Habitat Preferences of Ground Beetle (Coleoptera: Carabidae) Species in the Northern Black Hills of South Dakota

Dylan Brandenburg, Samantha Petit, Brian Smith, Mark Gabel, and David Bergmann*
Black Hills State University, Spearfish, SD 57799
*to whom correspondence should be addressed

ABSTRACT: Ground beetles (Coleoptera: Carabidae) were collected from pitfall traps at two sites in each of five kinds of habitats (native grassland, burr oak-ironwood forests, ponderosa pine – common juniper forests, aspen-pine forests, and a spruce forest) in the Black Hills of Lawrence County, SD, from which habitat structure characteristics and plant abundance data were collected. A total of 25 species of ground beetles were identified, most of which were collected only once or twice. While some species, such as *Dicaelus scultpilis* Say were found in most habitats, other species showed distinct habitat preferences: *Poecilus lucublandus* (Say) preferred oak forests, *Pasimachus elongatus* LeConte preferred grasslands , and *Calathus ingratus* Dejean preferred high-altitude aspen-pine forests. *Pterostichus adstrictus* Escholtz was found only in woodlands, and *Carabus taedatus* Say strictly in high-altitude (over 1500 m) aspen or coniferous woods.

KEY WORDS: ground beetles, Coleoptera, Carabidae, Black Hills, vegetation

The Black Hills has sometimes been referred to as a forested island surrounded by the mixed-grass prairies of the Great Plains. It possesses an interesting mix of plant species; many of Rocky Mountain or Great Plains affinity but others with boreal, eastern, or southwestern affinity as well (Larson and Johnson 1999). The Black Hills has been described to have four major vegetation complexes which include 1) Rocky Mountain coniferous forest, 2) boreal forest, 3) grassland complex and 4) the deciduous forest complex (Froiland 1990). A fifth vegetation complex, the southern Great Plains, was described in the Black Hills by Marriott (1985). An extensive northern coniferous forest covered the northern and central Great Plains during the late Wisconsin glaciation. It was replaced across most of the range by grasslands (Wright 1970). The timing of specific climate changes in the Black Hills during the Holocene is unclear (Gabel.et al 1997 Parrish et al. (1996) noted understory diversity, a general decline in riparian habitats and introductions of exotic plant species in the Black Hills ecosystem since the invasion of European-Americans. Fire intervals increased after about 1900 due to fire suppression (Fisher et al. 1987), and resulted in an increase in *Pinus ponderosa* Laws. (Covington and Moore 1994). Previous vegetation studies of the Black Hills include Rydberg (1986), Hayward (1928), McIntosh (1931), Thilenius (1971), Dorn (1977) Marriott (1985), Van Bruggen (1996), Marriot et al. (1999) and Gabel and Gabel (2007).

Disjunct populations of some vertebrates, such as the American Dipper *(Cinclus mexicanus*) and Redbelly Snake (*Storeria occipitomaculata* (Smith and Stephens 2003) are found in the Black Hills. With the exception of Tiger Beetles (Coleoptera: Cicindelidae) (Backlund et al. 2001) and Click Beetles (Coleoptera: Elateridae) (Johnson 2007) communities of invertebrates in the Black Hills have not been characterized in detail. It is known that there are about 120 species of ground beetles in the Black Hills (Kirk and Balsbaugh 1975). The Black Hills has experienced various sorts of natural and anthropogenic habitat disturbances, such as crown-replacing forest fires, Mountain Pine Beetle defoliation of Ponderosa Pine stands, logging, grazing, and mining. How local invertebrate communities are impacted by these factors is not known, and hence additional data on habitat requirements of some terrestrial invertebrate species would be informative. Here we present data on the abundance and habitat preferences of species of ground beetles (Coleoptera: Carabidae) in the northern Black Hills, focusing on Spearfish Canyon and the surrounding region.

Ground beetles are relatively large and abundant insects in many terrestrial habitats. Most species are polyphagous and largely predaceous on invertebrates, while others may consume seeds. They have been used as "bioindicators" of natural (fire) and anthropogenic (logging) disturbance to boreal forests, because they constitute a significant amount of insect biomass, are relatively easy to systematically collect by pitfall trapping, can usually be identified to species, and because the abundance of individual species may change dramatically in response habitat changes (Pearce and Venier 2006) such as fire (Moretti and Duelli 2004) logging (Heliola et al. 2001), and grazing (Dennis et al. 2002). Most of these studies have been conducted in northern Europe and in the boreal forests of Canada. One recent study in ponderosa pine forests of northern Arizona indicated that both mechanical thinning of forest stands and wildfire resulted in significant changes in composition of communities of carabid and tenenebrionid beetles (Chen et al. 2005). However, before assessing the roles of fire and anthropogenic agents in shaping ground beetle communities in the Black Hills, baseline data on these communities must be acquired.

In addition to traditional morphological methods for identifying arthropods, molecular methods of taxonomy, based on extraction of DNA from specimens, polymerase chain reaction (PCR) amplification of a gene, and sequencing PCR products, have allowed identification of specimens whose morphological traits are uncertain, especially larval forms of holometabolous insects. The sequence variability of the mitochondrial gene for cytochrome oxidase subunit I (*co*I) has proved useful for identifying arthropods, especially Ground Beetles ("barcoding") because its sequence is generally unique in each species (Greenstone et al. 2005). This data may also be useful in studying the genetics of isolated populations of ground beetles.

In this project we describe the communities of ground beetles in five different kinds of vegetation in the northern Black Hills of South Dakota, and correlate the abundance of individual ground beetle species with floristic and structural features of their habitat. For several species of Black Hills ground beetles, we compiled a small database of mtDNA *Co*I sequences.

Materials and Methods

Sites. Ground beetles were collected and plant cover was surveyed in five different kinds of plant communities: (a) wheatgrass-needlegrass mixed-grass prairie, (b) burr oak-ironwood forest, (c) ponderosa pine common juniper woodland, (d) aspen-ponderosa pine woodland, and (f) white spruce forest; all located in Lawrence County, SD (Marriott and Faber- Langendoen 2000)(Table 1). For the first four plant communities, two separate sites were sampled, while only a single spruce forest site was sampled.

Ground Beetle Collection. At each site, two lines of five pitfall traps, 20 m apart, were set in place. Each trap consisted of plastic cups 9 cm in diameter and 11 cm deep, filled with 100 ml of undiluted propylene glycol antifreeze (Sierra antifreeze/ coolant, Old World Products, Northbrook, IL) and covered with a 15 cm X 15 cm shingle lid to prevent dilution by rain. Four pieces of wooden lath, 4 cm high and 30 cm long, radiated from the trap and supported the shingle. The traps were sampled for two week periods in early June, early July, and early August. Specimens were transported to the laboratory in antifreeze and were and identified using keys in Lindroth (1961) and Downie and Arnett (1995). Most specimens were rinsed in ethanol and mounted on insect pins, while several specimens of each species were rinsed in ethanol and kept for mtDNA extraction and *co*I barcoding.

Habitat and Plant Surveys of Sites. Habitat characteristics were surveyed and specimens of vascular plants were collected within a ten meter radius of each pitfall trap at each of the nine sites monthly from June through September. Plants were collected in flowering or fruiting condition when possible, and vouchers were deposited in the BHSU herbarium. Diameter breast heights were recorded of any live tree over two meters tall and 12 cm or greater in circumference. Trees not meeting these requirements, along with all other woody plants, were recorded shrubs, and the percent of area covering each 20m diameter plot was noted. The slope and aspect of each trap plot were recorded using a clinometer. Three times during the summer, a densiometer was used to measure the percent sun over each trap, and readings were averaged for each location. Finally, a one meter squared area around each trap was measured in order to assess the immediate ground cover/litter, which was recorded as type present and percent area covered.

The soil survey of Lawrence County, SD (Meland, 1979) indicated that soils of the study areas (Table1) include Citadel Association, hilly (CBE) which has deep well-drained soils along drainage ways with dark gray loam covered by forest litter, Vale silt loam, (VaC) with deep, well-drained soils on terraces, uplands and alluvial fans with a surface layer of 15 cm of dark silt loam), Paunsaugunt-Rock outcrop complex (PbE) which has shallow well-drained soils with moderate to steep slopes with most areas in rangelands, Rock outcrop Vanocker association (RCF) which is very steep, drained, and on the side of mountains, and the Stovho association (SEE) which has deep well-drained soils with smooth upland divides and gray brown silt loam covered with forest litter and moderately low organic matter.

Principal component analyses (PCA) were conducted on habitat and plant structure, plant species presence, and abundance of ground beetle species using NTSYSpc (Rohlf, 2005). Variables were first standardized to eliminate the effects of different scales of measurement. The data were standardized using the formula for a linear transformation of the variables in the data matrix: $Y' = (Y-a)/b$ where "a" is the mean of each variable and "b" is the standard deviation. Correlations were calculated among variables, and eigen values were calculated to extract the first three principle components. The results were graphed to produce a three dimensional diagram.

DNA Extraction from Ground Beetles and *co*I PCR. DNA was extracted from a leg of each specimen stored in ethanol using the DNAeasy tissue extraction kit (Qiagen Inc., Valencia, CA). PCR of the *co*I gene was performed using 3 μM primers CIJ1751 and C1N2191 (Simon et al. 1994) with a touchdown PCR program modified from Greenstone et al. (2005): initial denaturation at 94 °C for 2 min; 6 cycles of denaturation at 94 °C from 45s, annealing at 40 °C (-0.5 °C/cycle) for 1 min, and extension at 68 °C for 2 min; 34 cycles of denaturation at 94 °C from 45s, annealing at 37 °C for 1 min, and extension at 68 °C for 2 min; final extension at 68 °C for 10 min; and storage at 10 °C for 1-18 hours. Portions of the PCR product were sequenced using the dideoxy-chain-termination method (Sequenase Version 3.1, ABI, Inc) using primers CIN2191 and CIJ1859 (Simon et al. 1994) at the BHSU Center for the Conservation of Biological Resources. *Co*I sequences were deposited in GenBank (accession numbers GQ502298 - GQ502307 and GQ502310- GQ502314).

Results

Plant Cover and Surface Characteristics of Sites. The nine sites examined ranged in elevation from 1243 m to 2059 m and exhibited considerable variation in slope, exposure to sunlight, plant litter present, and cover of tree and shrub species (Table 1). We found that the total percent shrub cover was highest for the two oak forest sites. The two pine forest sites contained the largest number of trees, with the McGuigan pine forest (MG Pine) having more than double the number of trees found in the Christensen Pine forest (CH Pine). The largest average tree DBH was found in the Ebbert spruce forest (EB Spruce). The number of vascular plant species at each site ranged from 12 to 62 (Table 1). A complete list of the vascular plant species present at each site is presented in Table 2.

Distribution of Carabid Species among Sites. A total of 1138 specimens were obtained, comprising 24 species (Table 3). Apart from relatively large numbers of individuals collected from traps along seasonal stream beds in the two oak forest sites (which may have trapped many beetles fleeing from flash floods), numbers of beetles collected at most sites were low. Less than 10 specimens were collected for each of 16 carabid species, so conclusions cannot be drawn concerning their habitat preferences. However, eight species appear to have distinct preferences for certain plant communities. *Pasimachus elongatus* LeConte and *Cyclotrachelus alternans* (Casey) were largely limited to grasslands, while *Pterostichus adstrictus* Escholtz was limited to woodlands. *Platyderus decentis* (Say), *Poecilus lucublandus* (Say), and to a lesser degree, *Dicaelus sculptilis* Say, preferred oak-ironwood forests. *Calathus ingratus* Dejean and especially *Carabus taedatus* Say preferred relatively high-altitude aspen-pine and spruce forests. *Pterostichus melanarius* Illiger, a species introduced from Eurasia, was abundant only in parts of an oak-ironwood forest (MG Oak) disturbed by a flash flood.

Some patterns in seasonality of a few carabid species can be discerned, despite the rather short collecting season (early June to early August)(Table 4). *P. elongatus*, *P. adstrictus*, *P. decentis*, and *P. lucublandus* were more abundant in June and July than in August. *D. sculptilis* was most abundant in July, while *C. taedatus* and *P. melanarius* were most abundant in July and August.

The abundance of several beetle species was significantly [P > 0.90] correlated with certain plant cover and site characteristics (Table 5). The abundance of *P. elongatus* was positively correlated with percent sunlight. The abundances of *C. ingratus* and *C. taedatus* were positively correlated with altitude. The abundances of *P. decentis, D. sculptilis*, and *P. lucublandus* were all positively correlated with (1) percent cover of all shrubs (2) percent cover of *Symphoricarpos* spp., and (3) density of *Quercus macrocarpus*. The abundance of *P. elongatus* was negatively correlated with the D.B.H. of the largest tree.

Number of Beetle Species and Sampling Effort. The cumulative number of species per site is plotted against sampling effort (number of individuals collected per site) in Figure 1. It is possible that enough individuals were collected at the MG Oak and UM Aspen sites to sample nearly all the species present, but at other sites, such as RN Aspen and EB Spruce, only a fraction of the species likely present may have been collected.

PCA Ordination of Plant and Ground Beetle Communities on Sites. PCA ordination of the nine sites according to their similarity in surface and plant structure characteristics accounted for 87.1 % of variance among the 3 main PCA axes, and resulted in the two grassland sites (MG Grass and CH Grass) clustering together, the two oak-ironwood forest sites (MG Oak and CH Oak) clustering together, and the two open pine-aspen forest sites (UM Aspen and RN Aspen) clustering together (Figure 2) although the two pine-juniper forest sties (MG Pine and CH Pine) and the spruce forest remain separated. Ordination of sites by similarities in abundance of plant species (Figure 3) accounted for only 54.7% of variance among the three main PCA axes, and did not group any sites closely together, except for the two pine-juniper forest sites. Ordination of sites by similarities in the abundance of ground beetle species (Figure 4) accounted for 78.8% of variance among the three main PCA axes, and resulted in three groupings of sites: the two grassland sites, the two pine-juniper sites, and the two oak-ironwood sites.

***co*I Amplification and Sequencing.** DNA extraction was attempted from single legs or tarsi of 26 carabid specimens of seven common species from pitfall traps. Although no genomic DNA band was visible when samples were analyzed by agarose gel electrophoresis and ethidium bromide staining, 20 samples yielded *co*I amplicons when PCR was conducted. Fourteen *co*I

PCR products, from *C. ingratus*, *C. taedatus*, *D. sculptilis*, *P. lucublandus*, *P. adstrictus*, and *P. melanarius*, were successfully sequenced (Table 6).

Discussion

Vegetation structure, if not diversity, appears to exert a strong influence on the abundance of ground beetle species in the northern Black Hills. For example, two species, *P. elongatus* and *C. alternans,* were largely restricted to grassland sites while others, such as *C. ingratus* and *P. adstrictus*, are found only in woodland sites. It is also possible that altitude, through its effects on climate or vegetation, may also be important; *C. taedatus* was noted only from sites above 1500 m. Although the species *P. lucublandus* was found only within oak-ironwood forest in our study area, literature indicates that this species is found in wide variety of habitats, including cultivated fields (Larochelleand Lariviere 2003). In our study area, it is possible that this species is limited to moister habitats, such as ravines, where oak-ironwood forests occur. An introduced species, *P. melanarius*, was abundant in part of an oak forest disturbed by a flash flood, hence, it is not likely that *P. melanarius* is displacing other carabid species from the northern Black Hills. Although Spence and Spence (1988) found a negative relationship between abundance of *P. melanarius* and both numbers and diversity of other species of ground beetles in human-disturbed sites in Alberta, Niemelae and Spence (1961) could find no evidence that *P. melanarius* was displacing other carabid species from less disturbed sites in central Alberta, despite its abundance in these sites.

Despite the influence of vegetation structure on the abundance of some ground beetle species, the diversity of vegetation appears to be less important in influencing the abundance of ground beetles. The two grassland sites, CH Grass and MG Grass, had similar assemblages of ground beetle species. However, the MG Grass site had far fewer plant species than the CH Grass site, as well as an extensive cover of *Bromus inermis*, indicating considerable disturbance to the site. The two grassland sites grouped together in PCA ordination of sites by plant structure and by beetle species abundance, but not in PCA ordination of sites by plant species.

It is likely that the total species richness is underestimated by our pitfall trap collections, because the majority of species collected are represented by only a few specimens, and also because the numbers of individuals collected at most sites are low. The large number of individuals collected at the MG Oak site may be due partly to the presence of a seasonal stream, which was flooding during the collecting season, adjacent to five of the 10 traps at this site. Ground beetles fleeing the flooding stream apparently became concentrated in the region of the traps.

Two species we found in frequently in spruce, or pine-aspen forests in the northern Black Hills, *Carabus taedatus* and *Calathus ingratus*, are found mainly in the boreal regions of North America (Lindroth 1961). Both have been previously recorded in extreme eastern South Dakota as well as the Black Hills, and appear to have disjunct distributions. Another species, *Pterostichus coracinus* (Newman), common at the UM Aspen pine-aspen forest, may have a similar distribution. Our study indicates that these species, which appear to be relicts of a boreal fauna now isolated in the higher portions of the Black Hills, may be more common than previously thought in favorable habitats. One specimen of *Notiphilius semistriatus* Say from the RN Aspen pine-aspen forest is a new state record for South Dakota.

Mitochondrial DNA was adequately preserved in ground beetles from pitfall traps containing commercial propylene glycol antifreeze and yielded *co*I PCR products which could be sequenced. The antifreeze preserved specimens despite being diluted by rainwater in some traps and being left at ambient temperatures for intervals up to two weeks. Future studies of the genetics of some isolated populations of ground beetles, in the Black Hills, such as those of *C. taedatus*, could be conducted using the pitfall trapping methods used in this study.

Acknowledgements: This project was funded by grant BA0800023 from the South Dakota Department of Game Fish and Parks. D. Brandenburg was supported by a Nelson Foundation Scholarship. We would like to thank Dr. Paul Johnson for his help with identification of specimens and Carolyn Farrell for help in DNA sequencing. We thank Dr. George Rinker, Elaine and Larry Ebbert, and Glen and Lori Umphries for permission to collect on their property.

References

Backlund, D.C., Backlund N., Marrone, G.L., and S. Wiens. New distribution records of cincindelids (Coleoptera: Cincindelidae) from South Dakota, USA. Cincindela 32: 9-12.

Chen, Z., Grady, K., Stephens, S., Villa-Castillo, J. , and M.R. Wagner. 2006. Fuel reduction treatment and wildfire influence on carabid and tenebrionid community assemblages in the ponderosa pine forest of northern Arizona, USA. Forest Ecology and Management 225: 168–177

Covington, W.W. and M.M. Moore. 1994. Southwestern ponderosa forest structure: Changes since Euro-American settlement. Journal of Forestry 92:39-47.

Dennis, P., Doering, J., Stockan, J.A., Jones, J.R., Rees, M.E., Vale, J.E., and A.R. Sibbald. 2003. Consequences for biodiversity of reducing inputs to upland temperate pastures: effects on beetles (Coleoptera) of cessation of nitrogen fertilizer application and reductions in stocking rates of sheep. Grass and Forage Science. 59: 121-135.

Downie, N.M., and R.H. Arnett, Jr. 1995. The Beetles of Northeastern North America.

Fisher, R. F., M. J. Jenkins and W.F. Fisher. 1987. Fire and the prairie-forest mosaic of Devil's Tower National Monument. American Midland Naturalist 117:250-257.

Froiland, S. 1990. Natural history of the Black Hills and Badlands. Center for Western Studies, Sioux Falls, SD 225 pp.

Gabel, A. C. and M. L. Gabel. 2007. Comparison of diversity of macrofungi and vascular plants at seven sites in the Black Hills of South Dakota. American Midland Naturalist 157:258-296.W.

Gabel, A.C. and M.L. Gabel. 2007. Comparison of macrofungi and vascular plants at seven sites in the Black Hills of South Dakota. Am. Midl. Nat. 157: 258-296.
Gabel, M. L., M. Cowan and L. L. Tieszen. 1997. Stable carbon isotopes in *Celtis* (Ulmaceae) from the Beaver Creek Shelter, Wind Cave National Park, South Dakota, and paleoclimatic interpretations. Proceedings of the South Dakota Academy of Science 76:131-137.

Greenstone, M.H., Rowley, D.L., Heimbach, U., Lundgren, J.G., Pfannenstiel, R.S., and S.A. Rehner. 2005. Barcoding generalist predators by polymerase chain reaction: carabids and spiders. Molecular Ecology 14: 3247-3266.

Hayward, H. E. 1928. Studies of plants in the Black Hills of South Dakota. Botanical Gazette 85:353-412.

Heliola, J., Koivula, M., and J. Niemala. 2001. Distribution of carabid beetles (Coleoptera: Carabidae) across a boreal forest-clearcut ecotone. Conservation Biology 15:370-377.

Johnson, P. Taxonomic Inventory of the Click Beetles of the Black Hills and Bear Lodge Mountains, South Dakota and Wyoming. http://nathist.sdstate.edu/smircol/nearctic/taxonlist.html, accessed 2-17-07.

Kirk V.M., and E.U. Balsbaugh. 1975. A list of the beetles of South Dakota. Tech. Bull. 42, Agric. Exper. Sta. South Dakota State University. Brookings, SD.

Larochelle, A., and M-C Lariviere. 2003. A natural History of the Ground-Beetles (Coleoptera: Carabidae) of America north of Mexico. Pensoft, Sofia, Bulgaria.

Larson, G.E., and J.R. Johnson. 1999. Plants of the Black Hills and Bear Lodge Mountains. South Dakota State University, College of Agriculture and Biological Sciences, Ag Communications, Brookings, SD.

Lindroth, Carl H. 1961. The ground-beetles of Canada and Alaska (Carabidae, excl. Cicindelinae) (Opuscula entomologica supplementa).

Marriot, H.J. and D.F. Faber-Langendoen. 200. Black Hills Community Inventory. Volume I. Plant community descriptions. The Nature Conervancy, Minneapolis, MN.

Marriott, H. 1985. Flora of the northwestern Black Hills, Crook and Weston Counties, Wyoming. M. S. thesis, University of Wyoming, Laramie. 93 pp.
McIntosh, A. C. 1931. A botanical survey of the Black Hills of South Dakota. Black Hills Engineer 19. Reprint 1949, 28 (4). Rapid City, SD.

McIntosh, A. C. 1931. A botanical survey of the Black Hills of South Dakota. Black Hills Engineer 19. Reprint 1949, 28 (4). Rapid City, SD.

Meland, A. C. 1979. Soil Survey of Lawrence County, South Dakota. United States Department of Agriculture, Soil Conservation Service, in cooperation with the Forest Service and the South Dakota Agricultural Experiment Station. 173 pp + maps.

Moretti, M., Obrist, M.K., and P. Duelli. 2004. Arthropod biodiversity after forest fires: Winners and losers in the winter fire regime of the southern Alps. Ecography. 27: 173-186.

Niemelae, J and Spence, JR. 1991. Distribution and abundance of an exotic ground-beetle (Carabidae): A test of community impact. Oikos 62:351-359

Parrish, J. B., D. J. Herman and D. J. Reyher. 1996. A century of change in Black Hills forest and riparian ecosystems. U. S. Forest Service and South Dakota Agriculture Experiment Station B722, South Dakota State University, Brookings, South Dakota, U.S.A. 20 pp.

Pearce, J.L. and L.A Venier. 2006. The use of ground beetles (Coleoptera: Carabidae) and spiders (Araneae) as bioindicators of sustainable forest management: A review. Ecological Indicators 6: 780-793.

Phillips, A.J., and C. Simon. 1995. Simple, Efficient, and Nondestructive DNA extraction protocol for arthropods. Ann. Entomol. Soc. Amer. 88:281-283.

Rohlf, F. J. 2005. NTSYSpc: Numerical Taxonomy and Multivariate Analysis System 2.2. Exeter Software, Setauket, NY.

Rydberg, P.A. 1896. Flora of the Black Hills of South Dakota. Contributions to the U. S. National Herbarium 3:463-523.

Simon, C., Frati, F., Beckenbach, A., Crespi, B., Liu, H., and P. Flook. 1994. Evolution, weighting, and phylogentic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. Ann. Enotomol. Soc. Amer. 87: 651-700.

Smith, B.E., and N.T. Stephens. 2003. Conservation assessment of the Black Hills Redbelly Snake in the Black Hills National Forest, South Dakota and Wyoming. USDA, Forest Service, Black Hills National Forest, Custer, SD.

Spence, J.R., and D. Spence. 1988. Of ground-beetles and men: introduced species and the synantrophic fauna of western Canada. Mem. Ent. Soc. Can. 144:151-168.

Thilenius, J.F. 1971.Vascular plants of the Black Hills of South Dakota and adjacent Wyoming. Rocky Mountain Forest and Range Experiment Station.

Van Bruggen, T. 1996. The vascular plants of South Dakota (3rd). University of South Dakota, Vermillion. 293 pp.

Wright, H. E. 1970. Vegetation history of the Great Plains, pp. 157-172. *In* W. Dort, Jr. and J. K. Jones, Jr. (eds.). Pleistocene and recent environments of the central Great Plains. Univeristy of Kansas Press, Lawrence. 433 pp.

Tables

1. Location and characteristics of study sites, including surface and structure of vegetation. Abbreviations: Avg = average, Lgst = largest, conif = coniferous, decid = deciduous, coryl = *Corylus* cornuta, J com = *Juniperus communis*, J hor = *Juniperus horizontalis*, Ostr = *Ostrya virginiana*, Pop = *Populus tremuloides*, Prun = *Prunus* species, Symp = *Symphoricarpus* species.

2. Occurrence of individual plant species at study sites. Plant species are designated as T (tree), S (shrub), G (graminoid), or F (forb). The presence of a species at a site is indicated by the number 1.

3. Abundance of individual species of ground beetles at each site, for the entire summer of 2008.

4. Abundance of individual ground beetle species at all sites during each of the three collecting periods in summer 2008.

5. Correlation coefficients for regression of the abundance of the eight most common species of ground beetles vs. habitat structure variables at sites. An asterisk indicates significance at the 5 % level.

6. Ground beetles specimens from which *co*I DNA sequences were obtained: specimen, species, site, and Genbank accession numbers.

Figures

1. Number of carabid species vs. number of specimens collected for each site.

2. PCA of sites by surface and vegetation structure variables.

3. PCA of sites by occurrence of plant species.

4. PCA of sites by abundances of the eight most common ground beetle species.

Site	MG GRASS	MG OAK	MG PINE	CH GRASS	CH OAK	CH PINE	EB SPRUCE	UM ASPEN	RN ASPEN
Latitude	N44 29.043'	N44 28.997'	N44 29.063'	N44 27.409	N44 27.143'	N44 27.095'	N44 17.644'	N44 11.491'	N44 11.867'
Longitude	W103 53.697'	W103 53.594'	W103 54.284'	W103 49.379	W103 50.064'	W103 50.671'	W103 53.369'	W103 59.729'	W103 58.048'
Vegetation Type	Grassland	Oak-Ironwood	Pine	Grassland	Oak-Ironwood	Pine	Spruce	Pine-Aspen	Pine-Aspen
Owership	SD GF&P	SD GF&P	SD GF&P	SD GF&P	SD GF&P	SD GF&P	R,E Ebberts	G,L Umphries	G Rinker
Elevation	1245	1243m	1248	1279	1294m	1374m	1691m	2059	2008
Avg. Slope	8 S	30 N	22 E	18 N	7 SE	9 SE	19 SE	5 E	10 SE
Soil Type	PbE	CBE	CBE	PbE	CBE	CBE	RCF	SEE	SEE
Avg Lgst DBH (cm)	0	32.8	37	0	37.6	35.1	46.7	41.2	33.9
Avg % sun	100	9.3	6	100	22.2	32.4	17	24.7	39.5
Avg % conif litter	0	0	86	0	0	83	29	32	54
Avg % decid litter	94	91	3	95	99	14	22	66	46
Avg % moss litter	1	<1	1	0	0	0	71	1	0
Avg % Coryl shrub	0	0	3	0	<1	15	<1	10	6
Avg % J com shrub	0	0	0	0	0	0	37	0	0
Avg % J hor shrub	13	0	4	0	0	0	0	0	0
Avg % Ostr shrub	0	12	0	0	5	0	0	0	0
Avg % Pop shrub	0	0	0	0	0	0	0	8	7
Avg % Prun shrub	0	12	4	0	3	13	2	0	0
Avg % Symp shrub	0	31	0	0	51	0	0	2	1
Total % shrub cover	13	55	11	0	59	28	39	20	14
total *Quercus*	0	162	17	0	159	3	0	0	0
total *Pinus*	0	4	470	0	4	226	3	39	68
total Populus	0	0	0	0	0	0	0	43	37
total *Picea*	0	0	0	0	0	0	92	0	17
total *Fraxinus*	0	44	0	0	0	0	0	0	0
total trees	0	210	487	0	163	229	95	82	122
Vascular Plant Spp.	40	49	12	52	62	47	51	24	41

Table 1. Sites used in this study, showing location, ownership, physical features, and plant cover characteristics. All sites are located in Lawrence County, South Dakota.

Table 2. List of plant species found on sites, June – September, 2008. Species are designated as F (forb), G (grass), S (shrub), or T (tree). The presence of a species at a site is designated by "1."

Ostrya virginiana (Mills.) K. Koch	T					1				
Oxytropis lambertii Pursh	F				1					
Packera pauperculus (Michx.) Love & Love	F				1					
Packera plattensis (Nutt.) Weber & Love	F				1		1			
Pascopyrum smithii Rybd.	G	1	1		1					
Pediomelum argophyllum (Pursh) J. Grimes	F		1							
Pediomelum esculentum (Pursh) Rybd.	F	1			1		1			
Penstemon gracilis Nutt.	F						1			
Penstemon grandiflora Nutt.	F						1			
Perideridia gairdneri (H. & A.) Mathias	F								1	1
Phleum pratense L.	G	1				1			1	1
Phlox alyssifolia Greene	F			1						
Phlox hoodii Richardson	F				1					
Piptatherum micranthum (Trin. & Rupr.) Barkworth	G			1						
Platanthera huronensis (Nutt.) Lindl.	F							1		
Poa pratensis L.	G	1	1		1	1				1
Polygala senega L.	F									1
Prosartes trachycarpa S. Watson	F							1		
Prunella vulgaris L.	F		1							
Prunus pumila L.	S	1								
Prunus virginiana L.	S		1			1	1	1		
Pterospora andromedea	F						1		1	
Quercus macrocarpa Michx.	T		1							
Ranunculus abortivus L.	F		1							
Ratibida columnifera (Nutt.) Woot. & Standl.	F	1			1					
Ribes lacustre (Pers.) Poir.	S							1		
Rosa acicularis Lindl.	S	1				1		1		
Rudbeckia hirta L.	F					1				1
Rudbeckia laciniata L.	F							1		
Rumex acetosella L.	F					1				
Sambucus nigra L.	S		1							
Sambucus racemosa L.	S							1		
Securigera varia (L.) Lassen	F			1						
Sedum lanceolatum Torr.	F					1	1			
Senecio integerrimus Nutt.	F	1								
Shepherdia canadensis (L.) Nutt.	S					1	1	1		1
Silene latifolia Poir.	F					1				
Silene vulgaris (Moench) Garcke	F	1								
Sisyrinchium montanum Greene	F	1	1		1			1		1
Spiraea betulifolia Pall.	S						1			
Symphoricarpos albus (L.) Blake	S		1				1			
Symphoricarpos occidentalis Hook.	S		1			1				
Symphyotrichum laeve (L.) Love & Love	F						1			
Taraxacum laevigatum (Willd.) DC.	F		1							
Taraxacum officinale Weber	F					1		1		1
Tetraneuris acaulis (Pursh) Greene	F	1			1		1			
Thalictrum dioicum L.	F							1		
Thalictrum venulosum Trel.	F		1			1				1
Thlaspi arvense L.	F	1								
Tradescantia bracteata Small	F				1		1			
Tradescantia occidentalis (Britt.) Smyth	F					1				
Tragopogon dubius Scop.	F	1	1		1	1				
Trifolium hybridum L.	F									1
Trifolium incarnatum L.	F								1	
Trifolium pratense L.	F	1				1				1
Trifolium repens L.	F								1	1
Urtica dioica L.	F							1		
Vaccinium scoparium Leiberg	S									1
Valeriana dioica L.	F							1		
Verbascum thapsus L.	F					1				
Veronica americana Schw.	F							1		
Viburnum edule (Michx.) Raf.	F							1		
Vicia americana Muhl.	F		1			1				1
Viola adunca Smith	F		1					1	1	1
Viola canadensis L.	F							1		1
Viola pubescens Ait.	F		1			1				
Zigadenus venenosus Wats.	F	1			1					
Zizia aptera (Gray) Fern.	F									1
Total species		37	45	12	49	56	46	45	21	33

Delphinium bicolor Nutt.	F		1		1		1			
Dianthus armeria L.	F	1								
Dodecatheon pulchellum (Raf.) Merr.	F								1	
Echinacea angustifolia DC.	F	1			1		1			
Elymus canadensis L.	G		1							
Elymus elymoides (Raf.) Swezey	G				1					
Elymus trachycaulus (Link) Gould ex Shinners	G						1			
Elymus villosus Muhl.	G		1			1	1			
Equisetum laevigatum A. Braun	A							1		
Erigeron philadelphicus L.	G		1							
Erigeron subtrinervis Rybd.	F					1				
Erysimum asperum (Nutt.) DC.	F				1		1			
Escobaria missouriensis (Sweet) D.R. Hunt	F				1					
Eupatoriadelphus maculatus (L.) King & Rob.	F							1		
Euphorbia spathulata Lam.	F	1								
Fragaria vesca L.	F							1		
Fragaria virginiana Duchne.	F							1	1	1
Fraxinus pennsylvanica Marsh.	T		1							
Gaillardia aristata Pursh	F									1
Galium aparine L.	F	1	1			1				
Galium boreale L.	F		1	1		1			1	
Galium triflorum Michx.	F							1		
Gaura coccinea Pursh	F	1	1		1					
Geranium richardsonii F. & T.	F							1	1	1
Geum aleppicum Jacq.	F							1		
Geum canadense Jacq.	F		1			1				
Glyceria striata (Lam.) Hitch.	F							1		
Halenia deflexa (Sm.) Griseb.	F							1		
Helianthus pauciflorus Nutt.	F				1					
Heracleum maximum Bartram	F							1		
Hesperostipa comata (Trin. & Rupr.) Barkw.	G				1					
Heterotheca villosa (Pursh) Shinners	F						1			
Hypericum perforatum L.	F					1	1			
Juniperus communis L.	S		1	1			1			
Juniperus horizontalis Moench	S	1	1	1						
Koeleria macrantha (Ledeb.) Schult	G				1		1			
Lactuca tatarica (L.) C.A. Mey.	F	1			1	1				
Lappula occidentalis (S. Watson) Greene	F				1					
Lathyrus ochroleucus Hook.	S					1		1		1
Lesquerella ludoviciana (Nutt.) Wats.	F				1					
Leucocrinum montanum Nutt. ex Gray	F	1								
Leymus innovatus (Beal) Pilger	G							1	1	1
Liatris punctata Hook.	F						1			
Lilium philadelphicum L.	F									1
Linnaea borealis L.	S							1		
Lithospermum incisum Lehm.	F				1	1				
Lonicera dioica L.	S							1		
Lonicera tatarica L.	S		1			1				
Lupinus argenteus Pursh	F						1		1	1
Lupinus sericeus Pursh	F								1	
Lysimachia ciliata L.	F							1		
Mahonia repens (Lindl.) G. Don	S		1	1		1	1	1	1	1
Maianthemum canadense Desf.	F							1		
Maianthemum stellatum (L.) Link	F		1			1		1		
Medicago lupulina L.	F	1	1			1	1			
Medicago sativa L.	F	1			1	1				
Melilotus alba Medic.	F					1				
Melilotus officinalis (L.) Lam	F	1	1			1	1			
Mentha arvensis L.	F							1		
Mertensia oblongifolia (Nutt.) G. Don	F					1				
Mimulus guttatus DC.	F							1		
Moehringia lateriflora (L.) Fenzl	F		1						1	1
Monarda fistulosa L.	F					1	1			
Myosotis scorpioides L.	F							1		
Nassella viridula (Trin.) Barkw.	G		1	1	1		1		1	
Onosmodium bejariense DC.	F		1		1	1				
Opuntia polyacantha Haw.	F		1							
Orthocarpus luteus Nutt.	F				1					
Oryzopsis asperifolia Michx.	G		1	1			1	1	1	1
Osmorhiza longistylis (Torr.) DC.	F					1		1		

Species	Type	MGGrass	MGOak	MGPine	CHGrass	CHOak	CHPine	EBSpruce	UMAspen	RNAspen
Acer negundo L.	T		1							
Achillea millefolium L.	F	1			1	1	1		1	1
Aconitum columbianum Nutt.	F							1		1
Agoseris glauca (Pursh) Raf.	F	1			1				1	1
Agropyron cristatum (L.) Gaertn.	G	1								
Allium textile Nels. & Mac Br.	F	1			1	1				
Alyssum alyssoides L.	F	1								
Alyssum desertorum Stapf	F					1				
Amelanchier humilis Wieg.	S					1	1	1		
Amorpha canescens Pursh	S	1			1	1				
Anaphalis margaritacea (L.) B. & H.	F						1			
Androsace occidentalis Pursh	F				1					
Anemone cylindrica A. Gray	F					1				
Anemone virginiana L.	F		1							
Antennaria microphylla Rybd.	F			1						1
Antennaria neglecta Greene	F									1
Antennaria parvifolia Nutt.	F	1			1					
Apocynum androsaemifolium L.	F		1			1				
Aquilegia brevistyla Hook.	F		1					1		
Arabis holboellii Hornem.	F					1				
Aralia nudicaulis L.	F							1		
Arctostaphylos uva-ursi (L.) Spreng	S									1
Arnica cordifolia Hook.	F							1		1
Artemisia campestris L.	F						1			
Artemisia frigida Willd.	F				1					
Artemisia ludoviciana Nutt.	F				1		1			
Asclepias ovalifolia Dcne.	F			1		1	1			
Asclepias viridiflora Raf.	F				1	1				
Astragalus alpinus L.	F									1
Astragalus crassicarpus Nutt.	F				1					
Astragalus laxmannii Jacq.	F				1		1			
Astragalus miser Dougl.	F				1					
Bromus arvensis L.	G					1				
Bromus inermis Leyss.	G	1	1			1	1		1	
Bromus racemosus L.	G	1	1		1					
Bromus tectorum L.	G						1			
Calochortus gunnisonii S. Wats.	F	1				1	1		1	1
Calochortus nuttallii T. & G.	F	1			1					
Calylophus serrulatus (Nutt.) Raven	F				1					
Calypso bulbosa (L.) Oakes	F							1		
Campanula rotundifolia L.	F	1	1	1	1	1	1			
Carex filifolia Nutt.	G				1					
Carex inops L.H. Bailey	G				1					
Carex obtusata Liljeblad	G					1				
Carex praegracilis Boott	G		1			1				
Carex sprengelii Dewey	G		1							
Carex utriculata Boott	G							1		
Castilleja sessiliflora Pursh	F				1					
Castilleja sulphurea Rybd.	F									1
Ceanothus herbaceus Raf.	S						1			
Cerastium arvense L.	F				1	1	1		1	1
Cirsium drummondii T. & G.	F									1
Cirsium undulatum (Nutt.) Spreng.	F				1					
Collinsia parviflora Lindl.	F								1	
Collomia linearis Nutt.	F	1					1		1	
Comandra umbellata (L.) Nutt.	F					1	1			
Convolvulus arvensis L.	F	1								
Corallorhiza wisteriana Conrad	F									1
Cornus canadensis L.	F							1		
Cornus sericea L.	S							1		
Corylus cornuta	T							1		
Crataegus chrysocarpa Ashe	T					1				
Cynoglossum officinale L.	F		1			1				
Cystopteris fragilis (L.) Bernh.	A		1			1		1		
Dactylis glomerata L.	G					1				
Dactylorhiza viridis (L.) R.M. Bateman, A.M. Pridgeon & M.W. Cha	F									1
Dalea candida Michx.	F					1	1			
Dalea purpurea Vent.	F				1					
Danthonia spicata (L.) Beauv.	G						1			

Genus and Species	MG Oak	CH Oak	MG Grass	CH Grass	MG Pine	CH Pine	UM Aspen	RN Aspen	EB Spruce
Agonum placidum Say		1							
Amara coelebs Hayward		2	2				5		
Calathus ingratus Dejean	4	2				1	25	33	3
Calosoma obsoletum			1						
Carabus taedatus Say							37	28	5
Chlaenius platyderus Chaudoir	5								
Chlaenius tomentosus (Say)								1	
Cyclotrachelus alternans (Casey)	5	4	38	16					
Cymindis cribicollis Dejean							1		
Cymindis neglectus Haldeman		1							
Cymindis pilosa Say			1	1					
Dichaelus sculptidis Say	13	27	4		1	8	2	1	
Euryderus grossus Say					1				
Harpalus fulgens Csiki			1						
Harpalus herbivagus Say		2							
Harpalus laeticeps LeConte	1								
Harpalus opacipennis Haldeman							1		
Hapalus pennsylvanicus (DeGreer)	1								1
Notiophilus semistriatus Say								1	
Passimachus elongatus LeConte			24	13		4			
Philophuga viridis (LeConte)		1		1					
Platynus decentis (Say)	9	5					1		
Poecilus lucublandus (Say)	119	138				1			
Pterostychus adstrictus Escholtz	35	9			7	23	20	20	8
Pterostichus coracinus Newman	2						32		1
Pterostychus melanarius (Illiger)	389								
Pterostychus pennsylvanicus Leconte									1
Unknown genus									1
Total individuals	581	119	62	31	9	37	122	84	21
Number of species	9	11	7	4	4	5	9	6	8

Table 3. Abundance of ground beetle species at each site, June – August 2008, showing numbers of individuals taken in pitfall traps.

Species	Genus	June 3-12	June 26- July 12	July 23 August 8
Agonum	*muellerii*	2	0	0
Agonum	*nutans*	0	0	1
Amara	*coelebs*	5	3	1
Calathus	*ingratis*	10	40	18
Calosoma	*obsoletum*	0	1	0
Carabus	*taedatus*	2	37	31
Chlaenius	*platyderus*	2	2	1
Chlaenius	*tomentosus*	0	1	0
Cyclotrachelus	*alternans*	0	12	51
Cymindis	*cribicollis*	0	0	1
Cymindis	*neglecta*	0	0	1
Cymindis	*pilosa*	0	0	2
Dihaelus	*sculptilis*	6	40	10
Euryderus	*grossus*	0	1	0
Harpalus	*laeticeps*	1	0	0
Harpalus	*opacipennis*	0	1	0
Harpalus	*pensylvanicus*	0	1	1
Harpalus	unknown	1	2	1
Notiophilus	*semistriatus*	0	0	1
Pasimachus	*elongatus*	12	26	4
Platynus	*decentis*	8	6	1
Poecilus	*lucublandus*	112	120	26
Pterostichus	*adstrictus*	74	37	11
Pterostichus	*coracinus*	0	10	22
Pterostichus	*melanarius*	43	44	292
Pterostichus	*pensylvanicus*	0	0	1
Unkown	genus	1	0	0

Table 4. Abundance of ground beetle species at all sites during each of three sampling periods, June – August, 2008.

Habitat Variable	*Calathus ingratus*	*Carabus taedatus*	*Dichaelus sculptidis*	*Pasimachus elongatus*	*Platynus decentis*	*Poecius lucublandus*	*Pterostychus adstrictus*	*Pterostychus melanarius*
Percent sunlight	-0.15	-0.15	-0.27	0.91*	-0.39	-0.36	-0.58	-0.26
Elevation	0.91*	0.94*	-0.38	-0.40	-0.31	-0.38	0.26	-0.27
Percent cover conifer litter	0.17	0.15	-0.38	-0.40	-0.48	-0.50	0.18	-0.38
Percent cover deciduous litter	-0.05	-0.06	0.45	0.43	0.50	0.53	-0.09	0.36
Percent cover moss	-0.13	-0.07	-0.27	-0.19	-0.20	-0.20	-0.19	-0.15
Percent cover shrubs	-0.18	-0.23	0.80*	-0.50	0.79*	0.85*	0.48	0.49
Total trees	-0.18	-0.23	0.10	-0.54	0.12	0.12	0.25	0.08
Total *Pinus ponderosa*	-0.17	-0.16	-0.22	-0.26	-0.31	-0.30	-0.01	-0.24
Percent cover *Symphoricarpos*	-0.18	-0.26	0.95*	-0.31	0.83*	0.98*	0.26	0.42
Number of vascular plant species	-0.16	-0.26	0.50	0.13	0.35	0.47	0.06	0.16
Quercus macrocarpa	-0.23	-0.33	0.83*	-0.32	0.94*	0.99*	0.41	0.65
Largest tree D.B.H.	0.31	0.33	0.19	-0.91*	0.19	0.20	0.53	0.02

Table 5. R-values for correlations between the abundance of individual ground beetles on sites and several habitat structure and plant cover variables. An asterisk (*) indicates a significant correlation.

Specimen	Species	Site	Date	Accession Number
BHSUGB1	*Poecilus lucublandus*	CH Oak	6-10-08	GQ502298
BHSUGB2	*Poecilus lucublandus*	CH Oak	6-10-08	GQ502299
BHSUGB3	*Poecilus lucublandus*	MG Oak	6-10-08	GQ502300
BHSUGB5	*Pterostychus melanarius*	MG Oak	7-09-08	GQ502301
BHSUGB6	*Pterostychus melanarius*	MG Oak	7-09-08	GQ502302
BHSUGB7	*Pterostychus adstrictus*	RN Aspen	6-20-08	GQ502303
BHSUGB8	*Pterostychus adstrictus*	RN Aspen	6-20-08	GQ502304
BHSUGB10	*Dicaelus sculptilis*	CH Pine	7-10-08	GQ502305
BHSUGB11	*Dicaelus sculptilis*	MG Oak	7-09-08	GQ502306
BHSUGB12	*Dicaelus sculptilis*	CH Oak	7-10-09	GQ502307
BHSUGB20	*Carabus taedatus*	UM Aspen	8-08-08	GQ502311
BHSUGB23	*Calathus ingratis*	UM Aspen	8-08-08	GQ502312
BHSUGB24	*Calathus ingratis*	UM Aspen	8-08-08	GQ502313
BHSUGB25	*Carabus taedatus*	UM Aspen	8-08-08	GQ502314

Table 6. Ground beetle specimens from which the *co*I gene was partially sequenced from mitochondrial DNA.

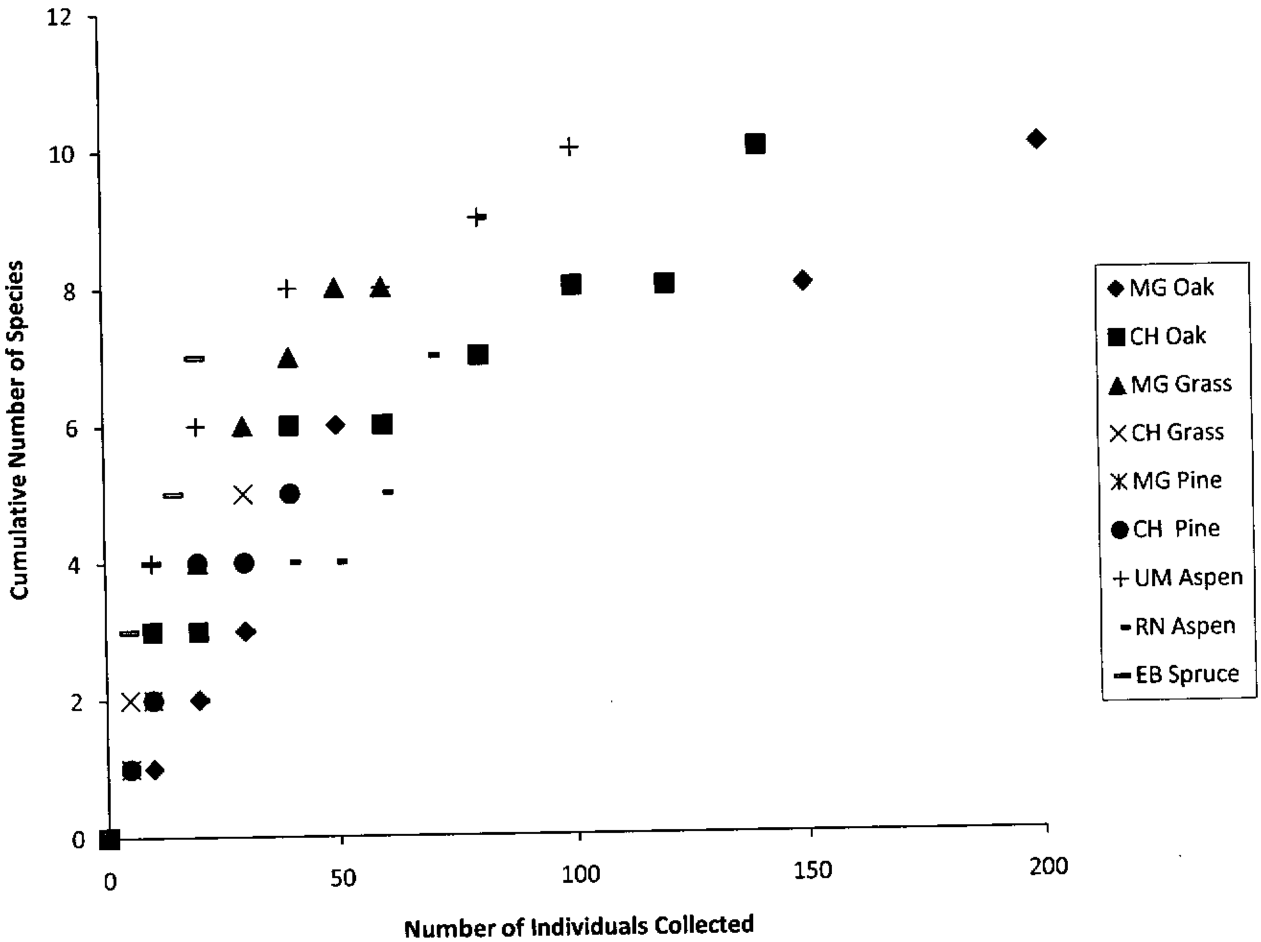

Figure 1. Cumulative numbers of ground beetle species collected vs. number of individuals collected, for each of nine sites sampled in 2008.

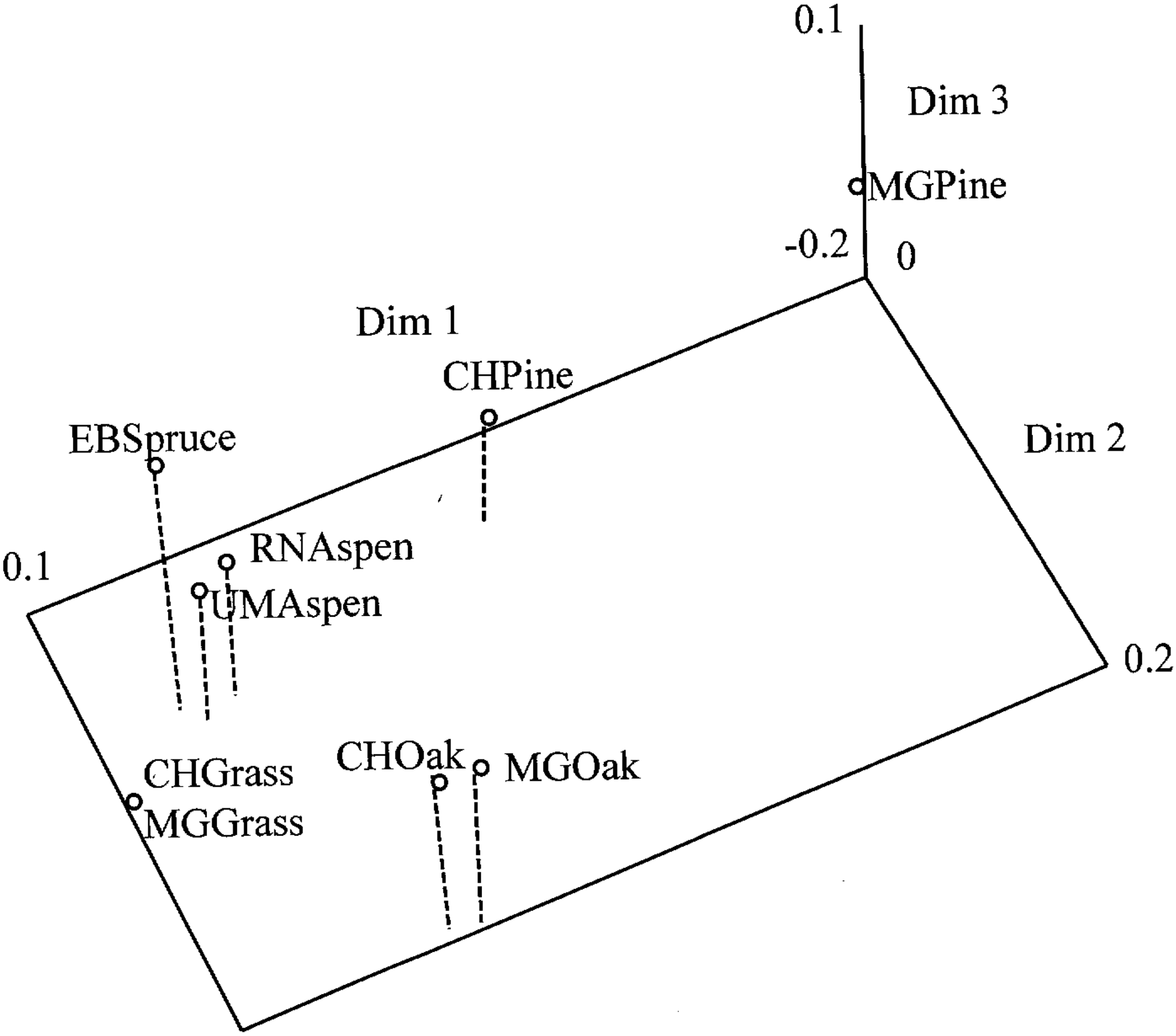

Figure 2. Principal components analysis of sites according to structural and plant cover variables.

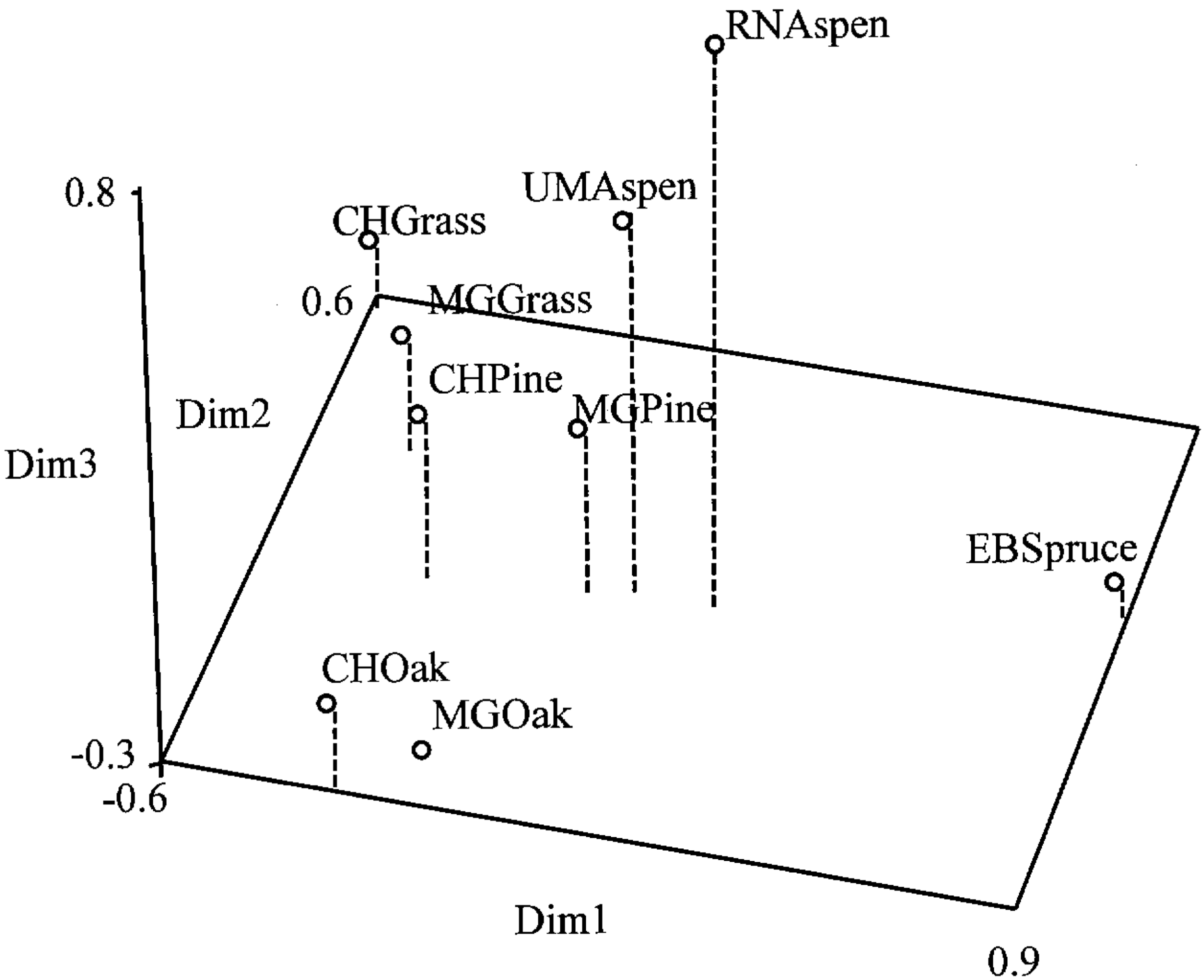

Figure 3. Principal component analysis of sites according to the presence of plant species.

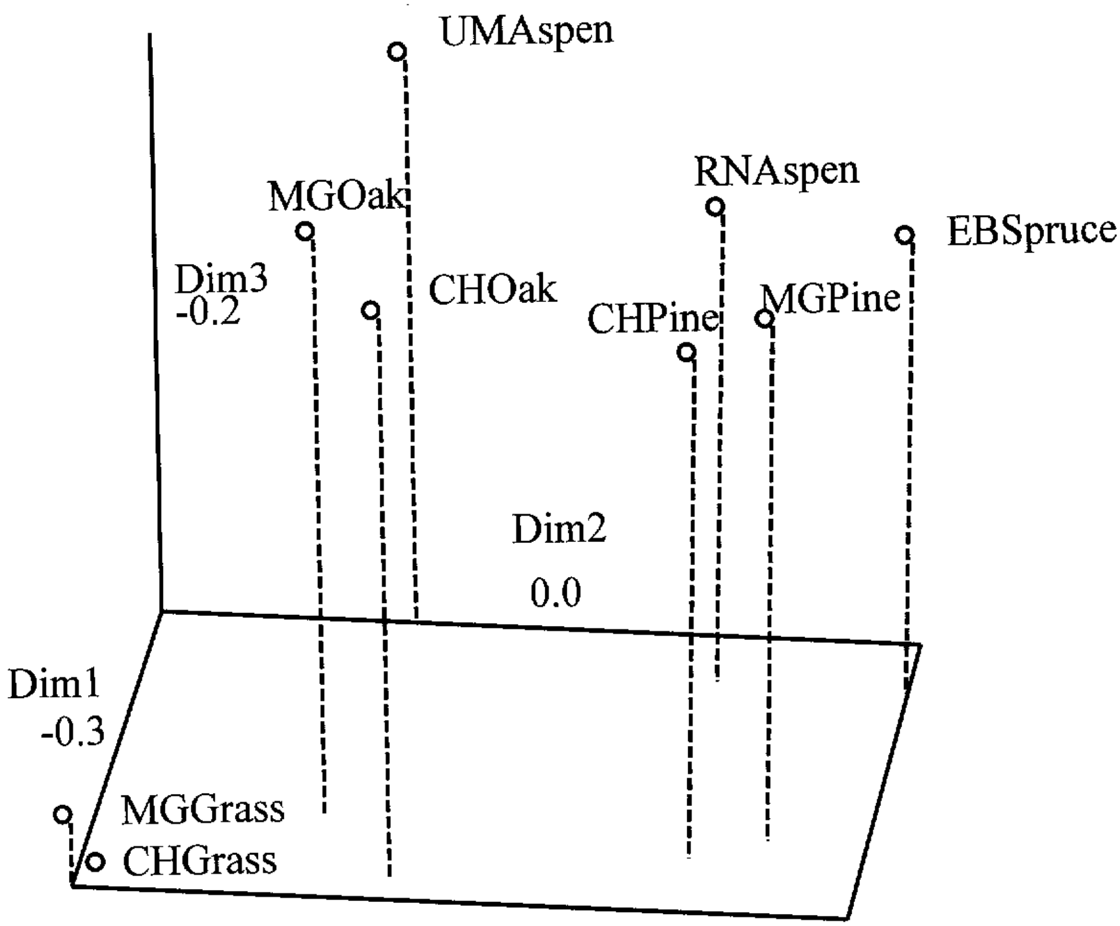

Figure 4. Principal components analysis of sites according to the abundance of the eight most common ground beetle species.