VEGETATIVE COMMUNITIES AS INDICATORS OF GROUND BEETLE (COLEOPTERA: CARABIDAE) DIVERSITY

BY

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THESIS

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ABSTRACT

Formally assessing biodiversity can be a daunting if not impossible task. Subsequently, specific taxa are often chosen as indicators of patterns of diversity as a whole. Mapping the locations of indicator taxa can inform conservation planning by identifying land units for management strategies. For this approach to be successful, though, land units must be effective spatial representations of the species assemblages present on the landscape. In this study, I 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. Beetles were sampled continuously via pitfall trapping across an entire active season from 2011–2012. Land unit characteristics were measured in July 2012. Nonmetric multidimensional scaling (NMDS) ordinated the land units by their carabid 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.

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CHAPTER 1: VEGETATIVE COMMUNITIES AS INDICATORS OF GROUND BEETLE (COLEOPTERA: CARABIDAE) DIVERSITY[1]

INTRODUCTION

The primary goal of conservation biology is the protection of biological diversity (Soulé 1985). An important part of conservation planning is measuring and mapping biodiversity (Margules and Pressey 2000). However, due to its complexity, the community structure and total diversity of an area cannot be measured and known completely. Thus, in order to plan conservation strategies, land managers rely upon indicators of biodiversity.

Biodiversity indicators serve to represent the unknown diversity and generally fall into two broad categories: (1) the use of species; and (2) the use of environmental features. With indicator species, the diversity of a set of taxa is used to infer the diversity of a separate group of taxa (McGeoch 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 (Favreau et al. 2006; Rodrigues and Brooks 2007).

A second approach is to use environmental characteristics as indicators of biodiversity. Environmental features can often be obtained remotely; and for many parts of the world, these are the only spatially consistent data available (Margules and Pressey 2000). 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 (e.g., the set of beetle species in savanna land units will be more similar to each other than to sets of beetle species from other land unit types.)

[1] This chapter has been prepared for publication in Biodiversity and Conservation following the journal's instructions for authors.

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 community structure of a diverse group of invertebrates—the ground beetles (Coleoptera: Carabidae). This family of beetles is well suited for biodiversity studies for several reasons. 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). Finally, it is easy and cost-effective to quantitatively collect data on carabids via 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.

I 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, I 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.

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) (Fig. 1). 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 (Phillippe et al. 2008; White 1978).

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 meters 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 meters (Digweed et al.

1995). From all the potential sample sites generated, 31 were randomly selected for the study (Fig. 1; Table 1). 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 (Conservation Design Forum 2010).

Carabid Sampling

A linear transect of four pitfall traps was set at each sample site (Fig. 2) with an inter-trap distance of 5 meters. Pitfalls consisted of two nested, 532 mL (18 oz.), plastic Hefty® drinking cups (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 cm x 15 cm x 2 cm) was supported with nails 2-3 cm above each pitfall to keep out rainwater and debris. To deter animal vandalism, chicken wire (61.0 cm x 61.0 cm; mesh: 2.5 cm) was laid over each trap and staked in place. Pitfalls were partially filled with approximately 150 mL of 20% ethylene glycol.

Pitfall traps were installed August 19, 2011. The initial disturbance from pitfall installation can affect the abundance of specimens collected (Greenslade 1973; Digweed et al. 1995), so sampling was delayed approximately one month. Pitfall traps were sampled roughly every two weeks from September 16, 2011 to November 11, 2011 and again from March 10, 2012 to September 22, 2012. The pitfall 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.

The raw abundance of each carabid species collected from each sample site over the course of the entire study was standardized to 1000 trap nights (number of traps x number of trap nights). This corrected for trap losses (i.e., flooding) and for any 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 (Fig. 2). 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 x 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 Soilmoisture Probe Series 2900 F1 (Soilmoisture Equipment Corp., California). The tensiometer of the probe was pushed into the soil to a depth of 5 cm. Eight soil moisture readings were averaged for each sample site (Fig. 2).

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 (Fig. 2). 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:

$$height\ index = \sum_{i=1}^{N} h_i n_i \Big/ \sum_{i=1}^{N} n_i$$

where N = 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). *K*-means clustering is a non-hierarchical clustering technique that partitions the points into *k* groups such that the total sum of squares of

the Euclidean distances from the points to their respective cluster centers is minimized (Legendre and Legendre 2012). Thus, sample sites with similar assemblages of carabid species cluster together. While the Euclidean distance is not appropriate for raw species counts, this issue can be circumvented by using a suitable transformation such as ln(x+1) (Legendre and Legendre 2012), as was done for this study. Firstly, the optimum number of *k*-means clusters suggested by the standardized and transformed carabid abundance data was identified by applying 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 1000 maximum iterations and 10,000 random starting sets (function kmeans in Stats; R Core Team 2012).

Multivariate analyses allowed the relationships between all dependent and all independent variables to be visualized and assessed simultaneously, with the plots of the variables represented in scatter diagrams with reduced dimensionality (e.g., two or three dimensions). Of the methods available, nonmetric multidimensional scaling (NMDS) (function metaMDS in Vegan; Oksanen et al. 2012) was performed with R 2.15.2 (R Core Team 2012). 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) created from the standardized, transformed carabid abundance data; the Bray-Curtis distance metric was chosen because of its robustness and ecological interpretability (Faith et al. 1987). The final ordination was produced in three dimensions from 1000 random starts.

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 *k*-means cluster and to test the significance of the *a priori* land unit classifications. Permanova is a nonparametric technique that calculates *p*-values from test statistics generated from rearrangements of the data, and thus does not need to conform to assumptions of multivariate normality (McArdle and Anderson 2001). For all tests, the data were permuted 1000 times. For the *k*-means clusters, 5 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, 6 tests were performed. All sample sites of the same land unit classification were grouped, and each group was tested individually to assess whether it was significantly different from all the other groups. Again, critical *p*-values were bonferroni corrected (Bonferroni 1935; Dunn 1961).

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 via 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 abundance data could be explained by the environmental parameters. This technique is similar to NMDS except that it allows the ordination of points to be influenced by a second set of variables (e.g., environmental parameters) such that the final ordination is maximally related to combinations of the variables from that second set (Legendre and Legendre 2012). The Bray-Curtis dissimilarity matrix of the standardized, transformed carabid abundance data 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 1000 permutations.

Diversity Indices

Six indices were used to estimate carabid beetle diversity for each *k*-means cluster:

(1) species richness (*S*);

(2) Fisher's alpha diversity index (Fisher et al. 1943) which approximates the number of species represented by a single individual (Magurran 2004);

(3) 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);

$$H' = -\sum p_i \ln p_i$$

where p_i is the proportion of individuals found in the *i*th species

(4) inverse Simpson's diversity index (1/*D*) (Simpson 1949; Magurran 1988). The Simpson's diversity index (*D*) gives the probability that any two individuals randomly drawn from a community will be of the same species. Diversity increases as its reciprocal (1/*D*) increases (Magurran 2004);

$$D = \sum p_i^2$$

where p_i is the proportion of individuals found in the *i*th species

(5) Shannon evenness (*J'*) (Pielou 1969, 1975) which is a measure of how equal the abundances of each species are. *J'* equals 1 when all species are equally abundant;

$$J' = H'/H_{\max} = H'/\ln S$$

(6) Simpson's evenness ($E_{1/D}$) (Magurran 2004) which is a measure of how equal the abundances of each species are. $E_{1/D}$ equals 1 when all species are equally abundant.

$$E_{1/D} = \frac{1/D}{S}$$

Indices 1-4 were calculated directly with EstimateS (Colwell 2013) for each of the 31 sample sites. Indices 5 and 6 were computed using Shannon diversity index and inverse Simpson's diversity index results from EstimateS (Colwell 2013). Raw carabid abundance data were randomized 1000 times without replacement. The mean and 95% confidence interval for the six indices were computed for each *k*-means cluster. The abundance of specimens (standardized by number of trap nights) and the mean abundance for the *k*-means clusters were also computed.

Statistical analyses were performed with SAS™ 9.3 software (SAS Institute Inc. 2011) to determine if the means of the diversity indices and of the abundance were statistically different among *k*-means clusters. Analysis of variance (ANOVA) for completely randomized designs (Ott and Longnecker 2001) and the Tukey-Kramer multiple comparison procedure (Kramer 1956; Tukey 1953) were used to assess the richness and Simpson's evenness

measures. For the Fisher's alpha, 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). The Shannon evenness and carabid abundance measures were heteroscedastic, so a Games and Howell test (Games and Howell 1976) was performed.

Sample-based species accumulation curves (Gotelli and Colwell 2001) were produced with EstimateS (Colwell 2013) to estimate the completeness of sampling (Colwell and Coddington 1994) across the entire study (31 sites x 18 sampling sessions). The expected number of species (S_{est}) (Colwell et al. 2004), first-order Jackknife richness estimator (Jack 1) (Burnham and Overton 1978, 1979; Heltshe and Forrester 1983), abundance coverage-based estimator of species richness (ACE) (Chao et al. 2000), Chao 1 richness estimator (Chao 1984), and bootstrap richness estimator (Smith and van Belle 1984) were computed with 1000 randomizations of the carabid abundance data 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 *k*-means cluster were produced with EstimateS (Colwell 2013) to make direct comparisons of species richness (Magurran 2004). Carabid abundance data were randomized 1000 times without replacement. To determine if species richness at n = 413 individuals (the lowest abundance collected from amongst the *k*-means 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 *k*-means 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 0–1 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. Only species with a minimum abundance of 20 individuals were included in the analysis. Significant indicator species were identified with permutation tests (1000 iterations) which determined the probability of observing a given indicator value.

RESULTS

Abundance

A total of 3859 carabid specimens belonging to 131 species from 48 genera were collected (Table 2; Table 3). The majority of species (63%) were represented by less than 10 specimens, and only seven species had abundances greater than 100 individuals (Fig. 3). The most abundant species, *Calathus opaculus*, made up 14.24% of the total specimens. The seven most abundant species made up 60.16% of the total catch and the twenty-one most abundant species made up 80.87% of the total catch.

Clustering and Ordination

K-means clustering optimally partitioned the 31 sample sites into 5 clusters of sizes 11, 10, 4, 3, and 3 (Table 2). These clusters were visualized with NMDS (K=3, stress=0.107, non-metric fit (R^2=0.988), linear fit (R^2=0.916)) (Fig. 4a–d). A stress of 10% is considered to have a "fair" goodness of fit (Kruskal 1964). Based on their similarity to the *a priori* land unit classifications and on field observations at the sample sites, I named the five ecologically meaningful clusters: Disturbed, Marsh, Prairie, Restoration, and Savanna. 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. 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. Permanovas detected significant differences between each of the five *k*-means clusters ($p < 0.05$) (Fig. 4a–c). For the *a priori* land unit classification types, only the prairie, savanna, and restoration habitats were significantly different ($p < 0.05$) (Fig. 4d) from the others.

Optimum Environmental Parameters

Of the 14 environmental parameters, 16,383 possible subsets were evaluated. Subsets ranged in size from 1–14 parameters. For each of the 14 subset sizes, the set of parameters with the strongest correlation was found (Table 4). The subset with the strongest overall correlation (correlation=0.5067) included the following four parameters: mean litter depth, mean soil moisture, mean percent canopy cover, and mean percent grass ground cover (Table 4).

Distance-based redundancy analyses (dbRDA) were conducted using the full model of all 14 environmental parameters as well as the reduced model using the optimum subset of four parameters. The model which included all of the 14 environmental parameters was globally significant (permanova, $p < 0.05$). The R^2 was 0.615, and the R^2_{adj} was 0.279. The constrained ordination included 14 canonical axes and 16 residual axes. The first four canonical axes were significant (permanova, $p < 0.05$). Axis 1 explained 6.65% of the total variance, axis 2 explained 2.25% of the total variance, axis 3 explained 1.76% of the total variance, and axis 4 explained 1.40% of the total variance (percentages have been adjusted by R^2_{adj}). Several environmental parameters had extremely high (>100) variance inflation factors (VIF) indicating that some of the parameters were strongly correlated with each other.

The reduced model using the optimum subset of environmental parameters (mean litter depth, mean soil moisture, mean percent canopy cover, and mean percent grass ground cover) was globally significant (permanova, $p < 0.05$) (Fig. 5). The R^2 was 0.317, and the R^2_{adj} was 0.212. The constrained ordination included 4 canonical axes and 26 residual axes. The first two canonical axes were significant (permanova, $p < 0.05$). Axis 1 explained 4.47% of the variance and axis 2 explained 1.12% of the variance (percentages have been adjusted by R^2_{adj}). R^2_{adj} from the optimum subset model was not drastically different from the full model's R^2_{adj} indicating that the reduced model explained nearly as much of the total variance as the full model did. Also, the VIFs of the optimum subset were much lower (all < 10).

Diversity

Carabid diversity measures, except Simpson's evenness, were highest for the Marsh and Restoration clusters (Table 5). Species richness for the Marsh and Restoration clusters differed significantly from the Disturbed, Prairie, and Savanna clusters (ANOVA with Tukey-Kramer test, $p < 0.05$). Fisher's alpha diversity index did not differ significantly among the five clusters. The exponential Shannon and inverse Simpson's diversity indices differed significantly among the five clusters (Kruskal-Wallis, $p < 0.05$). However, the multiple comparisons tests with bonferroni correction failed to detect the source of significance for the two indices. Neither Shannon evenness nor Simpson's evenness differed significantly among the clusters. Mean carabid abundances for the Disturbed and Restoration clusters differed significantly from the Savanna and Prairie clusters (Games and Howell test, $p < 0.05$).

Species accumulation curves failed to reach an asymptote (Fig. 6), indicating that additional species would likely be collected if further sampling had been conducted. The number of species at the point in the rarefaction curves (Fig. 7) where n = 413 individuals (the lowest abundance collected from amongst the *k*-means clusters) differed significantly among the five clusters (chi-square = 12.36, 4 df, $p < 0.05$). Species richness for the Disturbed cluster differed significantly from the Marsh and Prairie clusters ($p < 0.05$).

Indicator Species

Of the 30 species where total abundance > 20 (see Table 4), 21 significant ($p < 0.05$) indicator species were identified (Fig. 8). Four species were found for the Disturbed cluster: *Cyclotrachelus sodalis sodalis*, *Dicaelus elongatus*, *Poecilus lucublandus*, and *Pterostichus permundus*; six species for the Marsh cluster: *Agonum gratiosum*, *Diplocheila striatopunctata*, *Galerita bicolor*, *Lophoglossus scrutator*, *Pterostichus caudicalis*, and *Pterostichus luctuosus*; eight species for the Restoration cluster: *Amara exarata*, *Amara* (*Celia*) sp., *Carabus serratus*, *Harpalus* (*Pseudoophonus*) sp., *Notiobia nitidipennis*, *Notiobia terminata*, *Pterostichus mutus*, and *Syntomus americanus*; and three species for the Savanna cluster: *Notiophilus aeneus*, *Platynus decentis*, and *Synuchus impunctatus*. No significant indicator species were identified for the Prairie cluster.

DISCUSSION

Diversity

Rarefied species richness was lowest for the Disturbed cluster, differing significantly from the Marsh and Prairie clusters (Fig. 7). 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 carabids 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 one year prior to the start of my 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 my 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 (Kruskal-Wallis, $p < 0.05$). 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.

Species accumulation curves failed to reach an asymptote (Fig. 6), indicating additional species would likely have been collected if further pitfall trapping had been conducted. However, this study likely recorded the majority of species collectable via pitfalls. Adult carabids vary in their annual rhythms of activity with many species categorized generally as spring or autumn breeders (Thiele 1977). As not all species were equally active over the course of the year, I continued to collect additional species even towards the end of the study. Had this study continued into the following year, carabid seasonality would have been largely accounted for, and the species accumulation curves would have been more asymptotic.

Clusters

The land units classified by their soils and vegetative communities are effective spatial representations of the ground beetle assemblages in 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 my study. Only the Restoration cluster was 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.

I 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 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 x 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 carabids, the classification system used in my study has found that equilibrium.

In contrast, a comparable study by Rykken et al. (1997) could find no significant link between carabid 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.

Environmental Parameters

The correlation of soil moisture, leaf litter depth, the percentage of canopy cover, and the percentage of grass ground cover with the carabid 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 distributions; some species are even generalized as open-habitat species and forest species to reflect their affinities (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 & Bonn 2001; Gardner 1991; Thiele 1977).

Environmental heterogeneity, particularly among Marsh and Prairie cluster sites, made interpretation of the dbRDA plot problematic. I 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.

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. 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.

Indicator Species

The Braidwood Dunes and Savanna Nature Preserve study demonstrates the affinity of certain carabid species to environmentally similar sample sites. Within the Preserve, 21 ground beetle species were found predominantly in single ecological clusters, with species specific to Disturbed, Marsh, Restoration, and Savanna clusters. Represented by at least 20 individuals, these species should be sufficiently abundant to be useful indicators.

For land managers seeking to classify land unit types, these species can potentially serve as indicators of the habitats they preferentially reside in. Additionally, it should be possible to assess the success of restoration efforts using these carabid indicator species. For example, one might expect to observe a transition from Disturbed and/or Restoration indicators to Savanna indicators as savanna habitat becomes more established; the presence of the appropriate ground beetle species could be used to determine whether the target habitat state has been reached. However, additional work is needed. When using indicator species, care should be taken to coordinate collection efforts with the species' activity patterns, as the abundance of each indicator species varied seasonally (Fig. 8).

No carabids 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 *Calathus opaculus*, a generalist species collected from nearly all of the sites in this study.

CONCLUSIONS

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 carabid 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, 21 carabid species were found to be useful in classifying land units; with further study these species may serve to evaluate the efficacy of restoration practices.

FIGURES AND TABLES

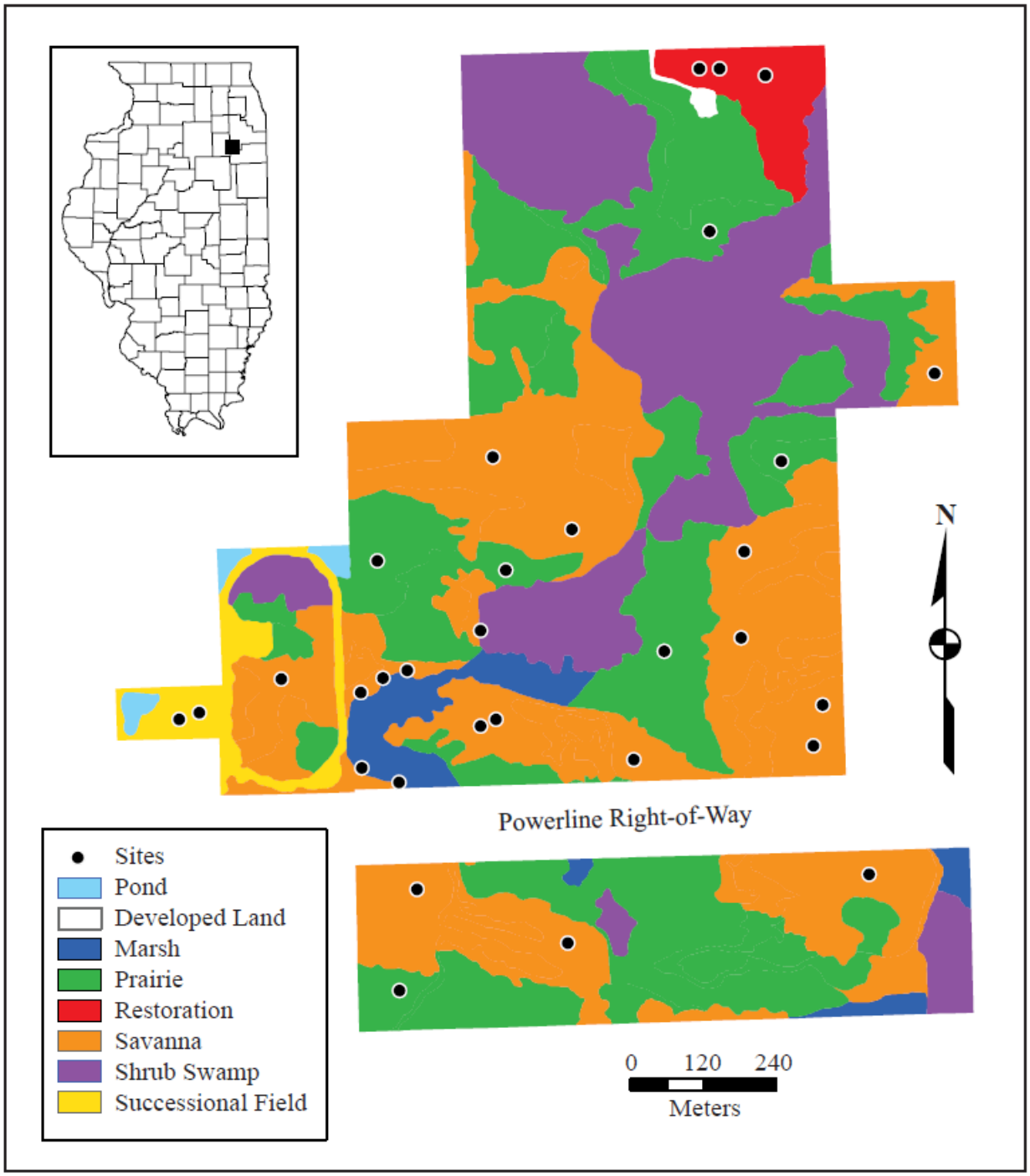

Fig. 1 Locations of the 31 sample sites in relation to the *a priori* vegetation-based classification within Braidwood Dunes and Savanna Nature Preserve. Inset map: approximate location of Braidwood Dunes and Savanna Nature Preserve within Illinois, USA

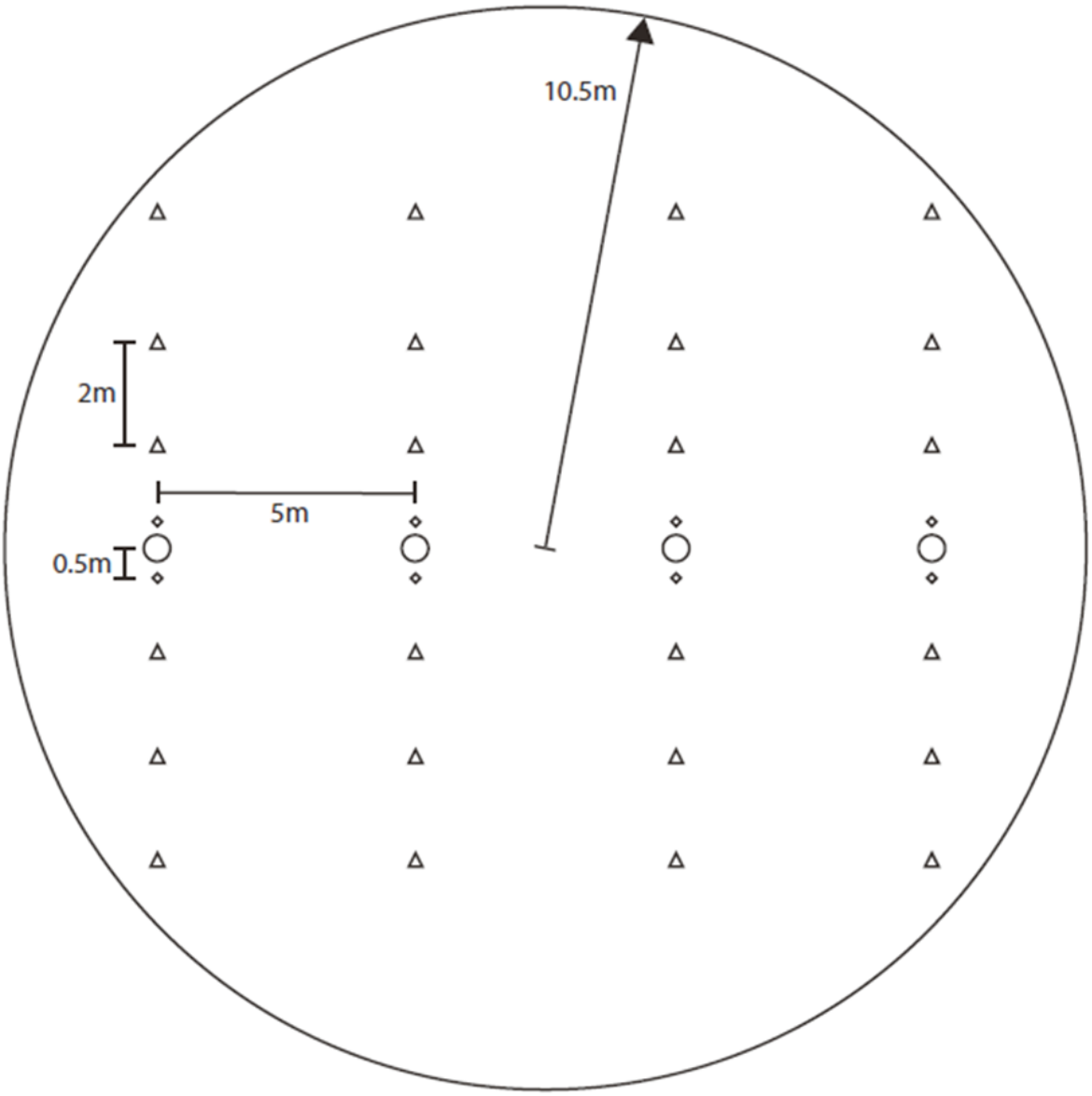

Fig. 2 Pitfall trap transect and locations of where the environmental parameters were measured. O: pitfall trap; Δ: vegetative structure and leaf litter measurements; ◊: soil moisture measurements

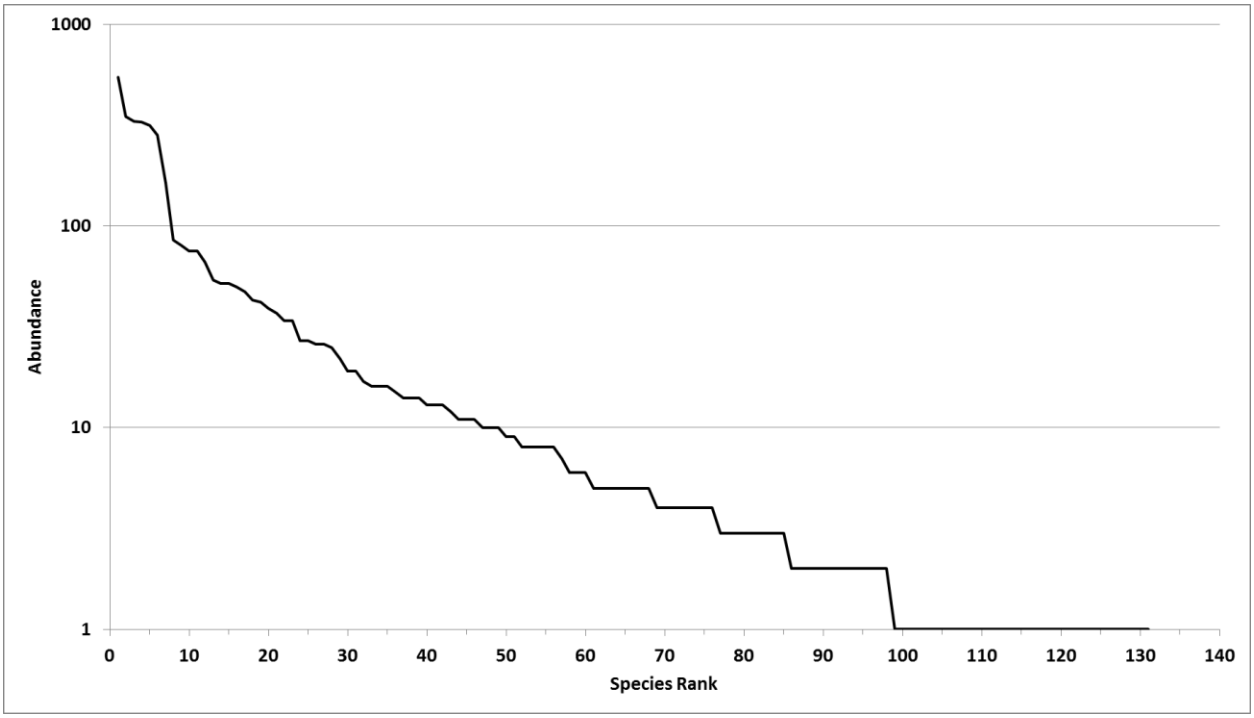

Fig. 3 Rank abundance diagram plotting carabid abundance measured on a log scale against species rank. Carabid species ranked in descending order of abundance

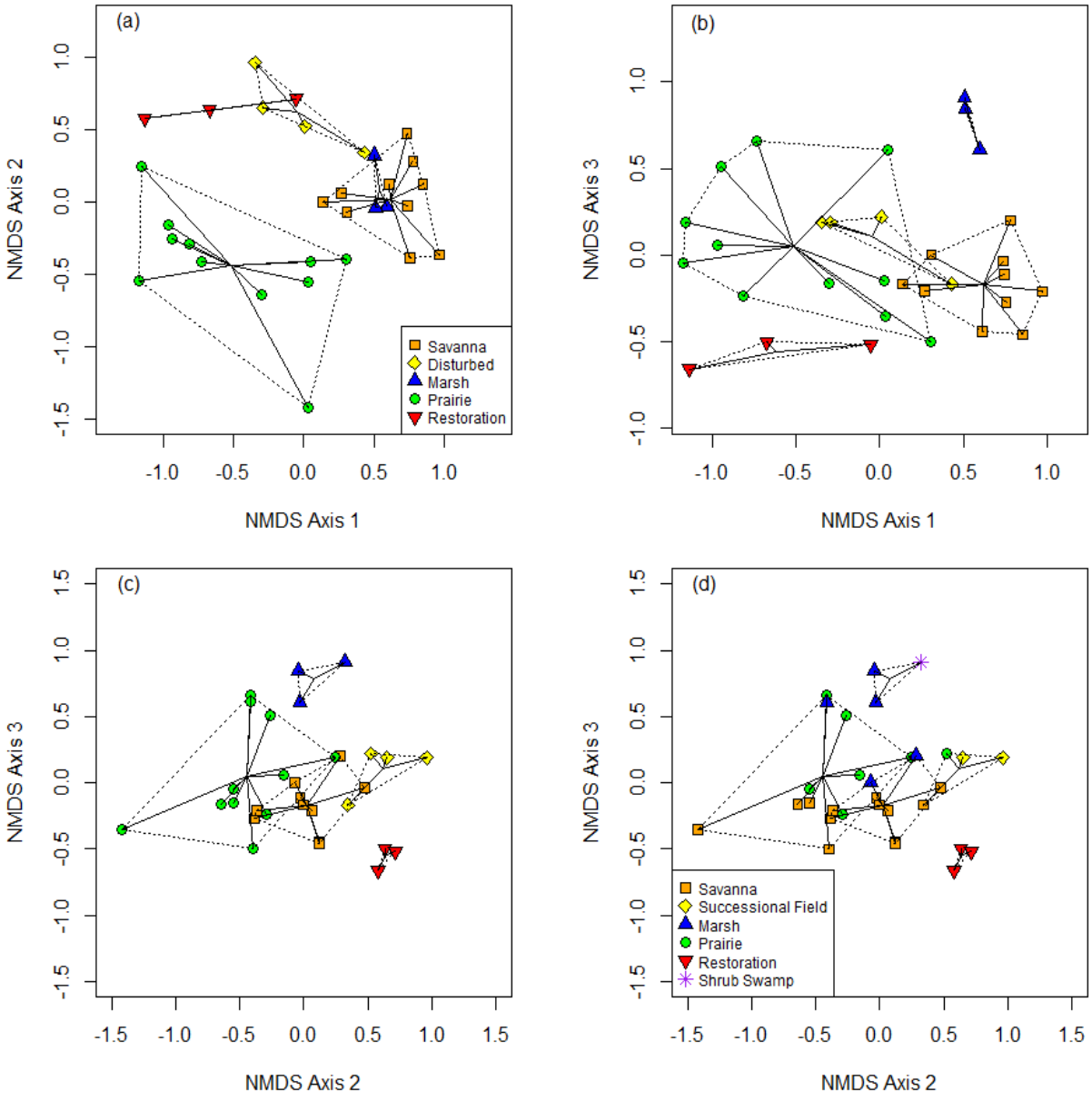

Fig. 4 Nonmetric multidimensional scaling (NMDS) plots of the sampling locations ordinated by the carabid assemblages and grouped according to *k*-means cluster. The ordination is displayed along (a) axis 1 and 2, (b) axis 1 and 3, and (c) axis 2 and 3. (d) The clusters and their correspondence to the *a priori* land unit classification types is displayed along axis 2 and 3

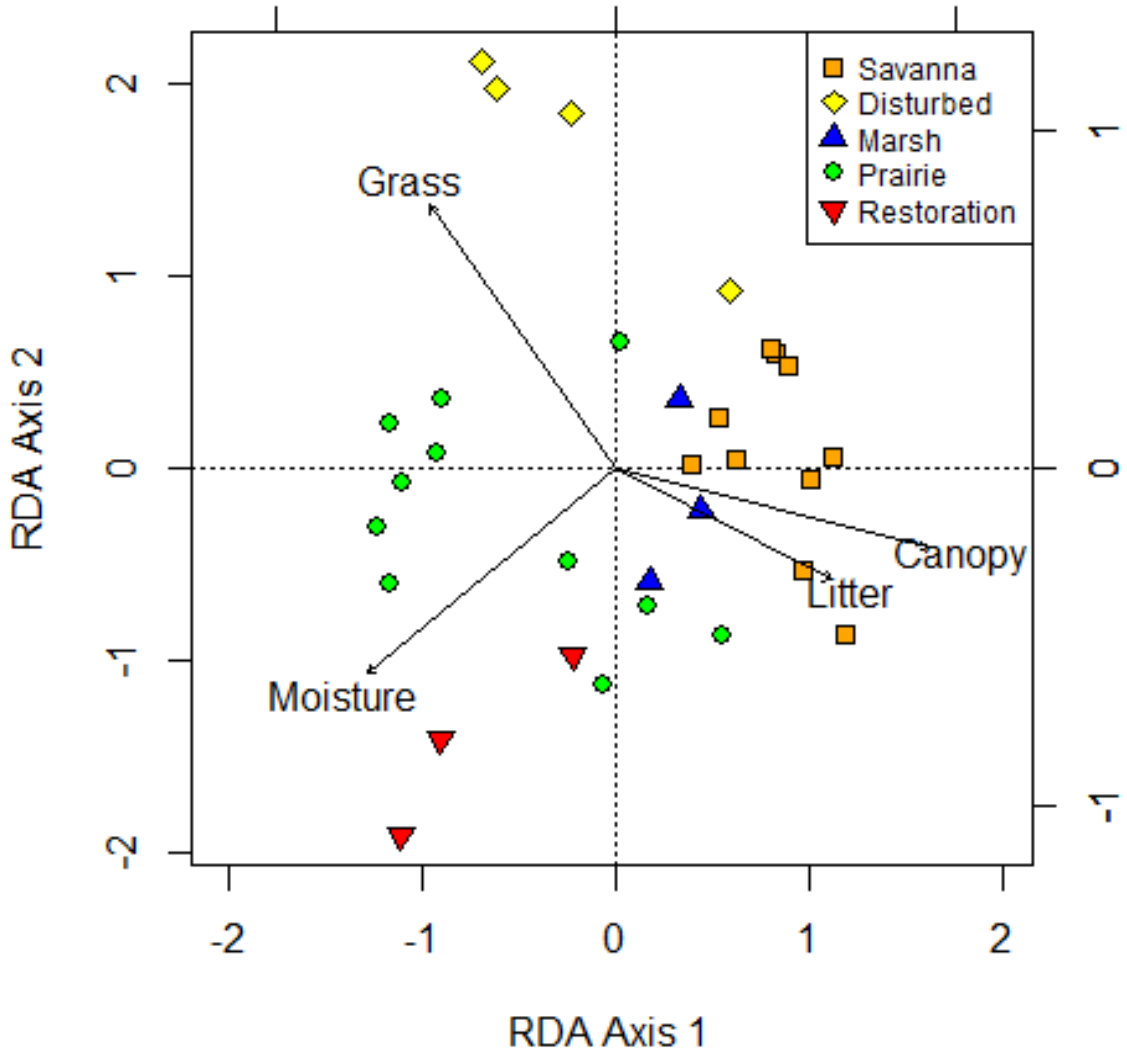

Fig. 5 Distance-based redundancy analysis (dbRDA) correlation biplot showing the relations between the sampling locations shaded by *k*-means cluster and ordinated by the carabid assemblages as constrained by the optimum subset of environmental parameters. Canopy = percentage of canopy cover; Grass = percentage of grass ground cover; Litter = mean leaf litter depth; Moisture = mean soil moisture

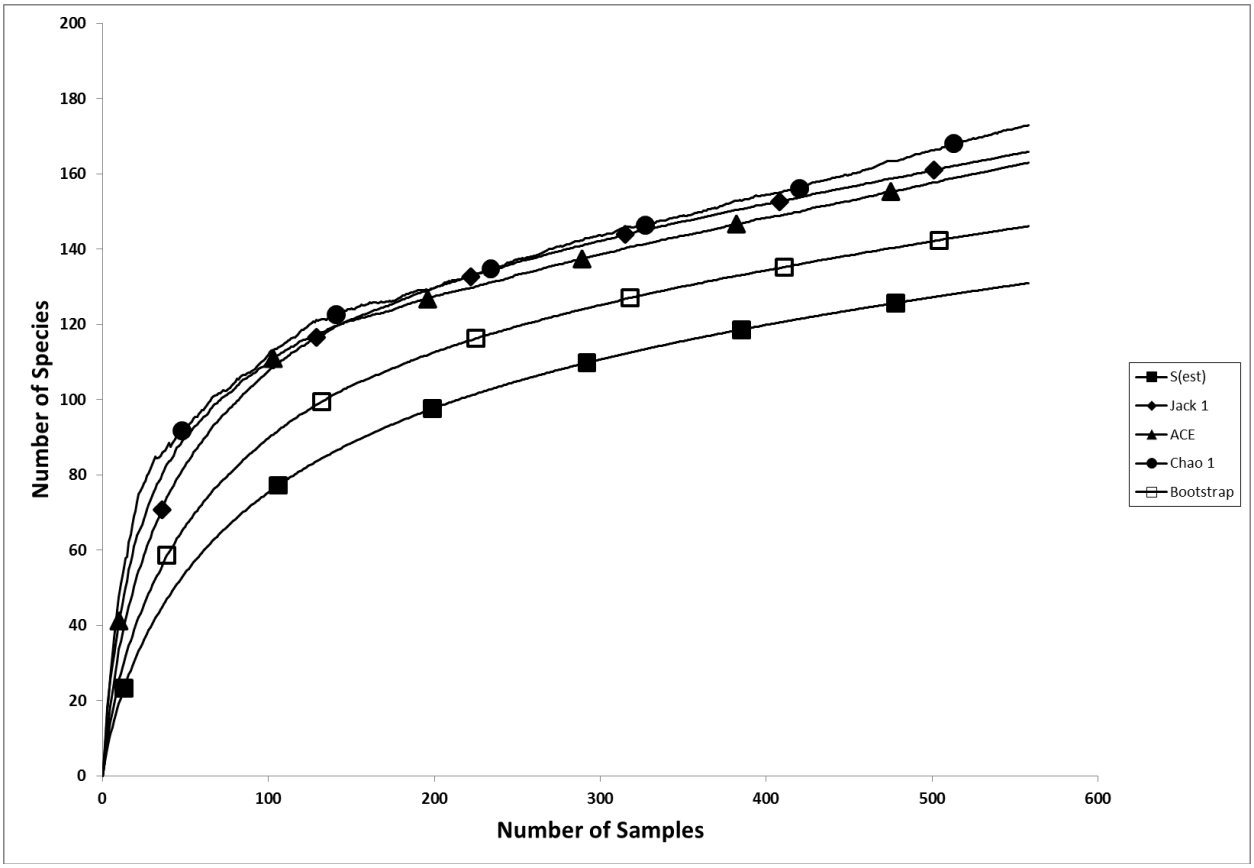

Fig. 6 Sample-based species accumulation curves for the entire study (31 sampling sites x 18 sampling sessions). S(est) = expected number of species; Jack 1 = first-order Jackknife richness estimator; ACE = abundance coverage-based estimator of species richness; Chao 1 = classic Chao 1 richness estimator; Bootstrap = bootstrap richness estimator

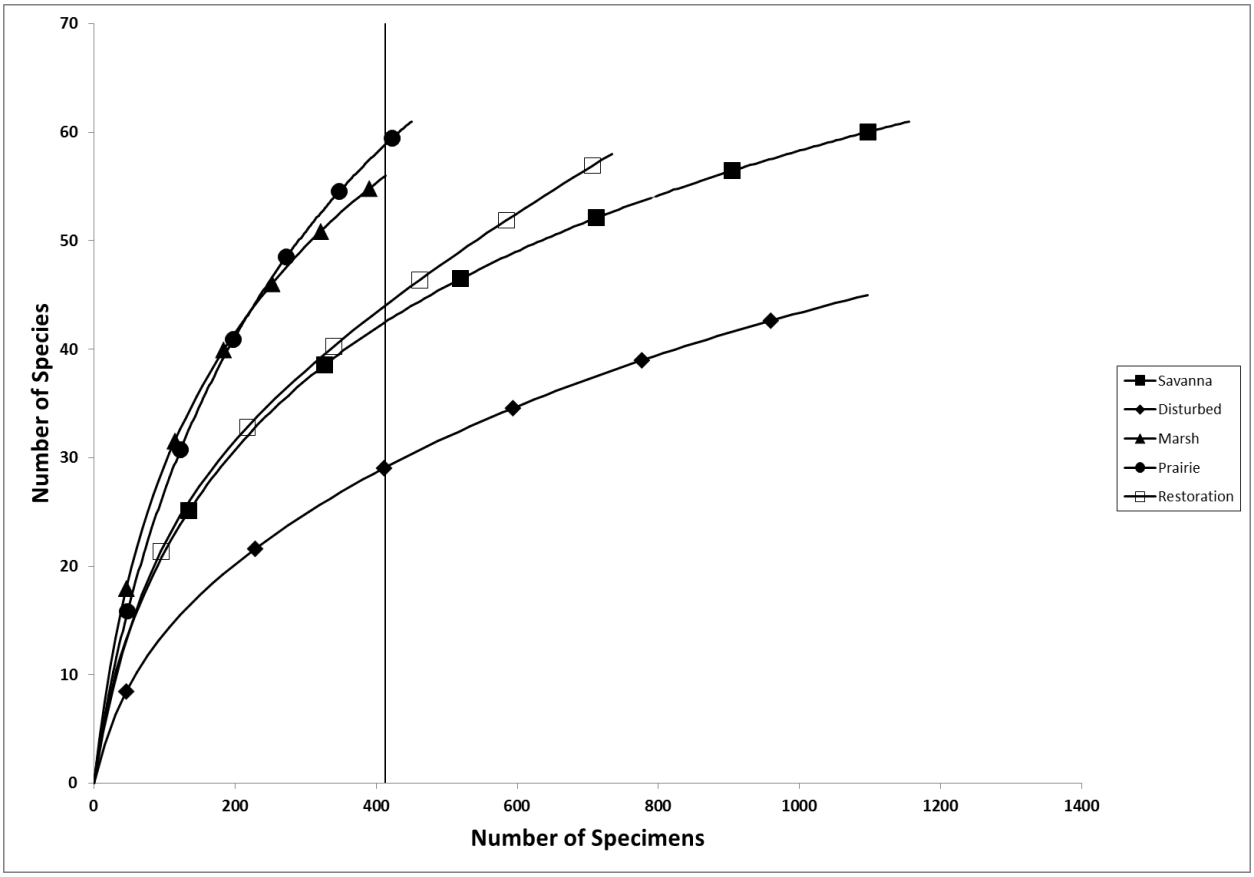

Fig. 7 Sample-based rarefaction curves for the five *k*-means clusters. Species richness for each cluster at n = 413 individuals is indicated by the vertical line

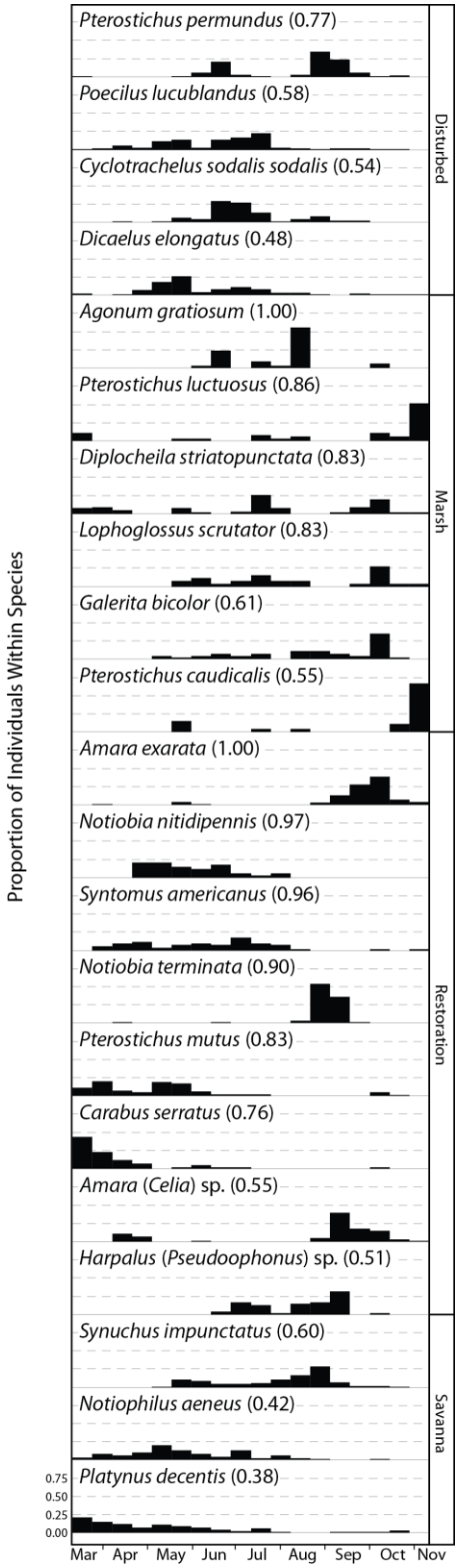

Fig. 8 The 21 indicator species with indicator values in parentheses. The proportion of individuals within each species collected at each of the 18 sampling sessions is plotted along a monthly axis. Species are in descending order of indicator value by *k*-means cluster

Table 1 Number (*n*) of sample sites, soil type, and characteristic vegetation for six land unit classification types (Conservation Design Forum 2010)

Land Unit Classification	*n*	Soil	Characteristic Vegetation	
			Species	Common Name
Savanna	13	Sandy, well drained to poorly drained sandy loam	*Andropogon scoparius*	Little Bluestem Grass
			Carex pensylvanica	Common Oak Sedge
			Quercus alba	White Oak
			Quercus velutina	Black Oak
			Salix humilis	Prairie Willow
Prairie	7	Sandy, well drained to poorly drained sandy loam	*Aletris farinose*	Colic Root
			Andropogon gerardii	Big Bluestem Grass
			Andropogon scoparius	Little Bluestem Grass
			Calamagrostis canadensis	Blue Joint Grass
			Helianthus mollis	Downy Sunflower
			Koeleria cristata	June Grass
			Opuntia humifusa	Eastern Prickly Pear
			Osmunda regalis	Royal Fern
			Parthenium integrifolium	Wild Quinine
			Pycnanthemum virginianum	Common Mountain Mint
			Scleria triglomerata	Tall Nut Rush
			Sorghastrum nutans	Indian Grass
			Viola lanceolata	Lance-Leaved Violet
Marsh	5	Fine sandy loam, standing water for part of the year	*Alisma subcordatum*	Common Water Plantain
			Carex lacustris	Common Lake Sedge
			Polygonum amphibium	Water Knotweed
			Polygonum coccineum	Water Heartsease
			Proserpinaca palustris	Mermaid Weed
			Scirpus fluviatilis	River Bulrush
			Typha latifolia	Broad-Leaved Cattail
Restoration	3	Sandy, well drained	*Carex pensylvanica*	Common Oak Sedge
			Phytolacca americana	Pokeweed
			Rubus allegheniensis	Common Blackberry
			Solidago altissima	Tall Goldenrod
Successional Field	2	Sandy, generally well drained	*Coronilla varia*	Crown Vetch
			Ligustrum vulgare	Common Privet
			Phragmites australis	Common Reed
			Solidago canadensis	Canada Goldenrod
Shrub Swamp	1	Fine sandy loam, standing water for part of the year	*Cephalanthus occidentalis*	Buttonbush
			Salix discolor	Pussy Willow
			Salix interior	Sandbar Willow

Table 2 *k*-means cluster size (number of sample sites), carabid abundance standardized by number of trap nights, mean standardized carabid abundance, and raw number of carabid genera and species for each *k*-means cluster

k-means cluster	Size	Abundance	Mean Abundance	Genera	Species
Savanna	10	1145.83	114.58	37	61
Disturbed	4	1087.30	271.83	29	45
Marsh	3	450.00	150.00	29	56
Prairie	11	447.53	40.68	34	61
Restoration	3	728.17	242.72	32	58
Total	31	3858.83	163.96	48	131

Table 3 Carabid species abundances (corrected by number of trap-nights) by *k*-means cluster

		Cluster				
Species	Total	Disturbed	Marsh	Prairie	Restoration	Savanna
Acupalpus canadensis	3.17		1.19	1.98		
Acupalpus hydropicus	8.93			1.98		6.94
Agonoleptus conjunctus	5.95			4.96	0.99	
Agonoleptus thoracicus	5.95	0.99		0.99	3.97	
Agonum gratiosum	35.32		35.32			
Agonum palustre	4.96	3.97			0.99	
Agonum albicrus	1.19		1.19			
Agonum melanarium	11.51		5.56	1.98		3.97
Agonum punctiforme	1.19		1.19			
Agonum (Olisares) sp.	0.99					0.99
Amara aenea	2.98	0.99		1.98		
Amara familiaris	7.94	1.98		2.98	1.98	0.99
Amara lunicollis	2.98	2.98				
Amara (Amara) sp. 1	14.88				14.88	
Amara (Amara) sp. 2	15.87			2.98	12.90	
Amara exarata	74.40				74.40	
Amara (Celia) sp.	74.56	28.77		14.04	31.75	
Amara quenseli quenseli	1.01			1.01		
Amerinus linearis	7.94	2.98	0.99			3.97
Amphasia interstitialis	0.99		0.99			
Anatrichis minuta	0.99	0.99				
Anisodactylus sanctaecrucis	1.98				0.99	0.99
Anisodactylus agricola	3.97	0.99			2.98	
Anisodactylus kirbyi	2.18		1.19			0.99
Anisodactylus melanopus	2.18		2.18			
Anisodactylus nigrita	1.19		1.19			
Anisodactylus (Anisodactylus) sp.	46.63	17.86		3.97	17.86	6.94
Anisodactylus merula	1.98			0.99	0.99	
Anisodactylus rusticus	2.98				1.98	0.99
Apenes sinuata	15.87	2.98		2.98		9.92
Axinopalpus biplagiatus	2.98			1.98	0.99	

Table 3 (cont.)

		Cluster				
Species	Total	Disturbed	Marsh	Prairie	Restoration	Savanna
Badister neopulchellus	0.99		0.99			
Badister notatus	3.98			2.99		0.99
Badister parviceps	1.19		1.19			
Bembidion hastii	13.89		13.89			
Bembidion affine	10.33		4.37	3.98		1.98
Bembidion mimus	0.99				0.99	
Bembidion (Notaphus) sp.	1.98		1.98			
Bembidion frontale	3.17		3.17			
Bradycellus rupestris	0.99				0.99	
Bradycellus lugubris	0.99				0.99	
Calathus gregarius	9.92	1.98				7.94
Calathus opaculus	549.44	76.39	51.79	239.72	93.25	88.29
Carabus serratus	43.06	0.99	2.38	0.99	37.70	0.99
Chlaenius emarginatus	41.87	5.95	5.16	1.98	0.99	27.78
Chlaenius impunctifrons	20.44	0.99	12.50			6.94
Chlaenius nemoralis	16.07	8.93	3.17			3.97
Chlaenius pennsylvanicus pennsylvanicus	1.19		1.19			
Chlaenius tricolor tricolor	1.98					1.98
Chlaenius erythropus	0.99					0.99
Chlaenius sp. 1	0.99	0.99				
Cicindela sexguttata	4.96	0.99		0.99		2.98
Cicindela punctulata punctulata	10.91			10.91		
Clivina americana	5.36	0.99	3.37	0.99		
Cyclotrachelus sodalis sodalis	324.40	197.42	1.98	4.96		120.04
Cyclotrachelus sp. 1	7.94	7.94				
Cymindis limbata	0.99			0.99		
Cymindis platicollis	2.98					2.98
Cymindis pilosa	4.00			2.01	1.98	
Cymindis sp. 1	21.83	1.98		1.98	2.98	14.88
Dicaelus elongatus	163.89	108.13	8.13	3.97	10.91	32.74
Diplocheila assimilis	1.98	1.98				
Diplocheila impressicollis	1.98		0.99			0.99

Table 3 (cont.)

		Cluster				
Species	Total	Disturbed	Marsh	Prairie	Restoration	Savanna
Diplocheila major major	15.28		15.28			
Diplocheila obtusa	8.93			8.93		
Diplocheila striatopunctata	75.40		65.48	2.98		6.94
Diplocheila sp. 1	0.99			0.99		
Dyschirius globulosus/longulus	9.92			8.93	0.99	
Elaphropus capax	3.97	0.99	1.98	0.99		
Elaphropus saturatus	0.99				0.99	
Elaphropus vivax	1.01			1.01		
Elaphropus xanthopus	1.98		0.99	0.99		
Galerita bicolor	54.56	1.98	32.74	0.99	0.99	17.86
Galerita janus	7.95		1.98	2.99		2.98
Harpalus erraticus	16.87				16.87	
Harpalus faunus	1.98			0.99	0.99	
Harpalus indigens	2.98				2.98	
Harpalus katiae	0.99			0.99		
Harpalus somnulentus	24.80	0.99		0.99	22.82	
Harpalus (Harpalus) sp. 1	0.99				0.99	
Harpalus (Harpalus) sp. 2	0.99				0.99	
Harpalus (Harpalus) sp. 3	10.91				10.91	
Harpalus (Pseudoophonus) sp.	53.67	4.96		18.95	23.81	5.95
Harpalus sp. 3	0.99				0.99	
Harpalus sp. 4	0.99	0.99				
Helluomorphoides praeustus bicolor	0.99					0.99
Lebia analis	0.99		0.99			
Lophoglossus scrutator	27.18		18.25			8.93
Loxandrus sp. 1	27.78		12.90		0.99	13.89
Loxandrus sp. 2	4.17		2.18			1.98
Notiobia nitidipennis	33.73			0.99	32.74	
Notiobia sayi	38.70			1.01	36.71	0.99
Notiobia terminata	51.60		0.99	1.01	49.60	
Notiophilus aeneus	84.33	4.96	12.90	5.95	2.98	57.54
Notiophilus novemstriatus	26.98		1.19	0.99		24.80

Table 3 (cont.)

		Cluster				
Species	Total	Disturbed	Marsh	Prairie	Restoration	Savanna
Notiophilus semistriatus	3.97			0.99	2.98	
Olisthopus micans	0.99					0.99
Oodes amaroides	4.17		3.17	0.99		
Oodes brevis	13.29		9.33	0.99		2.98
Paraclivina bipustulata	5.97			2.00	0.99	2.98
Pasimachus depressus	13.90			9.93	3.97	
Patrobus longicornis	4.96	0.99	0.99		0.99	1.98
Platynus decentis	328.20	34.72	13.69	14.91	17.86	247.02
Poecilus chalcites	2.20		1.19	1.01		
Poecilus lucublandus	312.50	250.00	0.99		45.63	15.87
Polyderis laeva	4.96	1.98		2.98		
Pterostichus adstrictus	1.98			0.99	0.99	
Pterostichus caudicalis	26.79		16.87	1.98		7.94
Pterostichus commutabilis	7.34	2.98	2.38			1.98
Pterostichus corvinus	14.88		11.90			2.98
Pterostichus femoralis	1.98				1.98	
Pterostichus luctuosus	38.29	1.98	34.33			1.98
Pterostichus melanarius melanarius	3.17		1.19		0.99	0.99
Pterostichus mutus	79.37			1.98	69.44	7.94
Pterostichus novus	18.85	8.93	2.98			6.94
Pterostichus permundus	278.77	258.93	2.98			16.87
Pterostichus praetermissus	13.69	1.98	4.76		0.99	5.95
Scarites subterraneus	7.94	1.98		1.98	0.99	2.98
Selenophorus ellipticus	4.96			4.96		
Selenophorus opalinus	4.97			1.01	1.98	1.98
Stenocrepis cuprea	0.99				0.99	
Stenolophus ochropezus	4.17	0.99	2.18			0.99
Stenolophus plebejus	0.99					0.99
Syntomus americanus	49.60				48.61	0.99
Synuchus impunctatus	348.02	22.82	4.76	16.87	0.99	302.58
Tachys proximus	1.19		1.19			
Tachys pumilus	4.96	0.99				3.97

Table 3 (cont.)

		Cluster				
Species	Total	Disturbed	Marsh	Prairie	Restoration	Savanna
Trichotichnus autumnalis	12.91	1.98		2.00		8.93
Trichotichnus dichrous	0.99				0.99	
Trichotichnus vulpeculus	0.99					0.99
Xestonotus lugubris	0.99				0.99	
Total	3858.84	1087.30	450.00	447.53	728.17	1145.83

Table 4 Subset of environmental parameters having the highest Spearman's rank correlation with the NMDS ordination for each size of subset (number of terms ranging from 1–14). Subset with the overall highest Spearman's rank correlation coefficient is in bold. HI = height index

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
Tree Diameter, Litter Depth, Soil Moisture, %Canopy, %Bare Soil, %Woody, %Herb, %Grass, %Leaf Litter, Grass HI, Shrub HI	0.4052
Tree Diameter, Litter Depth, Soil Moisture, %Canopy, %Bare Soil, %Woody, %Herb, %Grass, %Leaf Litter, Grass HI, Shrub HI, Herb HI	0.3728
Tree Diameter, Litter Depth, Soil Moisture, %Canopy, %Bare Soil, %Woody, %Herb, %Grass, %Leaf Litter, Grass HI, Shrub HI, Herb HI, Tree HI	0.3205
Tree Density, Tree Diameter, Litter Depth, Soil Moisture, %Canopy, %Bare Soil, %Woody, %Herb, %Grass, %Leaf Litter, Grass HI, Shrub HI, Herb, HI, Tree HI	0.2503

Table 5 Species richness, Fisher's alpha diversity index, exponential Shannon diversity index, inverse Simpson's diversity index, Shannon evenness, and Simpson's evenness for each *k*-means cluster. The 95% confidence interval is included for each value

Cluster	Richness (S)	Fisher's Alpha	Exponential Shannon ($e^{H'}$)	Inverse Simpson's ($1/D$)	Shannon Evenness (J')	Simpson's Evenness ($E_{1/D}$)
Savanna	16.30 ± 4.51	7.15 ± 2.39	8.96 ± 2.82	5.87 ± 2.12	0.72 ± 0.07	0.31 ± 0.08
Disturbed	19.75 ± 5.72	5.39 ± 3.50	6.94 ± 4.32	4.50 ± 3.06	0.63 ± 0.21	0.24 ± 0.20
Marsh	31.67 ± 13.68	13.29 ± 3.44	16.55 ± 3.15	10.30 ± 1.84	0.81 ± 0.07	0.33 ± 0.16
Prairie	11.18 ± 1.94	8.94 ± 5.91	6.15 ± 2.23	4.39 ± 1.93	0.71 ± 0.12	0.40 ± 0.16
Restoration	30.33 ± 12.25	9.45 ± 5.51	13.68 ± 2.33	9.40 ± 0.83	0.77 ± 0.06	0.32 ± 0.14

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