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Vegetative communities as indicators of ground beetle (Coleoptera: Carabidae) diversity

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Abstract Accurately measuring biodiversity is essential for successful conservation planning. Due to biodiversity's complexity, specific taxa are often chosen as indicators of patterns of diversity as a whole. Such taxa can include vegetation which can inform conservation decisions by demarcating land units for management strategies. For land units to be useful, they must be accurate spatial representations of the species assemblages present on the landscape. In this study, we determined whether land units classified by vegetative communities predicted the community structure of a diverse group of invertebrates—the ground beetles (Coleoptera: Carabidae). Specifically, that (1) land units of the same classification contained similar carabid species assemblages and that (2) differences in species structure were correlated with variation in land unit characteristics, including canopy and ground cover, vegetation structure, tree density, leaf litter depth, and soil moisture. The study site, the Braidwood Dunes and Savanna Nature Preserve in Will County, Illinois is a mosaic of differing land units. Carabid beetles were sampled continuously with pitfall trapping for 1 year (excluding winter) from September 2011 to November 2011 and from March 2012 to September 2012. Land unit characteristics were

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measured in July 2012. Nonmetric multidimensional scaling (NMDS) ordinated the land units by their carabid species assemblages into five ecologically meaningful clusters: disturbed, marsh, prairie, restoration, and savanna. The subset of land unit characteristics with the highest rank correlation with the NMDS ordination included soil moisture, leaf litter depth, percentage of canopy cover, and percentage of grass ground cover. Land units classified by vegetative communities effectively represented carabid species assemblages.

Keywords Carabidae · Species assemblages · Vegetative communities · Habitat delineation · Biodiversity indicator · Conservation planning

Introduction

The primary goal of conservation biology is the protection of biological diversity (Soulé 1985). Due to the complexity of biodiversity, indicators are used to measure and map biodiversity so that conservation strategies can be planned (Margules and Pressey 2000). Biodiversity indicators serve to represent the unknown diversity and generally fall into two broad categories. The first approach uses indicator species in which the diversity of a set of taxa is used to infer the diversity of a separate group of taxa (McGeogh 1998). Areas of conservation can then be defined by the range/presence of the indicator species with the expectation that their protection would consequently protect the unknown diversity (Lambeck 1997; Roberge and Angelstam 2004). However, the success of indicator species in accurately representing the diversity of other taxa has been mixed. While in some instances the presence of certain taxa can be predicted by the presence of other taxa, variation in results across study sites, ecosystems, and spatial, temporal, and taxonomic scales limit the application of broad generalizations (Favreau et al. 2006; Rodrigues and Brooks 2007).

The second approach uses environmental characteristics as indicators of biodiversity. Characteristics can include climate, landform and topography, geology, soils, hydrology, and vegetative communities (Cleland et al. 1997). Land units with similar environmental features are classified together (e.g., by habitat type) and can be delineated across landscapes to guide management strategies (Zonneveld 1989). In order for these strategies to be successful, land units must be effective spatial representations of the species assemblages present on the landscape. The distribution and relative abundance of a species is governed by its physiological response to its environment as well as by its interactions with other species (Hutchinson 1957). Because the same environmental features used to classify the land units also contribute to a species' spatial distribution and relative abundance, it is expected that land units of the same classification type should contain similar assemblages of species.

The primary goal of this study was to assess whether land units delineated according to vegetation and soil mapping in a sand prairie/sand savanna ecosystem predicted ground beetle (Coleoptera: Carabidae) community structure. This family of beetles is well suited for biodiversity studies because they are one of the most speciose beetle families with over 30,000 described species worldwide (Bousquet 2012). The taxonomy and ecology of the group are well studied (Lövei and Sunderland 1996; Niemelä 1996), and ground beetles respond to environmental parameters such as temperature and moisture (Thiele 1977). The Carabidae includes both habitat generalists and habitat specialists (Niemelä et al. 1992;

Larsen et al. 2003; Larochelle and Larivière 2003). Ground beetles can serve as bioindicators (Rainio and Niemelä 2003); assemblages of carabid species have been used to classify habitat types (Luff et al. 1992) and to identify areas of conservation concern (Butterfield et al. 1995). However, carabid species vary in seasonal abundance and activity (Niemelä et al. 1992; Lövei and Sunderland 1996) which can be a disadvantage to their use as bioindicators (Rainio and Niemelä 2003). Sampling over an entire growing season is recommended (Niemelä et al. 2000). Finally, it is easy and cost-effective to quantitatively collect data on Carabidae with pitfall trapping (Spence and Niemelä 1994).

A secondary goal of this study was to measure environmental parameters of the different land unit types to identify characteristics that affect the composition of carabid species assemblages. If ground beetle communities vary between land units of different vegetative classifications, then carabid species should be responding to the parameters' ranges expressed within each land unit type. Alternatively, carabid communities might not correspond to the delineated land units; and instead, the beetles might be responding to other environmental parameters that, if mapped, would result in a different set of land units within which conservation efforts should be focused. In this case, identifying the parameters which best characterize the ground beetle assemblages could then lead to adjustments to the land classification scheme allowing implementation of more effective management.

We examined carabid species assemblages sampled across Braidwood Dunes and Savanna Nature Preserve, a landscape composed of six predefined (Conservation Design Forum 2010) land unit types: marsh, prairie, restoration, savanna, shrub swamp, and successional field. For each land unit type, we compared the composition of the ground beetle species assemblages and examined the relationship between the environmental parameters and the species distributions. The expectation was that assemblages from the same type of land unit would be more similar to each other than to assemblages from other land unit types, suggesting that carabid species respond to environmental parameters that are within the ranges of those parameters for land units delineated on the basis of vegetation and soil types. Indicator species analyses were also performed to determine if certain ground beetle species are indicative for certain land classifications.

Materials and methods

Study area

The 357 acre Braidwood Dunes and Savanna Nature Preserve is located in southwestern Will County, Illinois (41.25519°N, 88.19605°W). The Preserve is a part of the Kankakee Sand Area Section of the Grand Prairie Natural Division, a region characterized by the extensive sand deposits left by the Kankakee Flood during the late Wisconsinan glaciation (Schwegman 1973). Established in 1981, the Preserve is owned and managed by the Forest Preserve District of Will County. Prior to 1981, portions of the Preserve had been used for horse racing, grazing, and agriculture, and adjacent lands to the north had been part of a strip-mine. A power line right-of-way passes through the southern third of the Preserve. Despite these disturbances, high quality remnants of sand prairie, sand savanna, and marsh still remain (White 1978; Phillippe et al. 2008).

As part of recent efforts to better understand the ecological communities in the Preserve and to improve conservation strategies, floristic inventories have been performed (Phillippe et al. 2008; Conservation Design Forum 2010). These inventories, along with soils data, have been used to delineate land units across the Preserve (Conservation Design Forum

2010). Identification and delineation of these land units followed the community classification system set forth by the Illinois Natural Areas Inventory (White 1978). The resulting demarcations revealed the Preserve to be a mosaic of community types including dry sand savanna, mesic sand savanna, wet-mesic sand savanna, dry sand prairie, mesic sand prairie, wet-mesic sand prairie, marsh, shrub swamp, successional field, and restoration (Conservation Design Forum 2010). To ensure sufficient sample size for statistical analyses in the present study, the three types of sand savanna and the three types of sand prairie were each considered as part of the same classification: savanna and prairie, respectively.

Sample sites

Potential sample sites within the Braidwood Dunes and Savanna Nature Preserve were randomly generated with ArcMap 9.3 (Environmental Systems Research Institute, Inc., California). Shapefiles delineating land unit boundaries (Conservation Design Forum 2010) served as a framework for selection of sample sites. Each site was generated such that it was at least 30 m from the nearest land unit edge, so as to reduce the potential for edge effects (Murcia 1995). However, sample sites in marsh land units were moved to the nearest edge to minimize the risk of flooding. To ensure independent sampling, each site was separated by at least 25 m (Digweed et al. 1995). From all the potential sample sites generated, 31 were randomly selected for the study: 13 savanna, 7 prairie, 5 marsh, 3 restoration, 2 successional field, and 1 shrub swamp site. The shrub swamp land units in the northern half of the Preserve were undergoing extensive active management; sample sites from those land units were replaced with sites randomly selected from the remaining land units. All sites, excluding those from restoration and successional field, were from land units that ranged in quality from late successional or lightly disturbed to relatively stable or undisturbed. Soils ranged from well drained to poorly drained sandy loam for savanna, prairie, restoration, and successional field sites. Marsh and shrub swamp soils were fine sandy loam that was under standing water for a portion of the year (Conservation Design Forum 2010).

Carabidae sampling

A linear transect of four pitfall traps was set at each sample site with an inter-trap distance of 5 m. Pitfalls consisted of two nested, 532 mL, plastic Hefty® drinking cups (Reynolds Consumer Products Inc., Illinois) (mouth diameter: 9.0 cm) whose lips were placed flush with the ground. The outer cup had drain holes punctured in its bottom. Styrofoam insulation ($15 \times 15 \times 2$ cm^3) was supported with nails 2–3 cm above each trap to keep out rainwater and debris. To deter animal vandalism, chicken wire (61.0×61.0 cm^2; mesh: 2.5 cm) was laid over each trap and staked in place. Traps were filled with approximately 150 mL of 20 % ethylene glycol.

Pitfall trapping has its disadvantages in that catches are an index of a species foraging activity and its density rather than actual abundance (Greenslade 1964). Pitfall trapping selects for larger ground dwelling beetles (Spence and Niemelä 1994) and can be affected by weather (Greenslade 1964) as well as the structure of surrounding vegetation; denser stands of vegetation limit foraging activity (Thomas et al. 2006). Despite these disadvantages, pitfall trapping is an efficient collecting technique, and its passive sampling approach reduces biases associated with actively searching for specimens. For studies such as this one that compare assemblages of ground beetle species rather than survey actual abundances, pitfall trapping is a suitable collecting method (Spence and Niemelä 1994).

Pitfall traps were installed August 19, 2011. The initial disturbance from pitfall installation can affect the number of specimens collected (Greenslade 1973; Digweed et al. 1995), so sampling was delayed approximately 1 month. Traps were sampled roughly every 2 weeks from September 16, 2011 to November 11, 2011 and again from March 10, 2012 to September 22, 2012. The trap contents were strained through a fine wire mesh and the Carabidae were stored in 80 % ethanol. Adult Carabidae were identified to species using Bousquet (2010), Ciegler (2000), and Pearson et al. (2006), and by comparing individuals to specimens from the Illinois Natural History Survey insect collection. Nomenclature follows that of Bousquet (2012). Individuals that could not be confidently identified to species were identified to morphospecies.

Carabidae captures were standardized to 1,000 trap-nights [captures per site/(number of traps $\times$ number of nights)] to correct for trap losses (i.e., flooding) and for variations in collection times. These standardized abundances were then $\ln(x + 1)$ transformed to reduce the asymmetry of the species abundances (Legendre and Legendre 2012).

Environmental parameters

The following environmental parameters were measured at each sample site once during the summer (mid-July 2012): tree density, tree diameter, leaf litter depth, soil moisture, percent canopy cover, percent ground cover (bare soil, dead wood, leaf litter, woody plants, herbaceous plants, and grasses), and vegetative structure.

Tree density was measured within a 10.5 m radius from the center of the pitfall transect at each sample site. All trees with a diameter at breast height (DBH) greater than 2.5 cm were included. Trees forking below breast height had each trunk measured as a separate tree. The DBH of each included tree was also recorded, and the average tree diameter for each sampling location was then computed.

Percent canopy and percent ground cover were estimated from photographs taken with a digital SLR camera. For canopy cover, a photograph was taken of the canopy directly above each pitfall trap with the lens at minimum zoom. For ground cover, a 0.5 m^2 quadrat was centered on each pitfall trap, with a photograph taken such that the quadrat filled the majority of the image. Scoring canopy and ground cover involved electronically overlaying a 10 $\times$ 10 grid of points on each photograph. This array of points was centered on each canopy cover photograph, and the number of points directly above canopy was recorded as percent canopy cover. For ground cover photographs, the grid of points had its scale, perspective, and depth adjusted so that it fit the 0.5 m^2 quadrat, and then the number of points for each of the following categories was recorded as percentages of those categories: bare soil, dead wood, leaf litter, woody plants, herbaceous plants, and grasses. An average percentage of canopy cover and an average percentage of the ground cover categories were calculated for each site.

Soil moisture was measured in centibars of soil suction with a Quickdraw Soil moisture Probe Series 2900 F1 (Soilmoisture Equipment Corp., California) at points 0.5 m above and below each pitfall trap. The tensiometer of the probe was pushed into the soil to a depth of 5 cm, and eight soil moisture readings were averaged for each sample site.

Vegetative structure was measured using a 3 m long rod (2.54 cm diameter PVC pipe) marked in 20 cm intervals (15 total intervals). Measurements were taken at 28 points at each sample site along four linear transects (seven points each spaced 2 m apart) perpendicular to and bisected by the pitfall trap transect. The four transects were each separated by 5 m. The number of grasses, herbaceous plants, shrubs (DBH: 0.5–2.5 cm), and trees (DBH: >2.5 cm) contacting each interval was recorded. From these data, a height index (Gibson et al. 1987) was computed for each vegetation type at each sample site:

$$\text{Height index} = \sum_{i=1}^{N} h_i n_i / \sum_{i=1}^{N} n_i$$

where N is the number of height classes (15 classes); h_i the midpoint of the height of the ith height class (e.g., 10, 30, 50 cm, etc.); and n_i the number of vegetation contacts in the ith class.

Statistical analyses

To compare the composition of carabid species assemblages from each sample site, k-means clustering (function cascadeKM in Vegan; Oksanen et al. 2012) was performed with R 2.15.2 (R Core Team 2012). Because this technique uses Euclidean distances to cluster points, which is not appropriate for raw species counts, Carabidae data were $\ln(x + 1)$ transformed (Legendre and Legendre 2012). The optimum number of k-means clusters suggested by the standardized and transformed carabid abundance data was identified using Hartigan and Wong's (1979) algorithm with k ranging from 2 to 30. The Calinski–Harabasz criterion (Caliński and Harabasz 1974) was used to select the optimum partition. Using this optimum partition, k-means clustering was performed again in order to identify the sample sites that formed each cluster, with 1,000 maximum iterations and 10,000 random starting sets (function k means in Stats; R Core Team 2012).

Nonmetric multidimensional scaling (NMDS) (function metaMDS in Vegan; Oksanen et al. 2012) was performed with R 2.15.2 (R Core Team 2012) to visualize the clusters. NMDS has several advantages: (1) it does not rely on a dissimilarity matrix of Euclidean distances; but instead, can utilize any distance measure including Bray–Curtis; (2) data are not assumed to have a multivariate normal distribution; however, any reduction in the asymmetry of the data (e.g., $\ln(x + 1)$ transformation) aids in making patterns more apparent; (3) a linear relation between the variables and underlying gradients is not assumed (Legendre and Legendre 2012). Sample sites were ordinated from a Bray–Curtis dissimilarity matrix (Bray and Curtis 1957) of the Carabidae data; the Bray–Curtis distance metric was chosen because of its robustness and ecological interpretability (Faith et al. 1987). Using 1,000 random starts, the final ordination was produced in three dimensions rather than two because of the substantial reduction in the lack of fit.

Permutational multivariate analyses of variance (permanova) (function adonis in Vegan; Oksanen et al. 2012) were performed with R 2.15.2 (R Core Team 2012) to test the significance of each cluster and to test the significance of the a priori land unit classifications. For all tests, the data were permuted 1,000 times. For the clusters, five tests were conducted, with each cluster tested individually to assess whether it was significantly different from all the other clusters. Critical p values were bonferroni corrected (Bonferroni 1935; Dunn 1961). For the a priori land unit classifications, six tests were performed in the same manner as for the clusters.

The environmental parameters were prepared for analysis by removing parameters with greater than 75 % zeroes from analyses; only the percent of dead wood ground cover was removed. The 14 environmental parameters that were included in analyses were the following: tree density, mean tree diameter, mean leaf litter depth, mean soil moisture, mean percent canopy cover, mean percent ground cover (bare soil, leaf litter, woody plants, herbaceous plants, and grasses), and vegetative structure (height indices for grasses, herbaceous plants, shrubs, and trees). The parameters were z score normalized because they were measured in different units.

To reduce the number of environmental parameters, the Vegan function bioenv (Oksanen et al. 2012) for R 2.15.2 (R Core Team 2012) was used. This function finds the subset of environmental parameters whose Euclidean distances have the maximum (rank) correlation with the community dissimilarity matrix (Clarke and Ainsworth 1993). The Spearman's rank correlation assessed the correlative strength between the Euclidean distance matrix for each subset of the 14 environmental parameters and the Bray–Curtis distance matrix of the sample sites.

Constrained ordination was performed with a distance-based redundancy analysis (dbRDA) (Legendre and Anderson 1999; function capscale in Vegan; Oksanen et al. 2012) with R 2.15.2 (R Core Team 2012) to determine how much variation in the carabid species data could be explained by the environmental parameters. The Bray–Curtis dissimilarity matrix of the sample sites and both the full set of environmental parameters and the "best" subset of environmental parameters were used. Significance of the models and of the axes was tested using permanovas with 1,000 permutations.

Diversity indices

Three indices were used to estimate carabid beetle diversity for each cluster: species richness (S); exponential Shannon diversity index ($e^{H'}$) (Shannon and Weaver 1949; Jost 2006) which estimates the number of species present in a sample had all species been equally common (Whittaker 1972); and inverse Simpson's diversity index ($1/D$) (Simpson 1949; Magurran 1988) which is the reciprocal of the probability any two individuals randomly drawn from a community will be of the same species (Magurran 2004). Indices were calculated using raw Carabidae count data (1,000 randomizations without replacement) with EstimateS (Colwell 2013).

Statistical analyses were performed with SAS™ 9.3 software (SAS Institute Inc. 2011) to determine which means of the diversity indices were statistically different among clusters. Analysis of variance (ANOVA) for completely randomized designs (Ott and Longnecker 2001) and the Tukey–Kramer multiple comparison procedure (Tukey 1953; Kramer 1956) were used to assess species richness. For the exponential Shannon diversity index and inverse Simpson's diversity index, the residuals were not normally distributed, so a Kruskal–Wallis one-way ANOVA (Kruskal and Wallis 1952) was performed. Multiple comparisons were made via Mann–Whitney–Wilcoxon tests (Mann and Whitney 1947; Wilcoxon 1945, 1947) with bonferroni correction (Bonferroni 1935; Dunn 1961).

Using raw Carabidae count data (1,000 randomizations without replacement), sample-based rarefaction curves (Gotelli and Colwell 2001) plotting the expected number of species (S_{est}) against the number of individuals for each cluster were produced with EstimateS (Colwell 2013) to make direct comparisons of species richness (Magurran 2004). To determine if species richness at $n = 413$ individuals (the lowest specimen total from amongst the clusters) was statistically different between clusters, a Chi square goodness-of-fit test (Pearson 1900) for equal proportions was performed with SAS 9.3 software (SAS Institute Inc. 2011). Multiple comparisons were made via additional Chi square goodness-of-fit tests with bonferroni correction (Bonferroni 1935; Dunn 1961).

Indicator species

To determine which carabid species could serve as indicators for each cluster, indicator species analysis (Dufrêne and Legendre 1997; function indval in Labdsv; Roberts 2012) was performed with R 2.15.2 (R Core Team 2012). This technique calculates an indicator value ranging from 0 to 1 for each species within a site grouping; indicator values are maximized (=1) when individuals of a species are observed in all sites of only one site group. Because few species had abundances greater than 50 specimens, and many of these more abundantly collected species were generalists, a minimum abundance of 20 individuals for a species was arbitrarily chosen as a threshold for its inclusion in the analysis. Significant indicator species were identified with permutation tests (1,000 iterations).

Results

Specimen totals

A total of 3,859 carabid specimens belonging to 131 species from 48 genera were collected (Online Resource 1). By *k*-means cluster, 1,087 specimens were sampled from 4 disturbed sites, 450 specimens from 3 marsh sites, 448 specimens from 11 prairie sites, 728 specimens from 3 restoration sites, and 1,146 specimens from 10 savanna sites. The majority of species (63 %) were represented by less than ten specimens, and only seven species had captures greater than 100 individuals. The most collected species, *Calathus opaculus*, made up 14.24 % of the total specimens. The seven most collected species made up 60.16 % of the total catch and the 21 most collected species made up 80.87 % of the total catch.

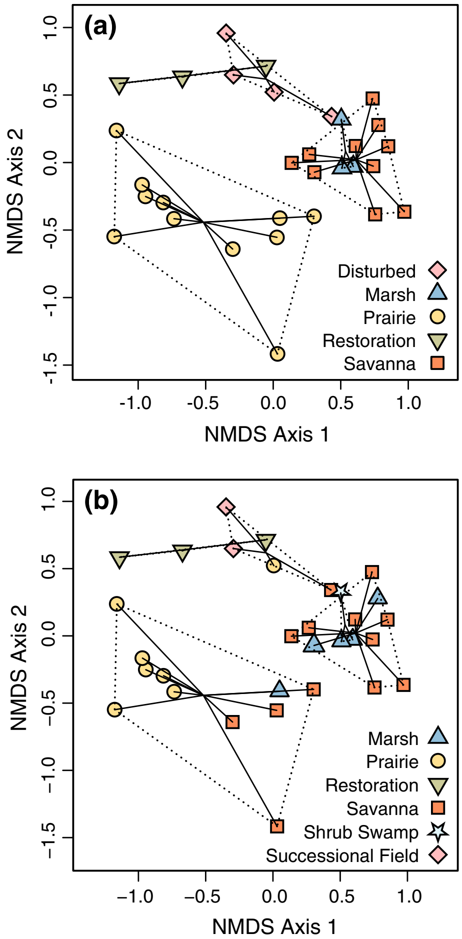
Clustering and ordination

Five ecologically meaningful clusters were identified: disturbed ($n = 4$), marsh ($n = 3$), prairie ($n = 11$), restoration ($n = 3$), and savanna ($n = 10$) (Fig. 1a). Cluster designations were based on the similarity of the sites to their a priori land unit classifications and on field observations. Overall, the sites' a priori classifications and their cluster identity partially agreed (Fig. 1b). The disturbed cluster included the two successional field sites as well as one prairie and one savanna site. The marsh cluster was comprised of the shrub swamp site and two sites initially categorized as marsh. The prairie cluster consisted of six prairie, four savanna, and one marsh site. All three restoration sites made up the restoration cluster. The savanna cluster was composed of eight sites that had initially been classified as savanna and two sites that had originally been classified as marsh.

Optimum environmental parameters

Mean litter depth, mean soil moisture, mean percent canopy cover, and mean percent grass ground cover formed the subset of environmental parameters with the highest overall correlation (Table 1). The model using these parameters in the dbRDA was globally significant (permanova, $p < 0.05$) (Fig. 2). The R^2 was 0.317, and the R^2_{adj} was 0.212. The constrained ordination included four canonical axes and 26 residual axes. The first two canonical axes were significant (permanova, $p < 0.05$). Axis one explained 4.47 % of the

Fig. 1 Nonmetric multidimensional scaling plots of the 31 sampling sites ordinated by each site's carabid species assemblage collected at the Braidwood Dunes and Savanna Nature Preserve from September 16–November 11, 2011 and March 10–September 22, 2012 (dimensions = 3, stress = 0.107, non-metric fit ($R^2 = 0.988$), linear fit ($R^2 = 0.916$)). *Dashed* and *solid lines* group the sample sites by *k*-means cluster. **a** The legend denotes which *k*-means cluster each site belongs to. Each cluster is significantly different (permanova with bonferroni correction, $p < 0.05$). **b** The legend denotes the a priori land unit classification of each site. *Dashed* and *solid lines* still group the sites by *k*-means cluster. Prairie, restoration, and savanna *k*-means clusters are significantly different (permanova with bonferroni correction, $p < 0.05$)



variance and axis two explained 1.12 % of the variance (percentages have been adjusted by R^2_{adj}). When compared to the full model using all 14 parameters, R^2_{adj} from the optimum subset model was not drastically different from the full model's R^2_{adj} (0.212 and 0.279, respectively) indicating that the reduced model explained nearly as much of the total variance as the full model did.

Diversity

Carabid diversity measures were highest for the marsh and restoration clusters (Table 2). Species richness for the marsh and restoration clusters differed significantly from the disturbed, prairie, and savanna clusters (ANOVA with Tukey–Kramer test, $p < 0.05$). The exponential Shannon and inverse Simpson's diversity indices differed significantly among the five clusters (Kruskal–Wallis, $p < 0.05$). However, Mann–Whitney–Wilcoxon multiple comparisons tests with bonferroni correction failed to detect the source of significance for the two indices.

Table 1 Best fit environmental parameter models for each size of model ranging from 1 to 10 terms[a]

Environmental parameters	Spearman's rank correlation coefficient
%Canopy	0.4501
Soil moisture, %canopy	0.4810
Soil moisture, %canopy, %grass	0.4945
Litter depth, soil moisture, %canopy, %grass	**0.5067**
Litter depth, soil moisture, %canopy, %bare soil, %grass	0.4981
Tree diameter, litter depth, soil moisture, %canopy, %bare soil, %grass	0.4854
Tree diameter, litter depth, soil moisture, %canopy, %bare soil, %grass, shrub HI	0.4771
Tree diameter, litter depth, soil moisture, %canopy, %bare soil, %grass, grass HI, shrub HI	0.4573
Tree diameter, litter depth, soil moisture, %canopy, %bare soil, %woody, %grass, grass HI, shrub HI	0.4382
Tree diameter, litter depth, soil moisture, %canopy, %bare soil, %woody, %herb, %grass, grass HI, shrub HI	0.4220

Models were fit to the nonmetric multidimensional scaling ordination of carabid species assemblages collected at the Braidwood Dunes and Savanna Nature Preserve from September 16–November 11, 2011 and March 10–September 22, 2012. Model with the overall highest Spearman's rank correlation coefficient is in bold. Environmental parameters measured in July 2012

HI height index

[a] Adding additional terms did not improve the model

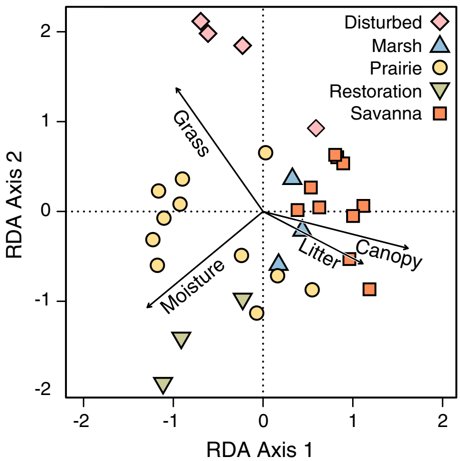


Fig. 2 Distance-based redundancy analysis correlation biplot of the sample sites shaded by *k*-means cluster and ordinated by their carabid species assemblages collected at the Braidwood Dunes and Savanna Nature Preserve from September 16–November 11, 2011 and March 10–September 22, 2012. The ordination is constrained by the optimum environmental parameters model that was fit to the nonmetric multidimensional scaling ordination of the carabid species assemblages. *Canopy* percentage of canopy cover, *grass* percentage of grass ground cover, *litter* mean leaf litter depth, *moisture* mean soil moisture

Table 2 Indices for mean (plus/minus 95 % CI) diversity of ground beetles captured at the Braidwood Dunes and Savanna Nature Preserve from September 16–November 11, 2011 and March 10–September 22, 2012 for each *k*-means cluster

Cluster	Richness	Exponential Shannon[a]	Inverse Simpson's[a]
Disturbed	19.75 ± 5.72^{B}	6.94 ± 4.32	4.50 ± 3.06
Marsh	31.67 ± 13.68^{A}	16.55 ± 3.15	10.30 ± 1.84
Prairie	11.18 ± 1.94^{B}	6.15 ± 2.23	4.39 ± 1.93
Restoration	30.33 ± 12.25^{A}	13.68 ± 2.33	9.40 ± 0.83
Savanna	16.30 ± 4.51^{B}	8.96 ± 2.82	5.87 ± 2.12

Means with different letters are significantly different (Tukey–Kramer test, $p < 0.05$)

[a] Overall significance (Kruskal–Wallis, $p < 0.05$)

The number of species at the point in the rarefaction curves (Fig. 3) where $n = 413$ individuals (the lowest number of specimens collected from amongst the clusters) differed significantly among the five clusters ($\chi^2 = 12.36$, 4 df, $p < 0.05$) with species richness for the disturbed cluster differing significantly from the marsh and prairie clusters ($p < 0.05$).

Indicator species

Of the 30 species where total abundance >20 (Online Resource 1), 21 significant ($p < 0.05$) indicator species were identified (Fig. 4). The most promising species for the disturbed cluster are *Poecilus lucublandus* and *Pterostichus permundus*. For the marsh cluster, *Diplocheila striatopunctata* serves as a useful indicator. *Amara exarata*, *Notiobia terminata*, and *Pterostichus mutus* are indicative of the restoration cluster. For the savanna cluster, *Platynus decentis* and *Synuchus impunctatus* are promising indicator species. No significant indicator species were identified for the prairie cluster.

Discussion

The land units classified by their soils and vegetative communities are effective spatial representations of the ground beetle assemblages in the Braidwood Dunes and Savanna Nature Preserve. Five ecologically meaningful clusters were identified across the Preserve: disturbed, marsh, prairie, restoration, and savanna. The majority of sites clustered according to the predefined classification system based on soils and vegetation. However, some of the marsh sites grouped with the savanna and prairie clusters, likely resulting from having to place the marsh site pitfall transects nearer the habitat edge to reduce the risk of flooding thus confounding the results because of the closer proximity of the adjacent savanna and prairie land units. Additionally, the prairie cluster included four savanna sites, perhaps due to habitat heterogeneity. Environmental parameter estimates varied widely for the sites initially classified as savanna; the savanna sites belonging to the prairie cluster were at the high end of the canopy openness and soil moisture spectrum. These sites may have been more prairie-like from the perspective of the ground beetles. The disturbed cluster consisted of sites that had experienced marked anthropogenic disturbance. These included the two successional field sites which had once been part of an agricultural field, as well as a prairie and savanna site that were immediately adjacent to land which had extensive vegetation removal just prior to the study. Only the restoration cluster was

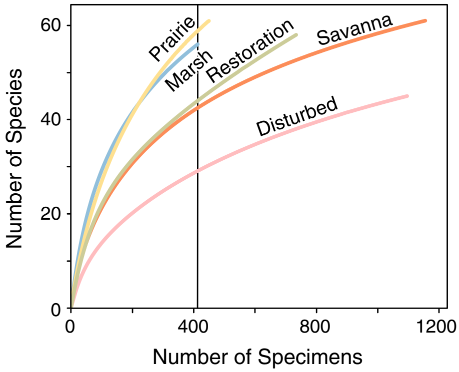


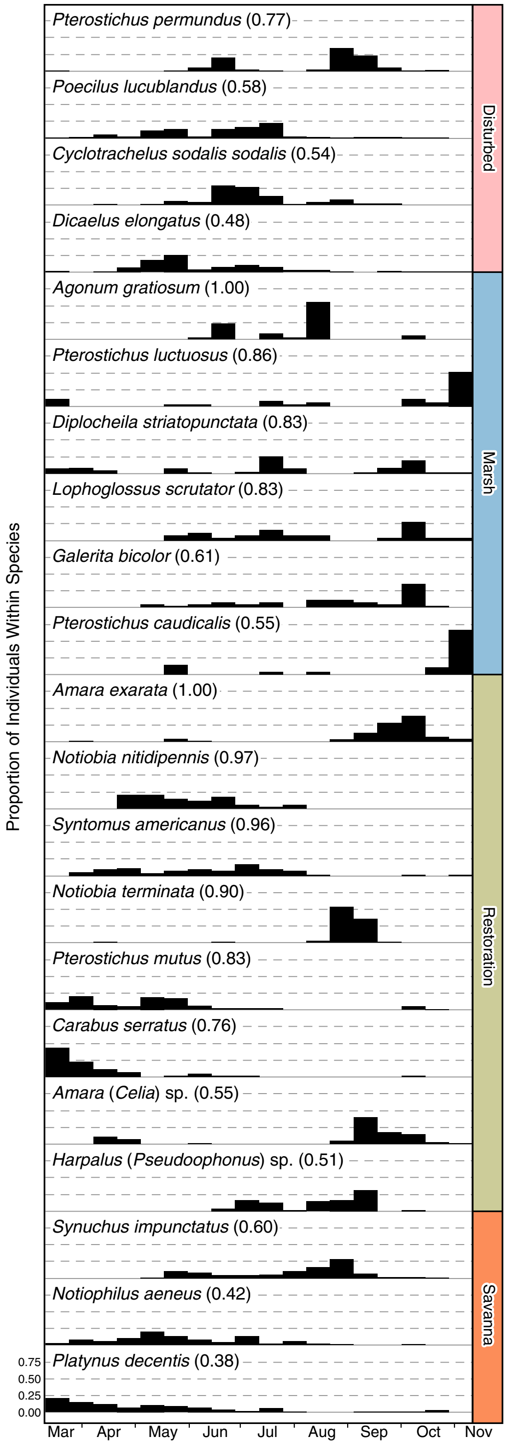
Fig. 3 Sample-based rarefaction curves for the five *k*-means clusters of the Braidwood Dunes and Savanna Nature Preserve. Carabid species richness for each cluster at $n = 413$ individuals (smallest catch size by cluster over a sampling period of September 16–November 11, 2011 and March 10–September 22, 2012) is indicated by the *vertical line*. Species richness for the disturbed cluster at $n = 413$ individuals is significantly lower than the species richness for the marsh and prairie clusters (multiple Chi squares with bonferroni correction, $p < 0.05$). Confidence intervals are removed for visual clarity

composed entirely of sites of one classification type. All the restoration sites formerly had been agricultural lands. Landscape reconstruction in the restoration sites began in 2005 with the removal of widespread Black Locust (*Robinia pseudoacacia*) thickets and has continued with re-sprout control (Conservation Design Forum 2010). In spite of the various exceptions discussed above, the initial land unit classification scheme reflected the carabid species assemblages reasonably well.

We examined ground beetle assemblages among habitat types (e.g., prairie, savanna, marsh) rather than within habitat types (e.g., wet-mesic sand savanna, mesic sand savanna, and dry sand savanna). At this broader scale of ecological resolution, several studies have succeeded in identifying distinct carabid species assemblages (Gardner 1991; Larsen et al. 2003; Luff et al. 1989; Willand et al. 2011). While ground beetle assemblages also have been utilized at finer scales to differentiate original and reconstructed tallgrass prairies (Larsen and Work 2003), forest stands of different successional ages (Koivula et al. 2002), and even microhabitats within a 100 × 120 m area of alluvial forest (Antvogel and Bonn 2001), results at too fine an ecological resolution may have limited practical application for land managers. Ultimately, a landscape classification system's effectiveness for predicting biodiversity depends upon its units being both easily identifiable to land managers and biologically relevant to a variety of species; with respect to carabid beetles, the classification system used in this study has found that equilibrium.

In contrast, a comparable study by Rykken et al. (1997) could find no significant link between carabid species distributions and an ecological classification system designed to represent biological diversity in the Green Mountain National Forest, Vermont. The classification system in their study ranged in scale from sites defined by landform, substrate, soils, drainage, and vegetation to sites demarcated by broad landscape characters such as climate, elevation, and geologic features. The authors suggested that the scale of habitat heterogeneity they examined was too fine to detect any patterns, and that at a broader scale, trends may become more apparent; all their sites had occurred within a northern hardwood forest habitat type.

Fig. 4 Carabidae indicator species for the *k*-means clusters of the Braidwood Dunes and Savanna Nature Preserve. Indicator values are in parentheses and can range from 0–1. Indicator values are maximized (= 1) when individuals of a species were collected in all the sites that form a single *k*-means cluster. Species are arranged in descending order of indicator value by cluster. The proportion of individuals within each species collected from September 16–November 11, 2011 and March 10–September 22, 2012 is plotted along a monthly axis. No indicator species were identified for the prairie *k*-means cluster



The correlation of soil moisture, leaf litter depth, the percentage of canopy cover, and the percentage of grass ground cover with the Carabidae dataset and the constrained ordination indicate that these measures reflect environmental parameters which influence the composition of ground beetle species assemblages within the Preserve. The degree of canopy cover at a site has been found by other studies to be an important factor explaining carabid species distributions; some species are even generalized as open-habitat species and forest species to reflect the habitats for which they are more specialized (Butterfield et al. 1995; Heliölä et al. 2001; Niemelä et al. 1993). Soil moisture also has been cited as a significant environmental characteristic shaping ground beetle distributions (Antvogel and Bonn 2001; Gardner 1991; Thiele 1977).

Environmental heterogeneity, particularly among marsh and prairie cluster sites, made interpretation of the dbRDA plot problematic. We expected soil moisture to have a positive effect on carabid species characterizing the marsh cluster rather than the restoration cluster. However, for the marsh sites, moisture measurements were taken along the marsh edges and after several of the marsh sites had already dried; the readings, which had been measured only once during the study, did not reflect the pronounced seasonal variation in marsh moisture. Additionally, 2012 was a year of abnormally low precipitation in Illinois; the entire state experienced extensive drought (Illinois Department of Natural Resources 2013).

The prairie cluster was characterized by generalist carabid species, ones that occurred across a wide spectrum of one or more environmental parameters. Ground beetle responses to grass ground cover ranged from positive to negative; while for soil moisture, responses were positive to none; and for canopy cover and litter depth, responses were negative to none. Alternatively, an unmeasured environmental parameter or combination of parameters may be affecting distributions of these carabid species. Biotic factors such as prey density can also play a significant role; *Pterostichus melanarius* forms aggregations in response to high slug density (Symondson et al. 1996), and the density of riparian carabid species is influenced by the availability of prey (Herring and Plachter 1997). Nevertheless, dbRDA did present clearer trends for the disturbed and savanna clusters. Species characterizing the disturbed cluster were positively influenced by grass ground cover, while canopy cover and litter depth had a positive effect upon the ground beetles characterizing the savanna cluster.

Rarefied species richness was lowest for the disturbed cluster, differing significantly from the marsh and prairie clusters. This did not follow the expected pattern. When a habitat experiences a physical disturbance, some or even all of its occupants are removed. Newly available niche spaces can then be filled by colonists and regenerating survivors; the initial increase in species richness is typically followed by a decline as the more competitive species come to dominate (Sousa 1984). Studies examining the effects of disturbance on carabid species had found that within 1–2 years following clear-cut harvesting, species richness was either maintained or increased when compared to undisturbed forest (Beaudry et al. 1997; Heliölä et al. 2001; Niemelä et al. 1993). Twenty years following a clear-cut harvest, species richness returns to undisturbed levels (Koivula et al. 2002; Niemelä et al. 1993).

The low rarefied species richness for the disturbed cluster likely was the result of a combination of factors. Two of the four disturbed sites were immediately adjacent to land which had been disturbed via tree and shrub removal and by spot-application of a broadleaf herbicide less than 1 year prior to the start of this study. It is possible that colonizing carabid species had yet to arrive. The other two disturbed sites were located in a successional field dominated by cool season grasses and woody plants that had been part of an agricultural field before the creation of the Preserve in 1981 (Conservation Design Forum 2010). By the time this study was conducted, any initial increase in species richness was no longer detectable for these two degraded sites.

Exponential Shannon and inverse Simpson's diversity indices significantly differed among the clusters, with values highest for the marsh cluster. This trend in species diversity could be due to the environmental complexity of the marsh sites. Both habitat heterogeneity (Tews et al. 2004) and temporal environmental variation (Chesson 2000) can act to increase species diversity by providing more niches and ways for species to access resources. The marsh sites varied by their degree of flooding, with some sites being submerged by several inches of water in the spring, while others had only been dampened. As the summer progressed, the sites dried at differing rates. Some were still moist at the end of the study, while others had dried completely. The affinity of ground beetles for moisture varies markedly by species (Thiele 1977), suggesting the wide moisture gradient of the marsh cluster may have driven the elevated species diversity.

The advantages to using carabid beetles as indicator species is that they can be efficiently sampled with pitfall trapping, they are sensitive to a variety of environmental factors, they have a well-studied taxonomy and ecology, and they occupy a broad geographic area in a wide range of habitats. Disadvantages are their seasonal variation in density and activity as well as the high number of generalist species (Rainio and Niemelä 2003). To reduce the impact of seasonal variation, sampling across the entire growing season is recommended (Niemelä et al. 2000). Alternatively, because the ecology of many species is well-known, sampling can be scheduled to match their seasonal phenology.

For the Braidwood Dunes and Savanna Nature Preserve, 21 carabid species displayed specificity to particular clusters. Of these, eight have the potential to be useful indicator species. *P. lucublandus* and *P. permundus* are both indicative of disturbed sites and were collected in high numbers ($n > 250$ for each). Previous studies have found these species to be common in disturbed areas. Relative abundance of *P. lucublandus* is high in tilled crop fields (Clark et al. 1997), following clear-cut forest harvesting (Duchesne et al. 1999), and in dairy pastures under intensive grazing (Byers et al. 2000). *P. permundus* is characteristic of crop fields (French et al. 2004; Gardiner et al. 2010). The indicator of the marsh cluster is *D. striatopunctata* ($n > 65$), a hygrophilous species found in moist habitats and near margins of water (El-Moursy and Ball 1959). The three indicators of the restoration cluster, *A. exarata* ($n > 70$), *N. terminata* ($n > 45$) and *P. mutus* ($n > 65$), may only be applicable for the Braidwood Dunes and Savanna Nature Preserve. *A. exarata*, while it occurs in a variety of open areas, is also common in disturbed habitats (Davidson et al. 2011). *P. mutus* is found in closed canopy forest (Liebherr and Mahar 1979) and in areas following clear-cut harvesting (Beaudry et al. 1997). The restoration sites in this study had no canopy and had not experienced recent disturbance. Indicator species for the restoration cluster should not be used to classify restoration areas outside the scope of this study. The savanna cluster's indicator species are two forest generalists: *P. decentis* ($n > 245$) and *S. impunctatus* ($n > 300$) (Epstein and Kulman 1990; Niemelä et al. 1992; Niemelä and Spence 1994; Beaudry et al. 1997). Their seasonal phenology was such that *P. decentis* was collected primarily in the spring and captures of *S. impunctatus* were higher in late summer/early fall, which provides a wide window over which these indicators can be utilized.

No carabid species were identified as being useful indicators for the prairie cluster. This may have been due to the environmental heterogeneity of the prairie sites. While some species were specific to the prairie cluster, they were only present in a few of the prairie sites. Additionally, none of these particular species were abundant enough to be considered useful indicators. The only species present in all of the prairie sites was *C. opaculus*, a generalist species collected from nearly all of the sites in this study.

The land unit classification system used to delineate the Braidwood Dunes and Savanna Nature Preserve by vegetation and soils is an effective spatial representation of Carabidae communities; ground beetle assemblages clustered into five ecologically meaningful groups including disturbed, marsh, prairie, restoration, and savanna. The classification system is both suitable to land managers and relevant to a diverse invertebrate group, supporting the use of environmental characteristics as indicators of biodiversity. Species richness and diversity were particularly high in the marsh sites, likely driven by heterogeneity in the presence and persistence of water. To protect diversity and avoid unintended losses, we must be cognizant of the effects that conservation efforts may have on marsh hydrology. Management planning should also consider the other important parameters influencing the ground beetle distributions across the Preserve: grass ground cover, canopy cover, soil moisture, and litter depth. Finally, eight carabid species were found to be potentially useful indicators of land unit type: *A. exarata*, *D. striatopunctata*, *N. terminata*, *P. decentis*, *P. lucublandus*, *P. mutus*, *P. permundus*, and *S. impunctatus*.

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