species (MacArthur and MacArthur 1961).

Arthropods, particularly ground-active ones, may respond more directly to soil properties such as hardness and texture (Crawford 1988; Stapp 1997; Whitford et al. 1999; Bestelmeyer and Wiens 2001) than those based on amounts of vegetation cover or leaf litter. The links between the soil and invertebrate organisms are appreciated for conservation (Lal 1991), and the impacts of soil management on invertebrates are well studied (e.g. Sharley 2008). It would be expected then that soil parameters would make useful habitat-based surrogates for invertebrate diversity.

71   Surrogates have also been used to represent environmental gradients and

72   subsequently used in environmental impact assessment. For example, assessment of

73   grazing impacts on biodiversity in rangelands used 'distance from artificial watering-

74   point' as a surrogate for grazing intensity (e.g. Ludwig et al. 1999; Hoffman 2000).

75   Based on the piosphere effect of radial grazing (Osborn et al. 1932), negative effects of

76   grazing are deduced when a positive trend between distance from watering-point and

77   measures of biodiversity are found. Whether positive or negative, distance from

78   watering sources could also prove to be a useful habitat-based surrogate.

79   In this study, we sought to identify habitat-based surrogates of invertebrate

80   biodiversity by testing the strength of a number of environmental correlates in a semi-

81   arid rangeland in northwest Australia. Many such rangelands throughout the world have

82   been substantially altered as a consequence of human activities, and almost all are

83   degraded to a greater or lesser degree (Perrings and Walker 1995). Efficient monitoring

84   strategies are required. Potential surrogates, namely distance from artificial watering-

85   point, soil hardness and habitat complexity have been shown to be important for

86   explaining invertebrate patterns elsewhere (as above), however their utility to act as

87   habitat-based surrogates in this environment is unclear. Total abundance and species

88   richness (as a measure of diversity) were used to describe invertebrate biodiversity.

89   Although there are problems with using species richness in conservation management

90   (Fleishman et al. 2005), modelling spatial variation in species richness is the most

91   common strategy when there is insufficient knowledge on the distribution of individual

92   species (Ferrier et al. 2007). Furthermore, species richness can contribute to biodiversity

93   conservation planning provided it is not used in isolation and other metrics are also used

94   (Fleishman et al. 2005). Therefore, we also examined how these environmental factors

95   were related to species composition.

96   **Methods**

97   **Study region**

98   This study was conducted on the Hamersley pastoral lease in the Pilbara region

99   of Western Australia (Figure 1, inset) in April 2005. The area is part of a zone that is

100   characterized by a hot and semi-arid climate, and extensive hummock grassland (Fisher

101   et al. 2004). The Pilbara is an important pastoral region and grazing is the dominant

102   (~60%) land use (Fisher et al. 2004). Permanent artificial watering-points are scattered

103   across the Pilbara's grazing region.

104   **Distance from artificial watering-points**

105   We chose five artificial watering-points (Ridge bore, Pindering well, Two-mile

106   bore, Balbina bore and Kangeenarina well) spaced 5–20 km apart (Figure 1). A 1-km

107   transect was established from each artificial watering-point. Four trapping lines

108   (perpendicular to each transects) of five pitfall traps were established at 100, 200, 500

109   and 1000 m intervals. Traps were positioned 5 m apart along each trapping line.

110   #Figure 1 approximately here#

111   **Invertebrate sampling**

112   Pitfall traps for invertebrate sampling were 9 cm in diameter and 14 cm deep.

113   All traps were: one-third filled with ethylene glycol as preservative; buried and placed

114   flush to the ground surface; covered by an upturned pot-plant base held above the

115   opening with clothes pegs; and, collected after nine days.

116   All traps and specimens were processed using the laboratory sorting protocols of

117   Wilkie et al. (2003), which is a quality control procedure for laboratory sorting and

118   identification of invertebrate specimens. In brief, the quality control procedure involves

119   a series of feedback loops and checks that are implemented throughout the sorting

120   stages so that errors are corrected as they occur, and errors that cannot be controlled, are

121   minimised. Ants (Formicidae), wasps (Hymenoptera but excluding Formicidae), beetles

122   (Coleoptera) and flies (Diptera) were identified to morphologically recognisable units

123   (morphospecies). Morphospecies are hereafter referred to as species for simplicity, and

124   species richness is used to refer to the number of morphospecies. All other taxa were

125   identified to ordinal level only and counted.

126   **Habitat-based surrogates and complexity**

127   We used a modification of the methods of Lassau and Hochuli (2005) to

128   measure seven habitat-based surrogates associated with habitat complexity. This

129   involved using an ordinal scoring system of habitat variables (tree canopy cover; shrub

130   canopy cover; ground herb cover; amount of leaf litter; amount of logs and debris;

131   substrate rockiness; soil moisture) at each trapping line (i.e. within 1-m either side of

132   the trapping line; Table 1). Soil moisture was excluded from analyses because it was

133   found that soil was very dry and there was little difference between sites. Habitat

134   complexity was then determined as a sum of six variables at each trapping line.

135   #Table 1 approximately here#

136   **Soil hardness**

137   Soil hardness was measured as the pressure (kg/cm^2) required for the end of a

138   hand-held soil penetrometer (Humboldt, 200 mm Pocket Penetrometer) to penetrate the

139   soil to a depth of 6.5 mm. Soil hardness was measured at three random points around

140   each pitfall trap (but within 1-m of each trap). The average of the 15 values recorded

141   along each trapping line was used in the analyses.

142   **Data analyses**

143   The samples from all five traps at each trapping line were pooled prior to

144   analyses. Several traps at 100, 200 m (Ridge bore) and 200 m (Pindering well) were lost

145   due to disturbance by cattle. As a consequence, for species richness (the total number of

6

146 species present on each trapping line), these three trapping lines were discarded. For

147 abundance (the absolute number of individuals on a trapping line), we discarded only

148 traps that were disturbed and standardized values as the number of individuals per trap.

149 Abundance and species richness were $\log_{10}(x + 1)$ transformed. Distance from

150 watering-point was also $\log_{10}(x + 1)$ transformed.

151 Relationships between environmental variables and: (1) ant, wasp, beetle, and

152 fly species richness; (2) species richness of the four groups combined (herein 'overall

153 species richness'); (3) total abundance of each of the 11 most abundant invertebrate

154 groups; and (4) total abundance of all invertebrates, were investigated using Generalised

155 Additive Models (GAMs) (Hastie and Tibshirani 1990). Distance from artificial

156 watering-point, tree canopy cover, shrub canopy cover, ground herb cover; habitat

157 complexity and soil hardness were considered as splines with two degrees of freedom.

158 The remaining habitat variables were included as linear terms since splines could not be

159 used (less than four unique values).

160 Environmental variables were assessed using a variation of the D^2 (deviance

161 explained) method. We calculated D^2 by disregarding each observation in turn and

162 determined the minimum deviance explained by the remaining observations. This

163 method was designed to penalise models that over-fitted to outliers (similar to Cook's

164 distance in linear regression; Cook 1977).

165 Models were created by testing each combination of one and two predictor

166 models. The best models were selected by maximising the D^2, and p-values for the

167 models were determined by simulating the modelling process using random response

168 variables. In short, we simulated the modelling process 1000 times using the real

169 predictor observations, but with random response variables. The p-value (0.05) was

170 determined as the D^2 threshold that only 50 of the 1000 models exceeded. This method

171   for determining *p*-values ensures that the entire model building process is considered

172   including how well the gradients were sampled, the correlation between predictor

173   variables, the sample size, the data type (categorical / continuous), the degrees of

174   freedom and our modification to the D^2 statistic. While we used a *p*-value of 0.05 to

175   determine significant relationships, we also examined near-significant relationships

176    $(0.05 < p < 0.20)$ to determine if different taxa displayed similar trends to each

177   potential surrogate.

178   The similarity in species composition was analysed for all 17 trapping lines

179   using cluster analysis (Bray-Curtis similarity using presence/absence data) for all four

180   target taxa individually, and in combination (hereafter 'overall composition'). The

181   resulting dendogram was used to determine if patterns in species composition were due

182   to differences between artificial watering-points (a potential spatial bias), distance from

183   artificial watering-point, soil hardness or habitat complexity.

184   **Results**

185   In total, 12 661 individuals were trapped. Ants and flies were the two most

186   abundant groups trapped (58% and 15% of total abundance, respectively). Of the four

187   taxa that were identified to species level, wasps were the most speciose, followed by

188   ants, beetles and flies (72, 60, 47 and 30, respectively).

189   Soil hardness was the habitat variable that was best able to explain multiple

190   components of invertebrate biodiversity. Hardness was selected in 19 of the 34 models

191   produced (56%), which was more than distance from water (12 of 34 or 35%), habitat

192   complexity (4 from 34 or 12%), and the individual components of habitat complexity

193   (up to five models each). Soil hardness was also selected in six of the eight models that

194   were significant $(P < 0.05)$, while no other factor was in more than two of the

195   significant models. Soil hardness could not be used as a surrogate for multiple

196   components of biodiversity, however, because taxa varied in their responses to the

197   gradient. For example, ant richness peaked on hard soils (Fig. 2b, $P < 0.05$),

198   Orthopteran abundance peaked in soft soils (Fig. 2j, $P < 0.05$), while Acarina abundance

199   peaked at intermediate values (Fig. 2l, $P < 0.05$).

200   Distance from water was significant ($P < 0.05$) in the two-parameter models for

201   Orthopteran abundance (Fig. 2i) and Araneae abundance (Fig. 2h), and near significant

202   ($P < 0.20$) in the two parameter model for ant abundance (Fig. 2c), the one parameter

203   model for overall abundance, and the one parameter model for wasp richness. In all five

204   cases, the responses peaked at low distances, indicating higher abundance and richness

205   of these taxa in close proximity to waterholes. The correlation between distance from

206   water and hardness was low ($r^2 < 0.03$), so the two most commonly selected predictors

207   each explained different aspects of the distribution of biodiversity.

208   Neither complexity, nor the individual components of complexity were selected

209   consistently across the 34 models. Trends in the significant and near significant models

210   were also variable, with different taxa peaking at either high or low complexity. Tree

211   canopy was significant ($P < 0.05$) in the models for ant and wasp richness, and ground

212   herbage was significant in the model for Acarina abundance. In all three of these models

213   the responses peaked at the more complex end of the gradient (Fig. 2a, e, k). However,

214   the abundance of ants (Fig. 2d, $P < 0.20$) and Araneae (Fig. 2g, $P < 0.05$) was higher at

215   the lower complexity end of the shrub canopy gradient, and the richness of wasps

216   peaked at low overall complexity (Fig. 2f, $P < 0.05$). Therefore, there was no consistent

217   trend that biodiversity was higher in either low or high complexity environments.

218   #Figure 2 approximately here#

219   Cluster analysis revealed that soil hardness was the most important factor in

220   explaining overall species composition. Three distinct site clusters: all soft (Cluster 1); a

221 mix of soft, medium and hard (Cluster 2); and all hard (Cluster 3) could be delimited

222 from the dendogram (Figure 3a). Soil hardness was also important for clustering sites

223 with respect to ants, but instead two distinct clusters: soft (Cluster 1), and a mix of

224 medium and hard (Cluster 2) could be delineated. However, two sites (Pw 1000 and Kw

225 500) were exceptions to this pattern (Figure 3b). Soil hardness did not appear important

226 for determining clusters of any other single taxa. There was no evidence to indicate that

227 location, distance from artificial watering-point and habitat complexity were important

228 for determining site clusters of overall species composition, or the species composition

229 of any single target taxon.

230   #Figure 3 approximately here#

231 **Discussion**

232   Habitat-based surrogates of biodiversity are potential cost-cutting tools and the

233 first step in identifying them is to determine the correlation between the potential

234 surrogate and the entity in which it is supposed to be a substitute for (McGeoch 1998).

235 In this study, we investigated strengths of correlations between the abundance and

236 species richness of different invertebrate groups, and a number of environmental

237 variables in a semi-arid rangeland. We also examined the influence of environmental

238 factors on community composition using cluster analysis.

239   We found that none of the environmental factors tested were adequate surrogates

240 for all components of invertebrate biodiversity. Soil hardness was the factor that was

241 best able to explain the distribution of abundance and species richness, but taxa varied

242 as to whether biodiversity peaked on hard, soft or intermediate soils. There was

243 consistently higher abundance and richness near watering-points, but this factor was not

244 as consistent as hardness in explaining all components of biodiversity. Habitat

245 complexity, and the individual components of complexity, also performed poorly. None

246 of the complexity predictors were consistently selected in the models, and taxa varied as

247 to whether they peaked at high or low complexity. Therefore, our results support the

248 notion that different taxa have difference habitat preferences, and one should consider

249 this when choosing surrogates. What this means is that one habitat variable should not

250 be used as a surrogate for all taxa.

251   Habitat-based surrogates have been used in attempts to cut costs in biodiversity

252 surveys, but there has also been interest in indicator taxa in recent years (Caro and

253 O'Doherty 1999). Indicator taxa are sub-components of the total community that are

254 correlated with the biodiversity of other groups (Noss et al. 1990). Ants (Formicidae) in

255 particular have been used extensively as focal taxa in studies of human impacts

256 throughout the world (Perfecto and Snelling 1995; Bestelmeyer and Wiens 1996, 2001;

257 Andersen 1997; Majer and Nichols 1998) because they are abundant, their taxonomy is

258 well-known relative to other groups, and their responses may indicate environmental

259 patterns that determine the distribution of other organisms over a wide range of scales

260 and environments (Andersen 1997). While an evaluation of the utility of ants as

261 bioindicators in rangelands, which includes parallel studies of the response of ants and

262 other taxa to environmental gradients, have been called for (e.g. Bestelmeyer and Wiens

263 2001), we found no evidence that other invertebrate groups show the same patterns for

264 ants. In fact, we found that orthopterans showed the opposite response to ants with

265 respect to soil hardness. Ants aside, it is generally unclear how species richness of

266 particular taxonomic groups are correlated with each other (Sauberer et al. 2004). The

267 parameters that we tested have potential to act as surrogates for some groups and for

268 some metrics, but not all. Thus, if different taxa are responding to different

269 environmental factors then we cannot expect one to act as an indicator of the other. Poor

270 correlation between species richness of different invertebrate groups have led authors to

271 suggest that a 'shopping basket' approach that estimates or monitors a variety of taxa is

272 required (di Castri et al. 1992). We also support a shopping basket approach with one

273 that also considers multiple habitat-based surrogates.

274 Our study has narrowed down a few habitat factors such as soil hardness and

275 habitat complexity for a few groups, but we must acknowledge that a limitation to our

276 study is the narrow scale of space and time that we have tested them at. Testing at

277 different spatial and temporal scales could clarify their usefulness over larger or smaller

278 areas, over seasons or years.

279 How our habitat-based surrogates predict different combinations of taxa may

280 also yield stronger relationships than we detected. Assuming that all invertebrates are

281 equally likely to fall into a pitfall trap is a limitation of pitfall data, and integrating other

282 collection techniques would be useful for investigation. Similarly, only including

283 species or groups that are most likely to fall into a pitfall trap might yield stronger

284 relationships. Although how this probability could be determined for every species is an

285 unfeasible task—if not an impossible one.

286 Assessments of the impacts of grazing on biodiversity use 'distance from

287 artificial watering-point' as a surrogate for grazing intensity (e.g. Ludwig et al. 1999;

288 Hoffman 2000). In our study, where distance from watering point was an important

289 predictor, partial response curves showed that there were more individuals and species

290 proximal to watering-points. This trend was particularly strong for beetles and overall

291 species richness, and abundance of Araneae, beetles, wasps, ants, Orthoptera and of all

292 individuals. While this could be a result of grazing, a negative relationship between

293 distance and abundance and species richness could also be an effect of the water and not

294 grazing per se. Indeed, grazing pressure is one of the hardest to quantify (Pringle and

295 Landsberg 2004). Thirteen important factors can modify the influence of distance from

296 water on the distribution of livestock grazing pressure (Pringle and Landsberg 2004).

297 Factors include: paddock and water source configuration; proximity to natural surface

298 water; salinity of water; and, the species of livestock. Alternatively, water is a resource

299 that is limiting in dry areas and a lack of water causes inactivity or death more quickly

300 than other essentials such as food (James et al. 1999). To separate the potential positive

301 effects of water from the effects of grazing, field-studies that use distance from

302 watering-point as a surrogate of grazing should include trapping lines close to watering

303 points that were not grazed.

304   We found poor relationships between habitat complexity and the species

305 richness and abundance of nearly all arthropod groups. However, wasp species richness

306 was negatively associated with habitat complexity in two-parameter models. Notably,

307 this is not consistent with the habitat heterogeneity hypothesis, which predicts that

308 habitat complexity would be positively correlated with species diversity (MacArthur

309 and MacArthur 1961). This result is also opposed to the findings of Lassau and Hochuli

310 (2005) who found higher species richness of wasps in highly complex woodland

311 habitats than ones with less structural diversity. In contrast to Lassau et al. (2005), we

312 also found no positive relationship between beetle richness and habitat complexity. Our

313 finding of poor relationships may not be surprising. Tews et al. (2004) review of habitat

314 heterogeneity-animal species diversity studies show variable responses between taxa

315 and structural parameters measured. Importantly, habitat complexity, and indeed other

316 habitat-based attributes, which are often inferred from remote sensing, may not

317 adequately reflect the variation that is important to some animal taxa. There may be

318 consequences for management strategies that use habitat-based surrogates developed in

319 other areas or under different sets of conditions—particularly when 'high' values of

320 complexity are used as surrogates of high diversity. For example, management

321 strategies using surrogate measures for one group of taxa might be detrimental for

322 others.

323   We found that soil hardness was a consistent predictor in two-predictor models

324 (8/12 and 4/5 for abundance and species richness, respectively), with ant abundance and

325 species richness and orthopteran abundance strongly related. Soil hardness was a factor

326 in overall species composition, although unduly influenced by ants, with the other three

327 taxa not clustered with respect to soil hardness. Bestelmeyer and Wiens (2001) also

328 found soil hardness important for explaining community variation of ants in a grazed

329 short-grass desert habitat in the south-west of the United States. Variations in soil

330 characteristics affect abundance and diversity of other surface-active arthropod groups

331 such as beetles in arid grasslands of New Mexico (Crawford 1988) and Colorado (Stapp

332 1997). Other soil factors, including erodibility and composition of clay and sand, are

333 associated with structure of rangeland orthopteran communities such as grasshoppers

334 (Quinn et al. 1991; Schell and Lockwood 1997). Soil parameters are clearly important

335 factors influencing invertebrate communities in rangelands—and an aspect that is often

336 neglected (Bestelmeyer and Wiens 2001).

337 **Conclusion**

338   Biodiversity in many parts of the world, including semi-arid regions in

339 Australia, is poorly understood and the means of tracking change in biodiversity are not

340 available (Fisher et al. 2004). Such limitations have prompted biologists to take

341 shortcuts in biodiversity assessment (Kerr et al. 2000). Shortcuts include both habitat-

342 based surrogates and indictor species. Samways (2007) noted that both surrogates and

343 indicators of invertebrate diversity are not perfect and there are inherent risks in using

344 them in ecological assessments. Our results support this notion and the need for

345 examining a variety of invertebrate taxa in order to obtain a more complete picture of

346 biodiversity and how human impacts might affect invertebrate communities. While we

347 found that soil hardness was the best habitat-based surrogate, measures of single habitat

348 features may not be relevant to all components of biodiversity and one cannot assume

349 that richness of one invertebrate group correlates with richness of others. As the

350 distribution of biodiversity is influenced by a variety of factors, we recommend that

351 predictions are based on models that include non-linear responses to multiple

352 environmental gradients, and not on the assumption that one gradient provides a

353 sufficient surrogate. If regional conservation strategies are to be effective for managing

354 biodiversity, monitoring and inventories need to be based on a set of factors reflecting

355 important aspects for varying groups of invertebrates. Thus, management plans will

356 need to vary accordingly.

357 **Acknowledgements**

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Captions, tables and figures

482 Figure 1. Map showing the location of the Hamersley pastoral lease in the Pilbara

483   region (inset) and the five artificial watering-points.

484 Figure 2. Partial response plots in two-parameter models between important

485   environmental attributes and: (a–b) ant richness; (c–d) ant abundance; (e–f)

486   wasp richness; (g–h) Araneae abundance; (i–j) Orthoptera abundance; and (k–l)

487   Acarina abundance. Dashed line shows the 95% confidence band.

488 Figure 3. Dendograms from cluster analysis showing the similarity in overall (a) and ant

489   (b) species composition between sites. Abbreviations for sites at each artificial

490   watering-point are: Rb = Ridge bore, Pw = Pindering well, Tb = Two-mile bore,

491   Bb = Balbina bore and Kw = Kangeenarina well. Following site abbreviations

492   are: distance from artificial watering-point (100, 200, 500 or 1000 m), hardness

493   of soil (kg/cm^2) as indicated by penetrometer (S)oft (<0.5), (M)edium (0.5–2.0)

494   and (H)ard (>0.5), and habitat complexity scores, respectively.

Table 1 Individual habitat attributes and visual scores used.

Habitat attributes	Score			
	0	1	2	3
Tree canopy (% cover)	0	< 30	30–70	> 70
Shrub canopy (% cover)	0	< 30	30–70	> 70
Ground herbage (height in m)	Sparse[a] (and < 0.5)	Sparse[a] (and > 0.5)	Dense[b] (and < 0.5)	Dense[b] (and > 0.5)
Logs and woody debris (% cover)	0	< 30	30–70	> 70
Substrate rockiness	None	Sparse small rocks	Moderate	Very rocky
Leaf litter (% cover)	0	< 30	30–70	> 70

[a]Sparse ground flora refers to grasses covering less than 50% of a study site, [b]Dense ground flora refers to grasses covering more than 50% of a study site
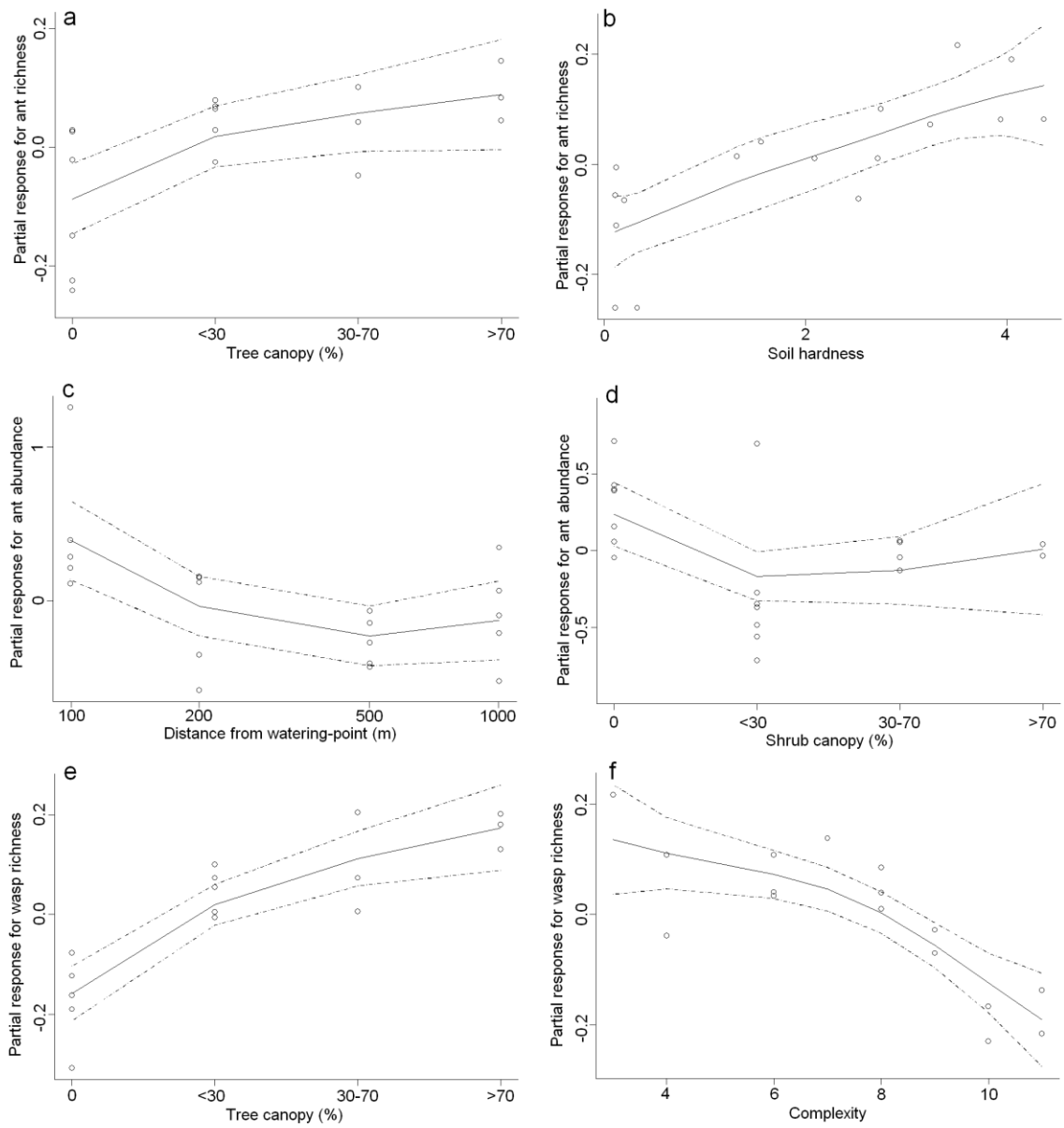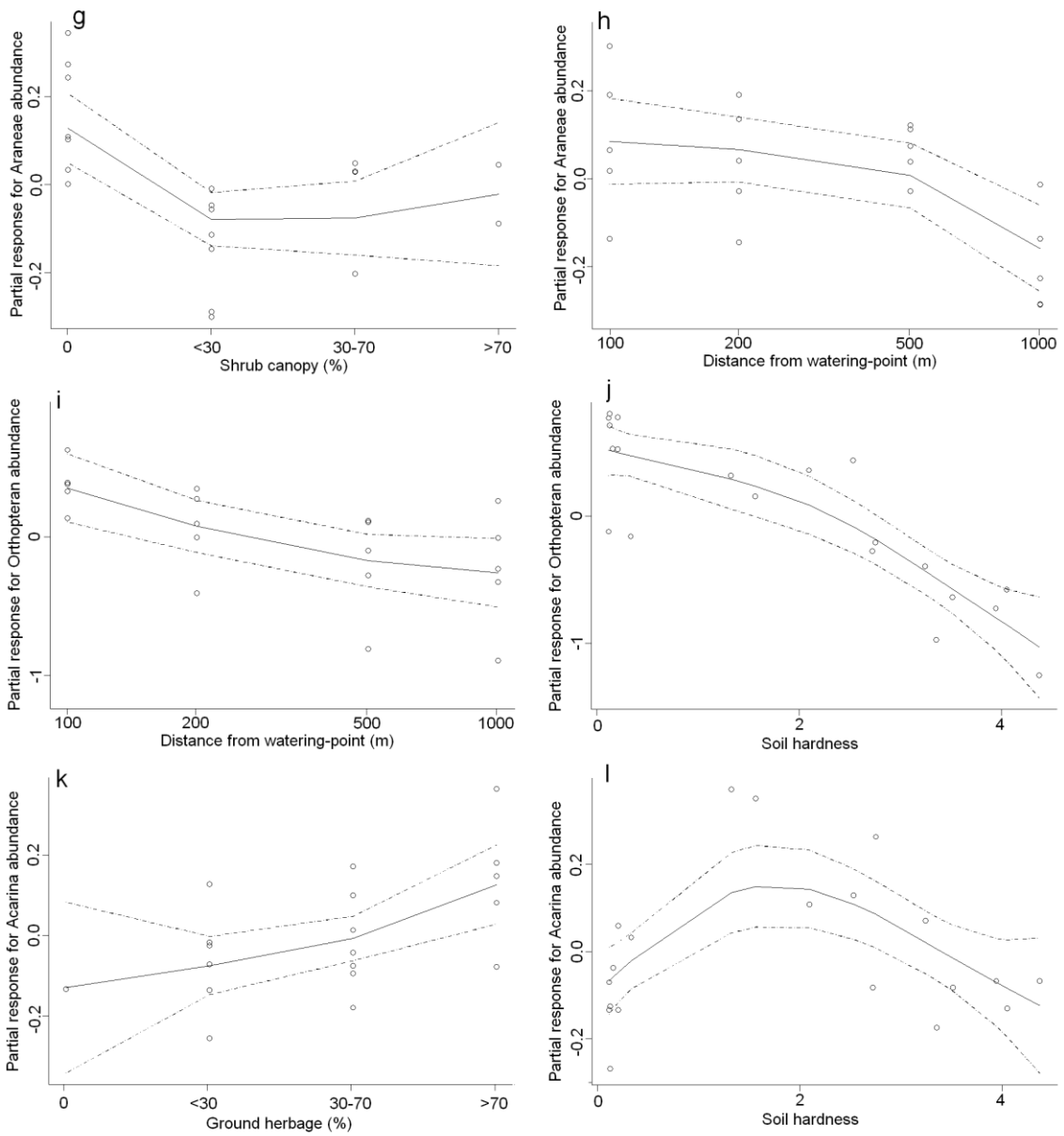
495   Figure 1
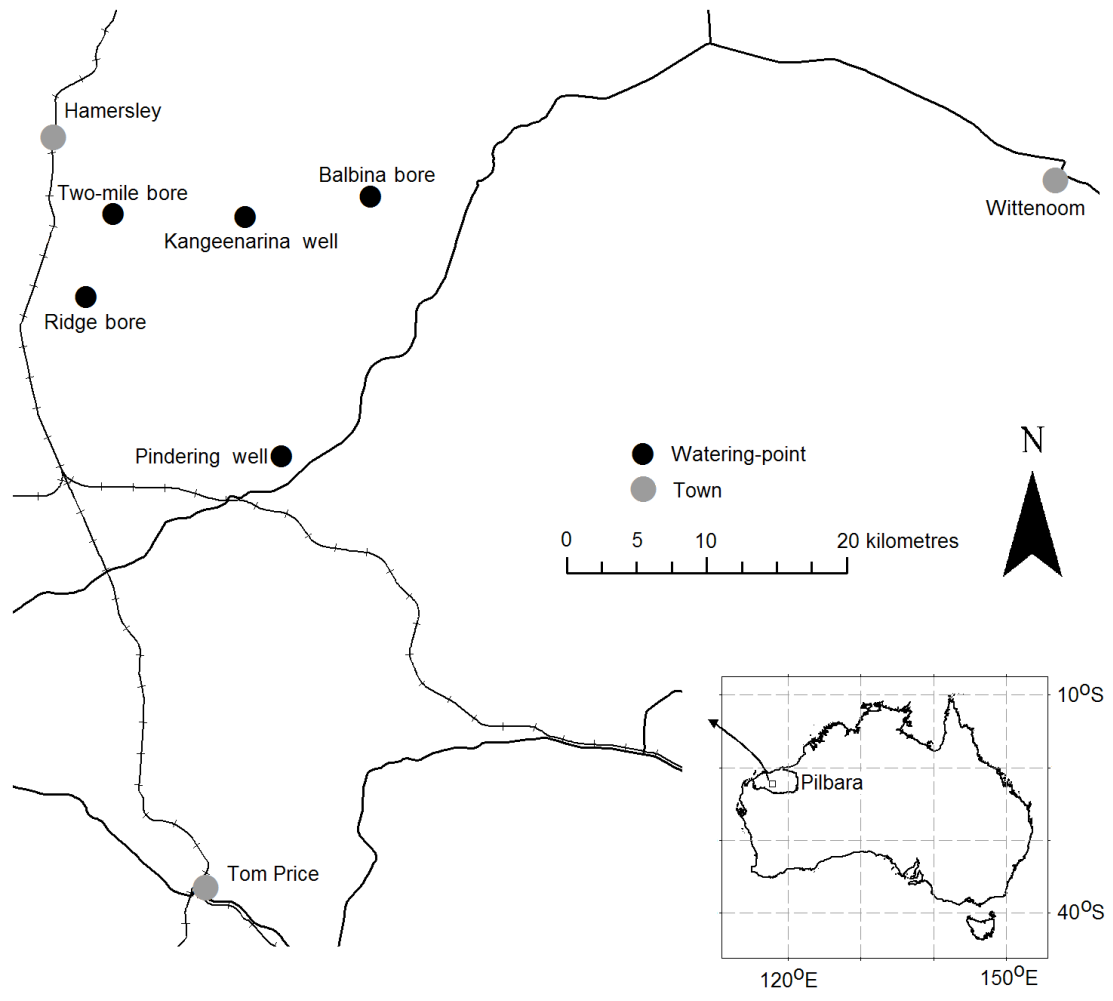
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498   Figure 2

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501   Figure 2 continued

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504   Figure 3

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