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Article

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

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Abstract

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

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

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

Habitat loss from urbanisation and modern intensive agricultural land use practices has contributed to the impoverishment of many invertebrate groups including carabids; thus habitat restoration potentially plays an important role in their conservation (Judd and Mason 1995; Sotherton and Self 2000; Meek et al. 2002). There are approximately 2,200 landfill sites in England and Wales covering 28,000 ha (EA 2006) representing a significant stock of land with conservation potential. Newly restored landfill sites potentially provide suitable habitats for carabids thereby compensating for the reduction of suitable habitat within the local area. It is expected the value of such newly created areas as habitat for carabids will vary depending on species-specific requirements and colonisation ability.
The influence of factors operating at differing scales is key to understanding the composition and diversity of invertebrate assemblages (Söderström et al. 2001; Collinge, Prudic, and Oliver 2003). Community composition of carabid assemblages may be influenced by local habitat to landscape-scale processes (Aviron et al. 2005). Recognising critical local habitat and landscape-level factors is important in developing effective conservation strategies of newly created invertebrate habitat sites. Invertebrate community composition and diversity, including those of carabids, have been found to be positively related to local habitat quality (Weibull, Ostman, and Granqvist 2003) whilst at the landscape scale, carabid assemblages are influenced by the amount and spatial arrangement of habitat patches and the surrounding landscape composition, specifically obstructing linear features such as road density (de la Pena et al. 2003; Aviron et al. 2005), and natural and semi-natural areas in the landscape (Liu et al. 2015). Although habitat quality and landscape pattern are known to explain the composition and diversity of other taxa in restored landfill sites (Rahman et al. 2011, 2012, 2013; Tarrant et al. 2013), few studies have considered both habitat and landscape factors simultaneously for carabid beetles, particularly on restored landfill sites.

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

Study sites

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

Sample collection

Two 100 m perpendicular transects crossing each other at the approximate centre point of each site were set out, with directions chosen using randomized bearing tables. Ten (5×2 transects) pitfall traps were set along the two transects using random points which were at least 1 m apart from each other. Each pitfall trap consisted of a plastic cup (5cm
diameter, 120ml) sunk flush with the ground. One pitfall per sampling point was half-filled with water (detergent was not added due to restrictions by landfill site operators) and exposed for five days. Longer exposure was not possible due to logistic constraints. Sampling from seven LF sites and their corresponding RF sites were conducted on three occasions April, June, and September 2007. Further, two more LF sites and their corresponding RF sites were surveyed for the same period during 2008 (no sampling could be conducted during 2007 due to flooding on these sites). To reduce the effects of temporal heterogeneity, sampling on both LF and their corresponding RF sites were conducted at the same period of time. All captured carabid beetles were dry mounted and identified to species using Forsythe (1987). Note that it was not our objective to obtain a full faunal list of carabid species for each of these sites, but to use standardised sampling as a means of comparing sites with different land use histories and landscape contexts.

**Local habitat and landscape variables**

From each of the LF and RF sites, five soil samples from a depth down to 10 cm were collected for soil analysis from random locations along the transects. The variables percentage of organic matter and bulk density were determined following Rowell (1994). Percentage of vegetation cover on each site was also calculated from 10 random 1m × 1m quadrats along transects. We used percentage of three non-crop features, grassland, woodland, and road networks, as indicators of the amount and diversity of perennial habitats in the surrounding landscape as perennial features should have a greater influence on composition of invertebrates on newly created habitats. Percentage area of grassland, woodland and a quantitative measure of the road networks, within a 1 km radius zone of each site’s margins, were determined from Land Cover Map 2000.
(Raster, 25m resolution) using a Geographical Information System to measure for potential landscape-scale effects (ESRI 1999).

**Statistical analysis**

All data on species richness and Shannon–Wiener diversity indexes were analysed using total number of species or number of individuals per site. As stated, we aimed at standardised comparison between LF and RF sites, and therefore the short sampling period may have an effect on the study. Carabid species composition and their abundance between site types were represented by non-metric multidimensional scaling (NMDS) by means of Euclidean distance, using the R package "vegan" (Oksanen et al. 2013). Generalised Linear Models (GLMs) were constructed to examine the effects of local habitat and landscape parameters, management, method of site plant colonization (seeded or natural), and age of the sites, on species diversity and richness of carabid species assuming Poisson and inverse Gaussian distributions. Within LF sites, we considered a set of models to test whether seeding, management and age of the LF sites have any influence on estimated species richness (Chao, 1984) and diversity. We restricted this analysis to only LF sites because we do not know the age of sites and methods of colonization on RF sites. Further, a separate set of models was constructed for diversity and richness by taking into account site type, year and soil organic matter, bulk density and vegetation cover in the sites, and percentage of grasslands, percentage of woodlands and percentage of road networks in the surrounding landscape. We checked the assumptions of normality of the residuals and homogeneity of the variances using the full models for each response variable. We compared candidate models using Akaike Information Criterion (AIC), one of the most powerful approaches for model selection from a set of alternative plausible models, and which solves the problems of
stepwise model selection (Burnham and Anderson 2002; Pinheiro and Bates 2000). Colinearity among independent variables was examined by Variance Inflation Factors (VIF) and inter-correlated variables with VIF>5 were omitted from the analysis (Crawley 2007). The analysis was carried out in R software (R Development Core Team 2013). Model selection and multi-model inference were implemented using “MuMIn” package in R (Barton 2013). Akaike weights were computed to assess the support in favour of each candidate models. Models with ΔAICc ≤ 2 were considered to be equally parsimonious (Burnham and Anderson 2002). We used multimodel inference to compute the model-averaged estimates of the explanatory variables that had a normalized ΔAIC ≤ 2 and their corresponding 95% confidence intervals. The response variable varied with the explanatory variables if 95% confidence interval excludes zero (Burnham and Anderson 2002)

Results

Carabid composition on LF and RF sites

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

Twenty species were found on both LF and RF sites; five species were found exclusively on LF sites; and 12 species were found exclusively on RF sites (Table 1).
However, nationally rare and scarce beetle species were not recorded from LF sites, and only one nationally scarce species (*Carabus monilis*) was found on an RF site. *Amara, Harpalus* and *Pterostichus* species were numerous, with 20 species of these three genera contributing 88% of the individuals captured.

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

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

Within the LF sites, the models of richness that included seeded sites and management independently were found to be most parsimonious (accumulated Akaike weight of 0.72). For diversity, the model that included seeded sites had the highest support (Akaike weight of 0.46) and the intercept model was the second ranked model for diversity (Table 2). Models incorporating age of the landfill sites were ΔAIC ≥4 with low Akaike weight in both richness and diversity which indicates no support for the hypothesis that age of the landfill sites has any effect on species richness and diversity. Seeding was found to have a strong positive effect on both richness and diversity (Figure 3), whilst management of the sites have a positive effect on carabid species richness (Table 3).
Effect of local and landscape factors on the richness and diversity of carabids

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

Discussion

Composition of carabid species assemblages on LF and RF sites

The carabid assemblages of LF sites consisted mostly of opportunistic, generalist, open habitat species, though limited sampling may have excluded rare species, and thus the species collected may not be completely representative of the assemblage in these areas (Lövei and Magura 2011). Generalist species from the genera *Amara*, *Harpalus* and *Pterostichus* were numerous and contributed most to the total abundance across all sites; all are at least facultative consumers of grass seeds (Honek and Jarosik 2003). These findings agree with the results of other studies of derelict urban sites where it was found that *Amara* and *Harpalus* species were numerous (Small, Sadler, and Telfer 2002; Eyre, Luff, and Woodward 2003).
No differences were found in the carabid assemblage composition between the LF and RF sites, and especially seeded LF sites indicating overlap of species amongst those sites. This reveals an important distinction that seeded LF sites replicate RF sites and therefore seeding has an important influence on carabid community composition.

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

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

Grassland management practices, including grazing and cutting, affect ground beetles (Rainio and Niemelä 2003). Because of intensive management and loss of natural and semi-natural habitats, carabids have undergone biotic homogenization with a few common species having become relatively more common at the expense of a large number of rare species, which have become even rarer (Desender, Dufrene, and Maelfait 1994). Management by grazing or mowing in our study sites was found have a positive effect on carabid species richness, echoing the findings of Woodcock et al. (2006). The explanation of a management effect on species richness could relate to timing of management relative to breeding time since the latter is an important factor affecting the survival of carabid populations. In most of the grasslands, cutting or mowing is done in spring time which is the peak breeding season for carabids.
However, in the restored LF sites, cutting and mowing usually occurred in summer which may not affect that many carabid species.

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

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

We found a stronger relationship between diversity and richness of carabids and local habitat factors compared to landscape factors, supporting the suggestion of Niemelä et al. (2002) that local factors are of primary importance for carabid community composition. Vegetation cover was found to be the most influential factor for richness and diversity of carabids in the study area. Vegetation cover might accelerate the establishment of the carabid community because it provides living space and modifies the microclimate to create a heterogeneous and stratified microenvironment supporting different carabid species. Judd and Mason (1995) also reported that vegetation cover could enhance the invertebrate community on a restored landfill site.
Carabid diversity and richness were also found to be related to the percentage of grassland in the surrounding landscape, probably because many carabids have excellent powers of dispersal if there is similar habitat nearby (Judd and Marson 1995). This indicates that the presence of grassland nearby favours movement of species that are open habitat specialists, due to the specific habitat preferences of these species. Landscape containing complex grassland structure should be maintained and sustainably managed as these habitats are important source of carabid species for colonization of newly created sites.

**Conclusions**

In conclusion, our results showed that the key drivers of carabid assemblage structure were both landscape and local habitat quality variables. More specifically, initial seeding coupled with management practices and vegetation cover of the sites were important at the local scale, whilst presence of grassland was the key landscape variable which dictated carabid composition of the restored sites. Given the effects of the grasslands in the landscape on overall ground beetle composition, future management of non-cropping habitats should be aimed towards creating a more complex landscape structure. In the light of the serious and widespread loss of carabid biodiversity in the UK (Brooks et al. 2012), re-creating clusters of grassland habitat within fragmented landscapes may have potential to enhance carabid conservation (Taboada et al. 2011), even if it is mainly of widespread, generalist carabid species. However, as we stated, more intensive sampling may show that rarer species can be supported in the grassland on restored landfill sites, especially those of greater age. Further detailed long term study to evaluate the success of restoration of landfill sites for carabid beetle
assemblages of landfill sites is recommended. Given the reduction and fragmentation of a number of important habitat types, these newly created habitats on restored landfill sites will be increasingly important for enhancing carabid populations, as well as populations of birds, plants and pollinators (Rahman et al. 2011, 2012, 2013; Tarrant et al. 2013). The development of detailed management prescriptions after seeding of restored sites could further enhance the conservation value of restored landfill sites.

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Tables:

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

<table>
<thead>
<tr>
<th>LF sites</th>
<th>LF sites</th>
<th>RF sites</th>
</tr>
</thead>
<tbody>
<tr>
<td>Agonum assimile</td>
<td>0</td>
<td>6</td>
</tr>
<tr>
<td>Amara aenea</td>
<td>11</td>
<td>17</td>
</tr>
<tr>
<td>Amara anthobia</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Amara aulica</td>
<td>0</td>
<td>5</td>
</tr>
<tr>
<td>Amara convexior</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Amara familiaris</td>
<td>7</td>
<td>18</td>
</tr>
<tr>
<td>Amara lunicollis</td>
<td>7</td>
<td>15</td>
</tr>
<tr>
<td>Amara ovata</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Amara plebeja</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>Bembidion lampros</td>
<td>5</td>
<td>3</td>
</tr>
<tr>
<td>Bembidion tetracolum</td>
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<td>4</td>
</tr>
<tr>
<td>Carabus monilis*</td>
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<td>14</td>
</tr>
<tr>
<td>Carabus problematicus</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>Carabus violaceus</td>
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<td>7</td>
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<tr>
<td>Dyschirius sp.</td>
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<td>Elaphrus riparius</td>
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<td>1</td>
</tr>
<tr>
<td>Harpalus affinis</td>
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<td>Harpalus rubripes</td>
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<td>1</td>
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<td>Loricera pilicornis</td>
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</tr>
<tr>
<td>Microlestes minutulus</td>
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</tr>
<tr>
<td>Nebria rufescens</td>
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<td>25</td>
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<tr>
<td>Nebria sp.</td>
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<td>0</td>
</tr>
<tr>
<td>Ophonus sp.</td>
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<tr>
<td>Pseudophonus rafipes</td>
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<td>Pterostichus capreus</td>
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<td>Pterostichus madidus</td>
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<td>Pterostichus melanarius</td>
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<td>1</td>
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<td>Pterostichus sp.</td>
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<td>6</td>
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<tr>
<td>Stomis punicatus</td>
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<td>1</td>
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<tr>
<td>Unidentified</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Mean species richness per site</td>
<td>7.9 ± 4.3</td>
<td>9.6 ± 4.0</td>
</tr>
<tr>
<td>Mean Shannon-Wiener diversity</td>
<td>0.51 ± 0.8</td>
<td>0.41 ± 0.1</td>
</tr>
</tbody>
</table>

*Carabus monilis* is the only nationally scarce species found in RF sites.
Table 2: Model selection results for richness and diversity of carabids with seeded sites, management and age of the LF sites

<table>
<thead>
<tr>
<th>Models</th>
<th>K</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>wi</th>
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<td><strong>Richness</strong></td>
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<td></td>
<td></td>
<td></td>
</tr>
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<td>Seeded</td>
<td>2</td>
<td>44.8</td>
<td>0.00</td>
<td>0.53</td>
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<tr>
<td>Management</td>
<td>2</td>
<td>46.0</td>
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<td>0.29</td>
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<tr>
<td>Seeded+Management</td>
<td>3</td>
<td>48.2</td>
<td>3.38</td>
<td>0.09</td>
</tr>
<tr>
<td>Seeded+Age</td>
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<td>49.6</td>
<td>4.79</td>
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<tr>
<td><strong>Diversity</strong></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Seeded</td>
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<td>20.9</td>
<td>0.00</td>
<td>0.46</td>
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<tr>
<td>Null model</td>
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<td>24.9</td>
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</table>
Table 3: Model-averaged estimates of explanatory variables only for LF sites with their respective unconditional standard errors (SE) and 95% confidence intervals (CI) and Relative importance (RI). Estimates in bold indicate a strong effect of that explanatory variable on the response variable.

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<thead>
<tr>
<th>Variables</th>
<th>Est.</th>
<th>SE</th>
<th>95% CI</th>
<th>RI</th>
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<tr>
<td><strong>Richness</strong></td>
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<td></td>
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</tr>
<tr>
<td>Null model</td>
<td>1.93</td>
<td>0.13</td>
<td>1.60, 2.25</td>
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<tr>
<td>Seeded</td>
<td>1.24</td>
<td>0.36</td>
<td>0.39, 2.08</td>
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<tr>
<td>Management</td>
<td>1.01</td>
<td>0.28</td>
<td>0.34, 1.68</td>
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<tr>
<td><strong>Diversity</strong></td>
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<td></td>
</tr>
<tr>
<td>Null model</td>
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<td>0.13</td>
<td>0.04, 0.65</td>
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</tr>
<tr>
<td>Seeded</td>
<td>0.63</td>
<td>0.25</td>
<td>0.05, 1.22</td>
<td>0.58</td>
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Table 4: Model selection results for richness and diversity of carabids with their local and landscape parameters. (Parameters: Veg.cover=percentage of vegetation cover, Blk.density=Bulk density)

<table>
<thead>
<tr>
<th>Models</th>
<th>df</th>
<th>AICc</th>
<th>∆AICc</th>
<th>wi</th>
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<tr>
<td><strong>Richness</strong></td>
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<tr>
<td>Veg.cover+grassland</td>
<td>3</td>
<td>100.15</td>
<td>0.00</td>
<td>0.15</td>
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<tr>
<td>Veg.cover</td>
<td>2</td>
<td>101.42</td>
<td>1.27</td>
<td>0.08</td>
</tr>
<tr>
<td>Veg.cover+grassland+woodland</td>
<td>4</td>
<td>101.67</td>
<td>1.52</td>
<td>0.07</td>
</tr>
<tr>
<td>Veg.cover+grassland+Site type</td>
<td>4</td>
<td>102.1</td>
<td>1.95</td>
<td>0.06</td>
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<tr>
<td>Veg.cover+grassland+Blk.density</td>
<td>4</td>
<td>102.61</td>
<td>2.46</td>
<td>0.04</td>
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<tr>
<td><strong>Diversity</strong></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Veg.cover</td>
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<td>32.42</td>
<td>0.65</td>
<td>0.08</td>
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<tr>
<td>Veg.cover +Blk.density</td>
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<td>32.56</td>
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<td>0.04</td>
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</tbody>
</table>
Table 5: Model-averaged estimates of explanatory variables only for both LF and RF sites with their respective unconditional standard errors (SE) and 95% confidence intervals (CI) and Relative importance (RI). (Parameters: Veg.cover=percentage of vegetation cover, Blk.density=Bulk density).

Estimates in bold indicate a strong effect of that explanatory variable on the response variable.

<table>
<thead>
<tr>
<th>Variables</th>
<th>Est.</th>
<th>SE</th>
<th>95% CI</th>
<th>RI</th>
</tr>
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<tbody>
<tr>
<td><strong>Richness</strong></td>
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<tr>
<td>Null model</td>
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<td>0.76</td>
<td>7.24, 10.20</td>
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<tr>
<td>Veg.cover</td>
<td><strong>4.72</strong></td>
<td><strong>1.35</strong></td>
<td><strong>2.06, 7.36</strong></td>
<td><strong>1.00</strong></td>
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<td>Grassland</td>
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<td>0.14, 6.95</td>
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<td>1.59</td>
<td>-5.11, 1.13</td>
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<td>Site type</td>
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<td>-5.84, 1.58</td>
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<tr>
<td><strong>Diversity</strong></td>
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<tr>
<td>Null model</td>
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<td>0.09</td>
<td>0.17, 0.52</td>
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<tr>
<td>Veg.cover</td>
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<td><strong>0.18</strong></td>
<td><strong>0.10, 0.81</strong></td>
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<td>-0.10, 0.61</td>
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</tbody>
</table>
Figures:

Figure 1
Figure 3

(a) Estimated species richness

(b) Species diversity

Natural vs. Seeded

Figure Legends

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

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

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