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5 Vegetation cover and grasslands in the vicinity accelerate development of carabid beetle
6 assemblages on restored landfill sites

7

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28 Abstract

29 There is increasing evidence that rare and scarce carabid species of conservation
30 importance are frequent in brownfield sites such as restored landfill. However, this
31 potential has largely been unexplored and was investigated here by examining carabid
32 species composition, richness, and abundance in relation to habitat quality and
33 landscape structure on landfill sites in comparison to paired reference sites of existing
34 wildlife value. Sampling was conducted by collecting carabids in ten pitfall traps set
35 along two 100 m transects on each of nine restored landfill and their paired reference
36 sites in the East Midlands region of the UK. A total of 1014 individuals representing
37 thirty seven carabid species were found during April to September in 2007 and 2008.
38 On the landfill sites, generalist species were common, while no nationally rare or scarce
39 species were found. Neither species richness nor diversity of carabid species was found
40 to be different from that of the reference sites. Seeding during restoration was found to
41 have a strong positive effect on richness and diversity, with seeded landfill sites tending
42 to be similar to reference sites in terms of carabid species composition. Marked
43 differences in diversity and richness were also attributed to variation in the amount of
44 local vegetation cover, with presence of grassland in the surrounding landscape having a
45 positive effect on carabid assemblages. We suggest that initial seeding may be an
46 appropriate conservation strategy to improve beetle diversity and richness, coupled with
47 management in terms of cutting to increase the potential of these sites for carabid
48 conservation at the landscape scale.

49 Keywords: ground beetles, restoration, habitat quality, landscape structure, grassland,
50 landfill.

51 **Introduction**

52 Carabid beetles (Coleoptera: Carabidae) are valuable indicators for habitat restoration
53 research as they are widely distributed and are well known both taxonomically and
54 ecologically, allowing comparisons to be made between a wide range of terrestrial
55 habitats; they are also sensitive to landscape change and disturbance (Butterfield et al.
56 1995; Niemelä et al. 2002; Rainio and Niemelä 2003; Vanbergen et al. 2005; Karen et
57 al. 2008). Man-made habitats support a rich carabid fauna, including 35% of the rare
58 and scarce carabid species in the UK (Eversham, Roy, and Telefer 1996; Gibbons 1998;
59 Small, Sadler, and Telfer 2002). There is increasing evidence that carabid species of
60 conservation importance are frequent in brownfield sites including former mineral
61 works and landfill sites (Judd and Mason 1995; Eyre, Luff, and Woodward 2003;
62 Morris et al. 2006). These habitats can serve as a novel habitat and have potential multi-
63 functional ecological and cultural roles as both natural conservation sites and amenity
64 land.

65 Habitat loss from urbanisation and modern intensive agricultural land use
66 practices has contributed to the impoverishment of many invertebrate groups including
67 carabids; thus habitat restoration potentially plays an important role in their
68 conservation (Judd and Mason 1995; Sotherton and Self 2000; Meek et al. 2002). There
69 are approximately 2,200 landfill sites in England and Wales covering 28,000 ha (EA
70 2006) representing a significant stock of land with conservation potential. Newly
71 restored landfill sites potentially provide suitable habitats for carabids thereby
72 compensating for the reduction of suitable habitat within the local area. It is expected
73 the value of such newly created areas as habitat for carabids will vary depending on
74 species-specific requirements and colonisation ability.

75 The influence of factors operating at differing scales is key to understanding the
76 composition and diversity of invertebrate assemblages (Söderström et al. 2001;
77 Collinge, Prudic, and Oliver 2003). Community composition of carabid assemblages
78 may be influenced by local habitat to landscape-scale processes (Aviron et al. 2005).
79 Recognising critical local habitat and landscape-level factors is important in developing
80 effective conservation strategies of newly created invertebrate habitat sites. Invertebrate
81 community composition and diversity, including those of carabids, have been found to
82 be positively related to local habitat quality (Weibull, Ostman, and Granqvist 2003)
83 whilst at the landscape scale, carabid assemblages are influenced by the amount and
84 spatial arrangement of habitat patches and the surrounding landscape composition,
85 specifically obstructing linear features such as road density (de la Pena et al. 2003;
86 Aviron et al. 2005), and natural and semi-natural areas in the landscape (Liu et al.
87 2015). Although habitat quality and landscape pattern are known to explain the
88 composition and diversity of other taxa in restored landfill sites (Rahman et al. 2011,
89 2012, 2013; Tarrant et al. 2013), few studies have considered both habitat and landscape
90 factors simultaneously for carabid beetles, particularly on restored landfill sites.

91 In this study, we evaluated the effects of local and landscape factors on diversity
92 and richness of carabids on newly created grassland on restored landfill sites.
93 Specifically, we determined the roles of local factors (vegetation cover, organic matter,
94 and soil bulk density) and landscape factors (grassland, road network, and woodland) on
95 carabid diversity and richness. This study also examined whether initial seeding during
96 restoration, management and age of restored landfill sites have any effect on carabid
97 assemblages.

98 **Material and Methods**

99 **Study sites**

100 The study was conducted in the four counties of Northamptonshire, Bedfordshire,
101 Warwickshire and Buckinghamshire in the East Midlands region of the UK (Figure 1).
102 Nine restored landfill (henceforth LF) sites were selected randomly from a pool of 42
103 based on minimum size and age of the sites since restoration. The mean size (\pm SE) of
104 LF sites was 14 ± 3.5 ha. The LF sites, all between 4 and 15 years old, were selected to
105 provide a gradient of ages of restored grassland communities. Three LF sites had been
106 naturally colonised by vegetation and six of the LF sites were seeded by locally
107 available seed mixes. The nine closest grassland sites of recognized nature conservation
108 value, all either designated Local Nature Reserves (LNRs) or Sites of Special Scientific
109 Interest (SSSIs) and not undergoing any specific carabid conservation measures were
110 selected as reference sites (henceforth RF). RF sites were close enough to the LF sites
111 (mean distance = 4.5 ± 3.5 km, range = 1.3 to 11.8 km) to experience similar local
112 climates, to have the same regional pool of species, and to have comparable landscape
113 contexts. Five of the LF sites were managed by mowing during summer and the
114 remainder had no management or grazing; all reference sites were managed by either
115 mowing or grazing.

116 **Sample collection**

117 Two 100 m perpendicular transects crossing each other at the approximate centre point
118 of each site were set out, with directions chosen using randomized bearing tables. Ten
119 (5 \times 2 transects) pitfall traps were set along the two transects using random points which
120 were at least 1 m apart from each other. Each pitfall trap consisted of a plastic cup (5cm

121 diameter, 120ml) sunk flush with the ground. One pitfall per sampling point was half-
122 filled with water (detergent was not added due to restrictions by landfill site operators)
123 and exposed for five days. Longer exposure was not possible due to logistic constraints.
124 Sampling from seven LF sites and their corresponding RF sites were conducted on three
125 occasions April, June, and September 2007. Further, two more LF sites and their
126 corresponding RF sites were surveyed for the same period during 2008 (no sampling
127 could be conducted during 2007 due to flooding on these sites). To reduce the effects of
128 temporal heterogeneity, sampling on both LF and their corresponding RF sites were
129 conducted at the same period of time. All captured carabid beetles were dry mounted
130 and identified to species using Forsythe (1987). Note that it was not our objective to
131 obtain a full faunal list of carabid species for each of these sites, but to use standardised
132 sampling as a means of comparing sites with different land use histories and landscape
133 contexts.

134 **Local habitat and landscape variables**

135 From each of the LF and RF sites, five soil samples from a depth down to 10 cm were
136 collected for soil analysis from random locations along the transects. The variables
137 percentage of organic matter and bulk density were determined following Rowell
138 (1994). Percentage of vegetation cover on each site was also calculated from 10 random
139 1m × 1m quadrats along transects. We used percentage of three non-crop features,
140 grassland, woodland, and road networks, as indicators of the amount and diversity of
141 perennial habitats in the surrounding landscape as perennial features should have a
142 greater influence on composition of invertebrates on newly created habitats. Percentage
143 area of grassland, woodland and a quantitative measure of the road networks, within a 1
144 km radius zone of each site's margins, were determined from Land Cover Map 2000

145 (Raster, 25m resolution) using a Geographical Information System to measure for
146 potential landscape-scale effects (ESRI 1999).

147 **Statistical analysis**

148 All data on species richness and Shannon–Wiener diversity indexes were analysed using
149 total number of species or number of individuals per site. As stated, we aimed at
150 standardised comparison between LF and RF sites, and therefore the short sampling
151 period may have an effect on the study. Carabid species composition and their
152 abundance between site types were represented by non-metric multidimensional scaling
153 (NMDS) by means of Euclidean distance, using the R package "vegan" (Oksanen et al.
154 2013). Generalised Linear Models (GLMs) were constructed to examine the effects of
155 local habitat and landscape parameters, management, method of site plant colonization
156 (seeded or natural), and age of the sites, on species diversity and richness of carabid
157 species assuming Poisson and inverse Gaussian distributions. Within LF sites, we
158 considered a set of models to test whether seeding, management and age of the LF sites
159 have any influence on estimated species richness (Chao, 1984) and diversity. We
160 restricted this analysis to only LF sites because we do not know the age of sites and
161 methods of colonization on RF sites. Further, a separate set of models was constructed
162 for diversity and richness by taking into account site type, year and soil organic matter,
163 bulk density and vegetation cover in the sites, and percentage of grasslands, percentage
164 of woodlands and percentage of road networks in the surrounding landscape. We
165 checked the assumptions of normality of the residuals and homogeneity of the variances
166 using the full models for each response variable. We compared candidate models using
167 Akaike Information Criterion (AIC), one of the most powerful approaches for model
168 selection from a set of alternative plausible models, and which solves the problems of

169 stepwise model selection (Burnham and Anderson 2002; Pinheiro and Bates 2000). Co-
170 linearity among independent variables was examined by Variance Inflation Factors
171 (VIF) and inter-correlated variables with $VIF > 5$ were omitted from the analysis
172 (Crawley 2007). The analysis was carried out in R software (R Development Core
173 Team 2013). Model selection and multi-model inference were implemented using
174 “MuMIn” package in R (Barton 2013). Akaike weights were computed to assess the
175 support in favour of each candidate models. Models with $\Delta AIC_c \leq 2$ were considered to
176 be equally parsimonious (Burnham and Anderson 2002). We used multimode inference
177 to compute the model-averaged estimates of the explanatory variables that had a
178 normalized $\Delta AIC \leq 2$ and their corresponding 95% confidence intervals. The response
179 variable varied with the explanatory variables if 95% confidence interval excludes zero
180 (Burnham and Anderson 2002)

181 **Results**

182 **Carabid composition on LF and RF sites**

183 A total 1014 individuals representing thirty-seven carabid species were identified from
184 nine LF and their corresponding RF sites from 15 survey days. The mean carabid beetle
185 species richness (\pm SE) per site on LF sites was 7.9 ± 4.3 (mean Shannon-Wiener
186 diversity: 0.51 ± 0.8), whereas that on the RF sites was 9.6 ± 4.0 (mean diversity: $0.41 \pm$
187 0.1). However, there was no significant difference between carabid species richness
188 (Paired t-test $t = -0.82$, $df = 8$, $p = 0.43$) nor diversity (Paired t-test $t = 0.20$, $df = 8$, $p = 0.84$)
189 between LF and RF sites.

190 Twenty species were found on both LF and RF sites; five species were found
191 exclusively on LF sites; and 12 species were found exclusively on RF sites (Table 1).

192 However, nationally rare and scarce beetle species were not recorded from LF sites, and
193 only one nationally scarce species (*Carabus monilis*) was found on an RF site. *Amara*,
194 *Harpalus* and *Pterostichus* species were numerous, with 20 species of these three
195 genera contributing 88% of the individuals captured.

196 The NMDS ordination of carabid species showed a clear separation between the
197 sites along the vertical axis (Figure 2). However, six of the nine LF sites were clustered
198 together, indicating that they share many of the carabid species. The RF sites have lower
199 variance in their spread, indicating that increased similarity to one another. Three of the
200 restored landfill sites which were found separated from each other had a lower
201 abundance of carabids, and also those sites were naturally colonized and not managed
202 by mowing.

203 **Effect of seeding, management and age of the LF sites on carabid richness and** 204 **diversity**

205 Within the LF sites, the models of richness that included seeded sites and management
206 independently were found to be most parsimonious (accumulated Akaike weight of
207 0.72). For diversity, the model that included seeded sites had the highest support
208 (Akaike weight of 0.46) and the intercept model was the second ranked model for
209 diversity (Table 2). Models incorporating age of the landfill sites were $\Delta AIC \geq 4$ with
210 low Akaike weight in both richness and diversity which indicates no support for the
211 hypothesis that age of the landfill sites has any effect on species richness and diversity.
212 Seeding was found to have a strong positive effect on both richness and diversity
213 (Figure 3), whilst management of the sites have a positive effect on carabid species
214 richness (Table 3).

215 **Effect of local and landscape factors on the richness and diversity of carabids**

216 Both species richness and diversity of carabid beetles on the LF and RF sites were
217 related to habitat quality and landscape variables. The richness model that included
218 additive effects of vegetation cover and grassland had the most support (Akaike weight
219 of 0.15). This model was about two-times more likely than the second-ranked model,
220 which considered vegetation cover only. The diversity models that contained vegetation
221 cover, intercept independently and additive effect of vegetation cover and bulk density
222 were found equally likely parsimonious ($\Delta AIC < 2$) though vegetation cover had higher
223 support (Akaike weight of 0.11) (Table 4). There was strong relationship between
224 vegetation cover and diversity and richness. Carabid species richness was found to vary
225 with grassland in surrounding landscape (Table 5). We found no evidence of an effect
226 of woodland, site type and bulk density on richness and diversity (Table 5).

227 **Discussion**

228 **Composition of carabid species assemblages on LF and RF sites**

229 The carabid assemblages of LF sites consisted mostly of opportunistic, generalist, open
230 habitat species, though limited sampling may have excluded rare species, and thus the
231 species collected may not be completely representative of the assemblage in these areas
232 (Lövei and Magura 2011). Generalist species from the genera *Amara*, *Harpalus* and
233 *Pterostichus* were numerous and contributed most to the total abundance across all
234 sites; all are at least facultative consumers of grass seeds (Honek and Jarosik 2003).
235 These findings agree with the results of other studies of derelict urban sites where it was
236 found that *Amara* and *Harpalus* species were numerous (Small, Sadler, and Telfer
237 2002; Eyre, Luff, and Woodward 2003).

238 No differences were found in the carabid assemblage composition between the
239 LF and RF sites, and especially seeded LF sites indicating overlap of species amongst
240 those sites. This reveals an important distinction that seeded LF sites replicate RF sites
241 and therefore seeding has an important influence on carabid community composition.

242 **Seeding, management and age of the LF sites**

243 This study found that carabid colonisation can be enhanced by seeding the newly spread
244 top soil. On restored flood-plain meadows, Woodcock et al. (2008) also found that the
245 structure of beetle assemblages was largely dependent on seed mixture, although
246 management also played an important role. Our findings suggest that restoration using
247 seed mixtures containing grasses and forbs would be expected to provide the greatest
248 resources for beetles, at least at local scales.

249 Grassland management practices, including grazing and cutting, affect ground
250 beetles (Rainio and Niemelä 2003). Because of intensive management and loss of
251 natural and semi-natural habitats, carabids have undergone biotic homogenization with
252 a few common species having become relatively more common at the expense of a large
253 number of rare species, which have become even rarer (Desender, Dufrene, and
254 Maelfait 1994). Management by grazing or mowing in our study sites was found have a
255 positive effect on carabid species richness, echoing the findings of Woodcock et al.
256 (2006). The explanation of a management effect on species richness could relate to
257 timing of management relative to breeding time since the latter is an important factor
258 affecting the survival of carabid populations. In most of the grasslands, cutting or
259 mowing is done in spring time which is the peak breeding season for carabids.

260 However, in the restored LF sites, cutting and mowing usually occurred in summer
261 which may not affect that many carabid species.

262 Wheeler and Cullen (1997) found that the age of old limestone quarries was
263 important in determining invertebrate community composition. This may be related to
264 the time available for establishment or a greater degree of stability within the biotic and
265 abiotic components of the site. That age of the LF sites was not found to be an
266 important factor may be due to the limited range of ages we studied, which spanned
267 only 4-15 years. Judd and Mason (1995) stated that invertebrate assemblages on newly
268 restored landfill sites are characterised by carabids as early colonisers. It is expected that
269 early dominance by opportunistic, dispersive, short-lived and generalist invertebrate
270 species will give way to a more stable mix of longer-lived, habitat-specific species as
271 these sites get older.

272 **Effect of local habitat and landscape factors on carabid richness and diversity**

273 We found a stronger relationship between diversity and richness of carabids and local
274 habitat factors compared to landscape factors, supporting the suggestion of Niemelä et
275 al. (2002) that local factors are of primary importance for carabid community
276 composition. Vegetation cover was found to be the most influential factor for richness
277 and diversity of carabids in the study area. Vegetation cover might accelerate the
278 establishment of the carabid community because it provides living space and modifies
279 the microclimate to create a heterogeneous and stratified microenvironment supporting
280 different carabid species. Judd and Mason (1995) also reported that vegetation cover
281 could enhance the invertebrate community on a restored landfill site.

282 Carabid diversity and richness were also found to be related to the percentage of
283 grassland in the surrounding landscape, probably because many carabids have excellent
284 powers of dispersal if there is similar habitat nearby (Judd and Marson 1995). This
285 indicates that the presence of grassland nearby favours movement of species that are
286 open habitat specialists, due to the specific habitat preferences of these species.
287 Landscape containing complex grassland structure should be maintained and
288 sustainably managed as these habitats are important source of carabid species for
289 colonization of newly created sites.

290 **Conclusions**

291 In conclusion, our results showed that the key drivers of carabid assemblage structure
292 were both landscape and local habitat quality variables. More specifically, initial
293 seeding coupled with management practices and vegetation cover of the sites were
294 important at the local scale, whilst presence of grassland was the key landscape variable
295 which dictated carabid composition of the restored sites. Given the effects of the
296 grasslands in the landscape on overall ground beetle composition, future management of
297 non-cropping habitats should be aimed towards creating a more complex landscape
298 structure. In the light of the serious and widespread loss of carabid biodiversity in the
299 UK (Brooks et al. 2012), re-creating clusters of grassland habitat within fragmented
300 landscapes may have potential to enhance carabid conservation (Taboada et al. 2011),
301 even if it is mainly of widespread, generalist carabid species. However, as we stated,
302 more intensive sampling may show that rarer species can be supported in the grassland
303 on restored landfill sites, especially those of greater age. Further detailed long term
304 study to evaluate the success of restoration of landfill sites for carabid beetle

305 assemblages of landfill sites is recommended. Given the reduction and fragmentation of
306 a number of important habitat types, these newly created habitats on restored landfill
307 sites will be increasingly important for enhancing carabid populations, as well as
308 populations of birds, plants and pollinators (Rahman et al. 2011, 2012, 2013; Tarrant et
309 al. 2013). The development of detailed management prescriptions after seeding of
310 restored sites could further enhance the conservation value of restored landfill sites.

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- 450

451 **Tables:**

452 Table 1: Carabid beetle species found only on LF sites, only on RF sites, and shared on both LF
 453 and RF sites. Total number of individuals sampled is in parentheses.

LF sites	LF sites	RF sites
<i>Agonum assimile</i>	0	6
<i>Amara aenea</i>	11	17
<i>Amara anthobia</i>	1	0
<i>Amara aulica</i>	0	5
<i>Amara convexior</i>	1	1
<i>Amara familiaris</i>	7	18
<i>Amara lunicollis</i>	7	15
<i>Amara ovata</i>	0	1
<i>Amara plebeja</i>	1	3
<i>Bembidion lampros</i>	5	3
<i>Bembidion tetracolum</i>	1	4
<i>Carabus monilis*</i>	0	14
<i>Carabus problematicus</i>	5	2
<i>Carabus violaceus</i>	6	7
<i>Chlaenius nitidulus</i>	0	1
<i>Dyschirius</i> sp.	1	3
<i>Elaphrus riparius</i>	0	1
<i>Harpalus affinis</i>	7	0
<i>Harpalus anxius</i>	6	3
<i>Harpalus rubripes</i>	3	0
<i>Leistus</i> sp.	1	1
<i>Loricera pilicornis</i>	0	3
<i>Microlestes minutulus</i>	4	0
<i>Nebria rufescens</i>	18	25
<i>Nebria</i> sp.	5	0
<i>Ophonus</i> sp.	0	1
<i>Pseudophonus rufipes</i>	9	5
<i>Pterostichus cupreus</i>	195	153
<i>Pterostichus macer</i>	5	11
<i>Pterostichus madidus</i>	35	228
<i>Pterostichus melanarius</i>	65	35
<i>Pterostichus niger</i>	15	1
<i>Pterostichus nigrata</i>	0	15
<i>Pterostichus</i> sp.	0	1
<i>Pterostichus</i> sp.	9	6
<i>Stomis pumicatus</i>	0	1
Unidentified	0	1
Mean species richness per site	7.9 ± 4.3	9.6 ± 4.0
Mean Shannon-Wiener diversity	0.51 ± 0.8	0.41 ± 0.1

454 **Carabus monilis* is the only nationally scarce species found in RF sites.

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456 Table 2: Model selection results for richness and diversity of carabids with seeded sites,
 457 management and age of the LF sites

Models	K	AICc	Δ AICc	w_i
<i>Richness</i>				
Seeded	2	44.8	0.00	0.53
Management	2	46.0	1.23	0.29
Seeded+Management	3	48.2	3.38	0.09
Seeded+Age	3	49.6	4.79	0.05
<i>Diversity</i>				
Seeded	3	20.9	0.00	0.46
Null model	2	21.5	0.66	0.33
Management	3	24.2	3.27	0.09
Seeded+Age	4	24.9	3.99	0.06

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460 Table 3: Model-averaged estimates of explanatory variables only for LF sites with their respective
 461 unconditional standard errors (SE) and 95% confidence intervals (CI) and Relative importance (RI).
 462 Estimates in bold indicate a strong effect of that explanatory variable on the response variable.

Variables	Est.	SE	95% CI	RI
<i>Richness</i>				
Null model	1.93	0.13	1.60, 2.25	
Seeded	1.24	0.36	0.39, 2.08	0.65
Management	1.01	0.28	0.34, 1.68	0.35
<i>Diversity</i>				
Null model	0.34	0.13	0.04, 0.65	
Seeded	0.63	0.25	0.05, 1.22	0.58

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 473 Table 4: Model selection results for richness and diversity of carabids with their local and
 474 landscape parameters. (Parameters: Veg.cover=percentage of vegetation cover,
 475 Blk.density=Bulk density)

Models	df	AICc	Δ AICc	w_i
Richness				
Veg.cover+grassland	3	100.15	0.00	0.15
Veg.cover	2	101.42	1.27	0.08
Veg.cover+grassland+woodland	4	101.67	1.52	0.07
Veg.cover+grassland+Site type	4	102.1	1.95	0.06
Veg.cover+grassland+Blk.density	4	102.61	2.46	0.04
Diversity				
Veg.cover	3.00	31.77	0.00	0.11
Null model	2.00	32.42	0.65	0.08
Veg.cover +Blk.density	4.00	32.56	0.79	0.07
Veg.cover+Site type	4	33.8	2.07	0.04

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478 Table 5: Model-averaged estimates of explanatory variables only for both LF and RF sites with their
 479 respective unconditional standard errors (SE) and 95% confidence intervals (CI) and Relative
 480 importance (RI). (Parameters: Veg.cover=percentage of vegetation cover, Blk.density=Bulk density).
 481 Estimates in bold indicate a strong effect of that explanatory variable on the response variable.

Variables	Est.	SE	95% CI	RI
<i>Richness</i>				
Null model	8.72	0.76	7.24, 10.20	
Veg.cover	4.72	1.35	2.06, 7.36	1.00
Grassland	3.55	1.74	0.14, 6.95	0.78
Woodland	-1.99	1.59	-5.11, 1.13	0.20
Site type	-2.13	1.89	-5.84, 1.58	0.16
<i>Diversity</i>				
Null model	0.35	0.09	0.17, 0.52	
Veg.cover	0.46	0.18	0.10, 0.81	0.70
Blk.density	0.25	0.18	-0.10, 0.61	0.28

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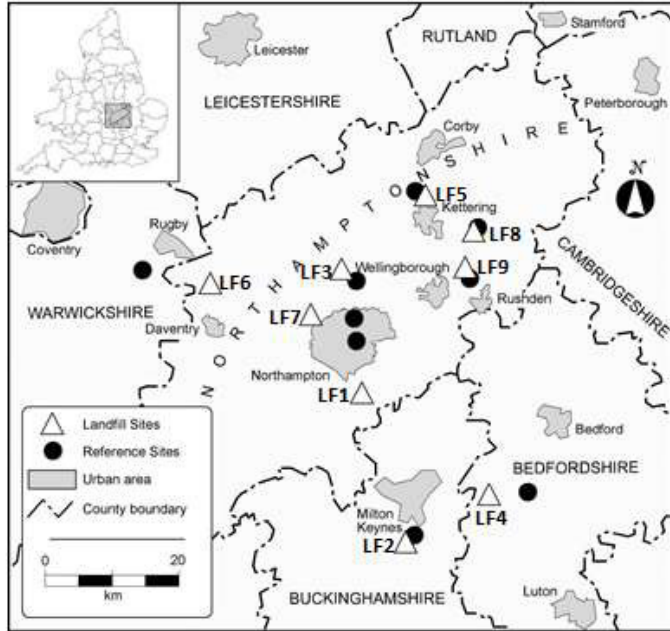
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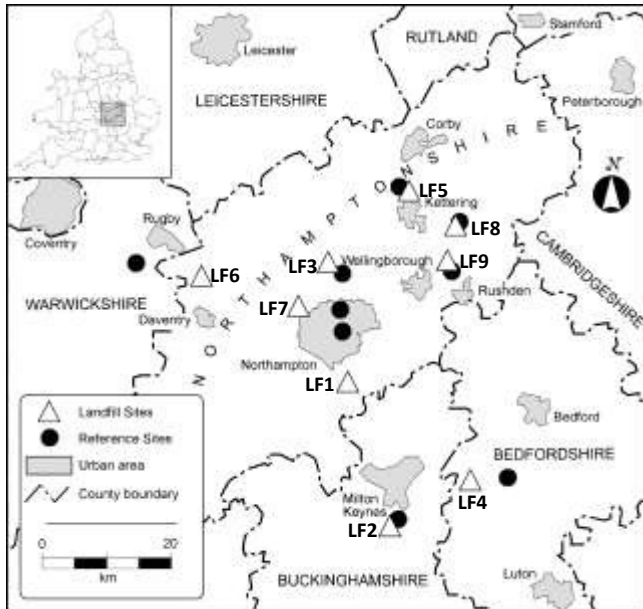
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488 **Figures:**
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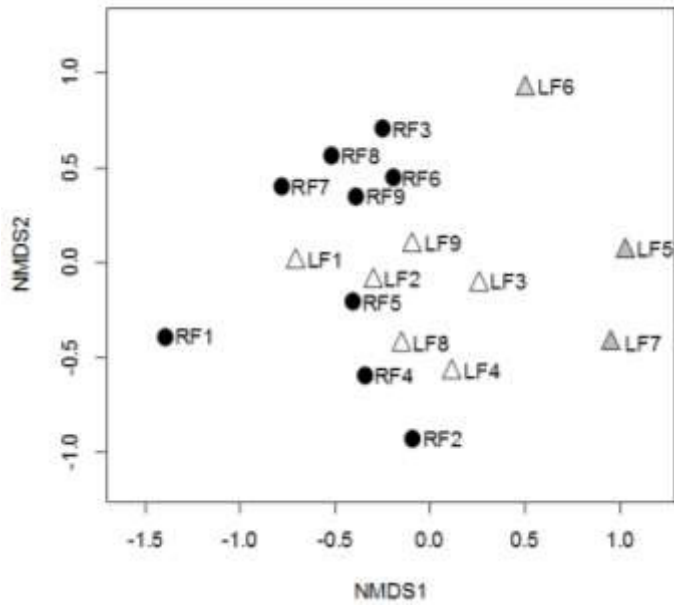


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Figure 1



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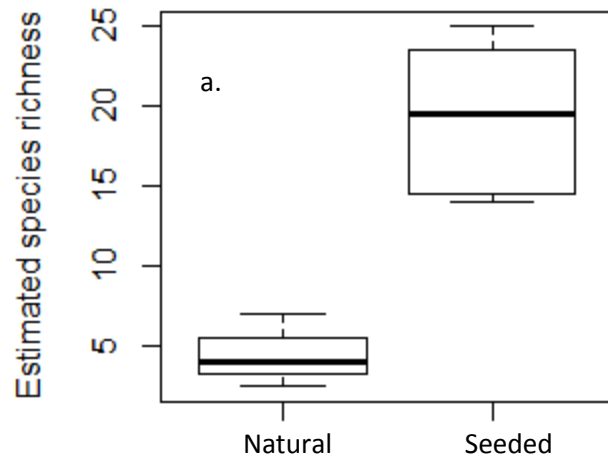
508 Figure 2

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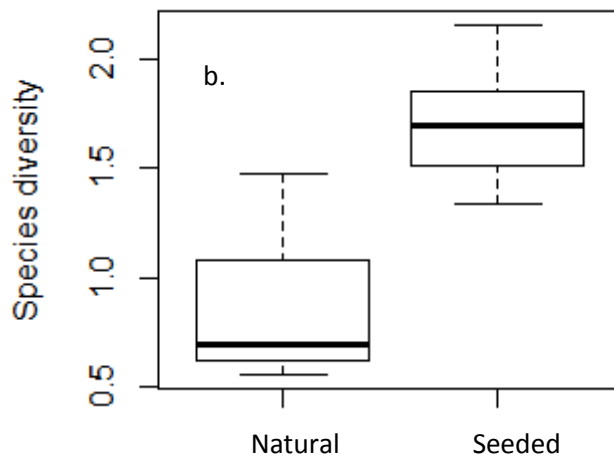
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517 Figure 3

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525 **Figure Legends**

526 Figure 1: Location of restored landfill (LP, triangles) and reference sites (black dots)
527 studied in Northamptonshire and its surrounding counties.

528 Figure 2: NMDS ordination of carabid species composition and their abundance on nine
529 restored landfill (LF 1-9) sites and nine reference (RF 1-9) sites. Two-dimensions used,
530 S-stress=0.113. Filled triangle=seeded landfill sites; open triangle=naturally colonized
531 landfill sites; filled circles=reference sites.

532 Figure 3: Estimated carabid species richness (a) and Shannon-Wiener diversity (b) on
533 seeded LF and naturally colonized LF sites. The horizontal line shows the median. The
534 bottom and top boxes show the 25th and 75th percentiles respectively. The vertical
535 dashed lines show interquartile range.