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Research Paper

A Comparison of an Ecological Model and GIS Spatial Analysis to Describe Niche Partitioning Amongst Carrion Beetles in Nebraska

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Abstract
Carrion beetles depend on vertebrate carcasses to rear their young. Carcasses are a limited resource with patchy distribution, and there is an intense competition among many species for these carcasses. This situation is expected to lead to niche partitioning, such that different beetle species use different resources and thus escape direct competition. Our project used a geographic information system (GIS) and pitfall sampling to characterize carrion beetle preferences for soil texture and land use in Kearney County, Nebraska. The GIS was used to select sites where sampling was conducted using pitfall traps baited with rat carcasses. Attracted beetles were counted, identified to species, and released. The resulting data were used to construct occurrence maps of eleven species of carrion beetles by overlaying soil texture and land use. We then compared the results of EcoSim (an ecological simulation model of niche overlap) with GIS-generated maps of probability of carrion beetle occurrence. Our results are consistent with landscape-level niche partitioning by seven of the eleven examined species. Our application of GIS to the spatial analysis of carrion beetle distributions demonstrates how this technology can be used to test ecological and evolutionary hypotheses, predict habitat associations, and examine the effects of land use on a community of

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insects. This work could easily be extended to study the habitat preferences of the federally endangered American burying beetle, *Nicrophorus americanus*.

1 Introduction

The role of geographic information systems (GIS) in biological and ecological studies has been rapidly expanding. Recently, GIS has been used for habitat conservation planning (Jones et al. 1997), to select habitat for re-introduction of rare species (Proctor et al. 1998, Gabler et al. 2000, South et al. 2001), and in predicting areas of high diversity (e.g. Sfenthourakis and Legakis 2001) and species richness (Hortal et al. 2001). GIS has also been applied to land use management (Wu et al. 2001) and its impacts on habitat (Dale et al. 1998) and rare species (Osborne et al. 2001). In addition, GIS has been used to improve scouting for insect pests (Lefko et al. 1998), to describe insect communities (Skinner et al. 2000), and for predicting and mapping the spread of invasive species (Yang et al. 1998, Haltuch et al. 2000).

Beyond these predictive and descriptive uses of GIS, the combination of digital map layers with field data offers the possibility of examining the abiotic parameters (e.g. soil texture, moisture requirements, etc.) of a species' observed or realized niche (Birnie et al. 2000). A niche is the specific set of resources and environmental conditions that allows an individual species to survive and reproduce (Hutchinson 1959). When multiple species share a habitat, competition for resources may be reduced through 'niche partitioning'. Niche partitioning most often occurs through differential use of space, food, and time among potential competitors (Schoener 1974). If species subdivide habitat based on physical characteristics that can be spatially referenced, then GIS may play a critical role in identifying and describing niche partitioning. The application of geographic information technologies to this aspect of community interactions represents a relatively unexplored role for GIS in ecological research.

In this paper, we compare spatial analysis using GIS with a standard ecological model (EcoSim) of niche partitioning to characterize habitat use by carrion beetles (Silphidae). A group of eight genera and 30 species of carrion beetles occur throughout North America, often forming species assemblages of five or more potentially competing species. In Nebraska, there are six genera and 18 species of carrion beetles (Ratcliffe 1996), including the endangered American burying beetle (*Nicrophorus americanus* Olivier). Within our study site in south-central Nebraska, there are 11 species belonging to two subfamilies, the Nicrophorinae and the Silphinae. Co-occurrence of so many closely related species suggests niche partitioning, but the mechanisms through which these species avoid or reduce competition are unknown.

One manner in which carrion beetles partition niche is the use of different-sized carcasses for reproduction. When a terrestrial vertebrate dies, a fierce competition begins for the nutrients stored in its decomposing carcass. The competitors that use carrion as food (for themselves and their young) include vertebrate scavengers; invertebrates, such as ants, flies, and beetles; soil dwelling fungi; and bacteria (Scott et al. 1987, Ohkawara et al. 1998). Among the competing scavengers are carrion beetles in the subfamily Silphinae, which arrive during the early to mid-stages of carcass decomposition. Adult Silphinae feed on carcasses of any size but only lay eggs on or near large (~1 kg or larger) carcasses such as those of rabbits and deer. Their larvae feed on fly maggots developing on the carcass (Ratcliffe 1996).

Unlike the Silphinae, carrion beetles in the subfamily Nicrophorinae display a unique behavior of burying carcasses, giving these species the common name 'burying beetles' (Milne and Milne 1976). Most burying beetles locate and use carcasses of animals such as birds and voles that die above ground. Upon discovery of a carcass, *Nicrophorus* beetles assess its mass (Lomolino and Creighton 1995) and if it is of appropriate size, a pair of beetles entombs the carcass for later use in rearing young. The burial process is thought to reduce the chances of discovery of the carcass by scavengers, including other carrion beetles that might displace the burying beetles from the carcass (Trumbo 1992, Lomolino and Creighton 1995, Scott 1998).

Numerous studies have examined habitat use and potential niche partitioning of the Nicrophorinae (Anderson 1982, Shubeck 1983, Peck and Kaulbars 1987, Creighton et al. 1993, Lingafelter 1995), while relatively few studies have considered the Silphinae (e.g. Anderson 1982). These studies have used predominant vegetation (e.g. forest, grassland, swampland) as a habitat indicator for species or have based species distributions on statewide physiographic regions (Lingafelter 1995). The results have been mixed and sometimes contradictory, showing the same species to prefer radically different habitat types across its range (Anderson 1982, Lomolino and Creighton 1995, Scott 1998).

Further, few of the previous studies addressed the role of soil texture in habitat preferences of carrion beetles, despite evidence that soil texture may be more important than dominant vegetative type for Nicrophorinae (e.g. Muths 1991, Scott 1998). Soil texture appears to be a critical component for burying beetle species because soil moisture, soil compaction, and soil composition are directly correlated to the speed of carcass burial and consequent removal from competition (Scott 1998). It is likely that the occurrence of a carcass in an inappropriate soil texture prevents burial and reproductive use, as seen for *N. orbicollis* Say in a laboratory setting (Muths 1991). Thus, Nicrophorinae may partition niche by soil texture while other carrion beetle species that do not bury carcasses may not partition niche by soil texture.

Our objectives in this study were to determine if carrion beetle species partition niche by soil texture, to establish baseline information for habitat occurrence for the Silphinae, and to examine the effects of land use on carrion beetle species distribution. To test for niche partitioning, we made an index of the probability of carrion beetle occurrence based on two geo-referenced data layers and field sampling. We compared these results to a niche overlap matrix generated using a standard ecological simulation model.

2 Methods

2.1 Soil Texture

Trap locations based on soil texture were selected to represent the four most prevalent soil textures of Kearney County, Nebraska, USA. These textures were extracted from the geographic soil survey (SSURGO) database for Kearney County provided by the United States Department of Agriculture Natural Resource and Conservation Service (USDA-NRCS) data clearinghouse (www.ftw.nrcs.usda.gov/ssur_data.html). The SSURGO data set consists of georeferenced digital map and attribute data in a 7.5-minute quadrangle format. The projection used for all georeferenced data was

Universal Transverse Mercator (UTM) Zone 14 using the North American Datum 1983 (NAD83).

A soil texture coverage was created from the SSURGO data and the surface texture attribute was linked to each map symbol unit (MUSYM) via the 'Join' function of ArcView 3.2a with MUSYM as the common field (ESRI 2000). In Kearney County, eight textures are identified by the USDA-NRCS classification system: sandy loam, coarse sand and gravel, loam, loamy fine sand, loamy sand, silty clay, silt, and sandy loam. To better represent the textures as they likely affect the distribution of beetles for this study, soils with close proximity and similar physical characteristics were merged into five textures: alluvial, loam, sand, loess, and mixed sand and loam (Plate 1, see plate section). The alluvial soil texture was created by combining the SSURGO coarse sand and gravel textures with the loamy sand texture. Spatially, these soils are found near river and stream systems of the county. The loam texture was created by combining the SSURGO fine sandy loam and loam soil textures. The sandy texture is the same as the SSURGO fine sand texture and was found only in a small band of sand hills in Kearney County. The loess soil texture was created by combining SSURGO silt and silty clay textures. These soils form part of the loess hills of the interior United States and are found in southern Kearney County. Soils that fell into the SSURGO mixed sand-loess texture were not sampled for carrion beetle occurrence because they represent a blend of two other recombined soil textures (sand and loess). These soils are classified as 'No Data' in Plate 1a.

2.2 Land Use

A land use map for southern Nebraska was obtained from the digital land use/land cover data developed for the Cooperative Hydrology Study (COHYST) of the Central Platte River Basin (CALMIT 2001). The COHYST data are in grid format at 30-meter resolution. To utilize this coverage with the SSURGO data set, it was re-projected from the state plane coordinate system, NAD 83, into UTM Zone 14, NAD 83. To acquire the land use map for Kearney County, the 'Grid Clip to Poly' script was executed in ArcView 3.2a. The ModelBuilder feature of ArcView's Spatial Analyst extension was then used to reclassify the land use grid coverage. The categories used in this study were: (1) urban land, (2) agricultural land, (3) range/grass/pasture land, and (4) riparian forests. The four category grid was then converted to a vector coverage. Urban land was not sampled because relatively few carrion beetle species survive in urban settings due to electric lights, pesticide use, and competition with urban scavengers (Ratcliffe 1996). Croplands comprised those areas utilized for the production of cash crops. In 1997, the total harvested acres in the study area was approximately 54% corn, 19% wheat, 8% soybeans, 3% sorghum, and 3% included oats, sugar beets, potatoes, and dry beans (Nebraska Department of Agriculture 1998). This land use category encompasses about 88% of Kearney County (289,799 of the 330,059 acres of Kearney County).

Approximately ten percent of the land (37,398 acres) along the Platte River in Kearney County is managed for hay, native grass, pasture, or rangeland for cattle. These areas comprised the range/grass/pasture land category of this study. Although the study area was originally mixed grass prairie dominated by big bluestem (*Andropogon gerardii* Vitman), little bluestem (*Schizachyrium scoparium* (Michx.) Nash), switchgrass (*Panicum virgatum* L.), and indiangrass (*Sorghastrum nutans* (L.)

Nash), use as rangeland has led to a domination of warm season annual grasses, although many of the native forbs, including stiff sunflower (*Helianthus rigidus* Cass.), rosinweed (*Silphium integrifolium* Michx.), compass plant (*Silphium laciniatum* L.), and dotted gayfeather (*Liatris punctata* Hook.) are still common (Great Plains Flora Association 1986).

The areas adjacent to the Platte River, which forms the northern border of Kearney County, are comprised of lowland prairies, wet meadows, and riparian forests. These land classes were combined into the riparian/scrub category. In the last 20 years, a majority of these lowland prairies have been drained and cultivated for cash crops. In the undisturbed areas, the dominant grasses include big bluestem, indiangrass, prairie cordgrass (*Spartina pectinata* Link), tall dropseed (*Sporobolus asper* (Michx.) Kunth), switchgrass, and sedges (*Carex* spp.). The floodplain or riparian forest communities have open canopies and are dominated by cottonwood (*Populus deltoides* Bartr. ex Marsh) with an under-story of eastern redcedar (*Juniperus virginiana* L.) and roughleaf dogwood (*Cornus drummondii* C.A. Mey) (U S Fish and Wildlife Service 1981).

2.3 Site Selection

Trap locations in Kearney County were selected using ArcView 3.2a to display the SSURGO soil layer and COHYST land use layer. Sites were chosen based on accessibility in geographic areas with greater than 20 ha of the desired soil texture or land-use category and were verified through differentially corrected global positioning system (GPS) measurements. Traps were separated by a minimum of 1 km. While obtaining the GPS positions, habitat characteristics were ground-truthed through visual examination for land use practice and through the 'feel' method for soil texture (Thein 1979). We located three replicate beetle traps in each of the four merged soil textures and three land-use categories of Kearney County.

2.4 Trapping Methodology

Trapping followed the U S Fish and Wildlife Service (1991) protocol as modified by Bedick et al. (1999). Baited pitfall traps were constructed using a five-gallon (18.9 L) plastic bucket with a diameter of 28.5 cm. These buckets were placed at selected sample sites and buried so the lip of the bucket was flush with the ground. The bottom of the bucket was filled with about 10 cm of soil. The carrion bait consisted of a $300\,g \pm 50\,g$ rat carcass which was allowed to decompose for four days prior to trapping. During trapping the bait was placed in a plastic container enclosed with a 0.5 cm screen top, which prohibited beetles or flies from contacting the carrion. A 2.8 cm screen was placed over the top of the bucket and was staked in place to deter scavenging vertebrates from disturbing the trap. A rain cover consisting of a piece of plywood approximately 30 cm by 30 cm was suspended above the trap by 2.5 cm by 5 cm boards. Traps were opened on the same day and were monitored in synchrony. All traps were opened twice per month and monitored every other day for five consecutive days. Localities were sampled from March to October 2000. This sampling period encompassed the seasonal activity period of the carrion beetle community (Wilson et al. 1984). Trapped beetles were identified to species, counted, and released 400 m from the trap after identification. Traps were re-baited as necessary during the sampling period. Data for individual traps were combined across dates for each species collected.

2.5 Statistical Analysis

To test carrion beetle preference for particular soil textures, occurrence by soil association was analyzed using a Kruskal-Wallace one-way analysis of variance (ANOVA) on ranks, based on the number of beetles collected. Where significant differences were detected, Dunn's method for multiple comparisons was used to separate means. The effect of land use on carrion beetle occurrence was tested similarly.

Niche overlap among carrion beetle species was tested by examining the percentage of each species collected in each texture and land use class with EcoSim software version 6.18 (Gotelli and Entsminger 2001). EcoSim is a null modeling program for community ecology investigations that compares observed data patterns with data patterns produced through iterative randomization. EcoSim creates an index of pairwise comparisons of all species (in this case, by soil texture and land use). The pairwise comparisons index ranges from 0 (no overlap) to 1 (complete niche overlap).

There are several options for the EcoSim model, based on assumed ecological interactions. For our test, we used the standard randomization algorithm 3 (RA3) for 1,000 iterations (Lawlor 1980). For each species modeled using RA3, increasing percent occurrence in a specific habitat parameter contributes to a species being interpreted as specialized for that habitat and, thus, defined as occurring in a narrow niche. Species that occur equally across several habitats are interpreted as being generalists and having a wide niche. Combinations of soil texture and land use where a given species was never found (zero states) are reshuffled at each iteration of the randomization algorithm, resulting in a null model in which the species has the ability to occur in any combination of soil texture and land use. RA3 then examines all species simultaneously and tests for overlaps in habitat use. This set of assumptions for RA3 has been found to be the most biologically realistic null model and provides the most conservative estimate of niche partitioning (Winemiller and Pianka 1990).

2.6 Species Occurrence Map Creation

Maps of carrion beetle species occurrence were created based on the percentage of the total number for each species collected from traps in soil classes or land use categories. Percent occurrence for each species in each soil class was calculated by dividing the number caught in a particular soil class by the total number collected in all traps and multiplying by 100. Similarly, percent occurrence for each species in each land-use category was calculated by dividing the number caught in a particular land use by the total number collected in all traps and multiplying by 100.

Maps of occurrence for 11 species of carrion beetles were then created using an 'Identity' overlay with the 'Xtools' extension of ArcView 3.2. Unsampled areas (sandy-loam soil texture and urban land use) were omitted. For each unique combination of soil texture and land use, we calculated the probability of species occurrence by multiplying the percent occurrence for the soil texture layer by percent occurrence in the land-use layer. Caution in interpreting the generated maps should be exercised because of geo-referencing errors that can be magnified through multiplying across layers to create the probability maps.

3 Results

3.1 Habitat preference

Carrion beetle occurrence differed among the soil textures of Kearney County, with most species collected from only one or two soil textures. For example, *Nicrophorus pustulatus* was only collected in habitats with alluvial soil, and *N. carolinus* was almost exclusively collected in sites with sandy soil (Table 1). Other species occurred in multiple soil textures. For example, large numbers of *N. marginatus* were collected in sandy, loess, and loam soils and *N. tomentosus* were collected almost equally from all examined soil textures (Table 1). There was a relatively high degree of variability in numbers of any species among the three traps within a single soil texture. Significant differences (P-value < 0.05) by soil texture were only detected for five species, three of which were burying beetles. Three of the five species occurred more often in alluvial soil, while the remaining two occurred more often in sandy soil (Table 1). These results suggest niche partitioning by soil texture among some burying beetles (e.g. *N. orbicolis* and *N. marginatus*). For those species that overlap in occurrence (e.g. *N. marginatus* and *N. tomentosus*), niche partitioning may occur because of some factor other than soil texture. As Table 1 shows, some species (e.g. *N. pustulatus* and *N. carolinus*) were rarely, if ever, encountered outside of a habitat with alluvial soils.

Carrion beetles also differed in their response to land use. Of the 11 species tested, three only occurred in undeveloped riparian habitat (Table 2). As with soil texture, *N. carolinus* and *N. marginatus* overlapped greatly in occurrence by land use, with the highest numbers of both species being collected in rangeland. As expected, because of disturbance and agricultural inputs, no species occurred more often in agricultural habitat compared to other land uses. However, *N. marginatus* and *N. tomentosus* appeared to be least affected by agricultural practices (Table 2). Significant differences in occurrence by land use were detected in four species, three of which occurred more often in rangeland (*N. carolinus*, *N. marginatus*, and *Thanatophilus laponicus*) and one, *Necrophila americana*, which occurred more often in riparian areas (Table 2). Two additional burying beetle species (*N. pustulatus* and *N. orbicolis*) were only collected in riparian areas.

3.2 Probability maps

Maps of carrion beetle occurrence by soil texture and land use show similar patterns to the statistical differences in relative abundance. The maps show that carrion beetle species can be broadly grouped as either generalists that are likely to occur over several soil textures in Kearney County or as specialists that are restricted to a small range of soil textures and are not likely to be found in other areas. Among species collected from multiple soil textures, the probability maps reveal effects of land use on species abundance. For example, *Nicrophorus carolinus* was most often collected from rangeland sites with sandy soils, while this species was seldom collected from sandy soils in center-pivot irrigated cropland, as shown by the low probability of occurrence in the circular areas in Plates 1 and 2 (see plate section). Additionally, *Necroides surinamensis* and *T. lapponicus* are found almost exclusively in rangeland with sandy soils and avoid sandy cropland (data not shown). In contrast, generalist species that appear to be less impacted by agriculture include *N. marginatus*, *N. tomentosus*, and *T. truncatus* (Plates 1 and 3).

Table 1 Average (±1 S.E.) number of carrion beetles by species collected in pitfall traps placed by soil texture. N.s. = *Necrodes surinamensis*, N.a. = *Necrophila americana*, O.i. = *Oiceoptoma inequale*, O.n. = *Oiceoptoma novaboracense*, T.l. = *Thanatophilus lapponicus*, T.t. = *Thanatophilus truncatus*, N.c. = *Nicrophorus carolinus*, N.m. = *Nicrophorus marginatus*, N.o. = *Nicrophorus orbicollis*, N.p. = *Nicrophorus pustulatus*, and N.t. = *Nicrophorus tomentosus*

	Species										
Soil texture	N.s.	N.a.	O.i.	O.n.	T.l.	T.t.	N.c.	N.m.	N.o.	N.p.	N.t.
Alluvial	3±1.2	27±9.3*	48±5.2	40±2.5*	0.7±0.7	0±0	0±0	1.3±0.9	70±16.8*	16±4.7	9±1.2
Loam	0±0	9.7±5.0	4.7±2.7	3±2.0	1±1.0	1.3±0.7	4.3±0.7	50±15.1	3.3±0.8	0±0	14.3±2.4
Sand	0.7±0.3	1.7±0.9	0±0	5.3±4.8	32±1.2	3±2.1	69±10	87±4.6*	6.7±1.5	0±0	28.7±3.4*
Loess	1±0.7	0±0	0±0	0±0	0±0	0.7±0.7	0±0	70±12.7	0±0	0±0	5.3±0.3

* Significant difference ($P < 0.05$) in abundance with Kruskal-Wallis ANOVA followed by Dunn's Method of mean separation

Table 2 Average (±1 S.E.) number of carrion beetles by species collected in pitfall traps placed by land use. N.s. = *Necrodes surinamensis*, N.a. = *Necrophila americana*, O.i. = *Oiceoptoma inequale*, O.n. = *Oiceoptoma novaboracense*, T.l. = *Thanatophilus lapponicus*, T.t. = *Thanatophilus truncatus*, N.c. = *Nicrophorus carolinus*, N.m. = *Nicrophorus marginatus*, N.o. = *Nicrophorus orbicollis*, N.p. = *Nicrophorus pustulatus*, and N.t. = *Nicrophorus tomentosus*

	Species										
Land use	N.s.	N.a.	O.i.	O.n.	T.l.	T.t.	N.c.	N.m.	N.o.	N.p.	N.t.
River	3.7±1.2	39±12.8*	125±67	62±26.6	1.3±0.3	2.7±1.5	0±0	1.3±1.3	57±6.5	19±8.5	20±4.6
Range	7±3.0	0±0	0.7±0.7	0.3±0.3	39±5.5*	9±0.3	108±41*	285±100*	0±0	0±0	31±4.9
Agriculture	1.7±0.9	0±0	0±0	0±0	11±2.3	0.7±0.7	1±0.6	107±13.7	0±0	0±0	16±5.3

* Significant difference ($P < 0.05$) in abundance with Kruskal-Wallis ANOVA followed by Dunn's Method of mean separation

Five species, *O. inequale*, *N. americana*, *O. novaboracense*, *N. orbicollis*, and *N. pustulatus*, have nearly identical occurrence maps and are found almost exclusively in undeveloped riparian areas with alluvial soil (Plates 1 and 4).

3.3 Niche overlap

Results from the EcoSim analysis show that niche overlap along the resource axes of soil texture and land use is significantly less than expected by the null hypothesis. The results of this model are similar to those obtained with the GIS-generated probability maps (Table 3; Plates 2–4). Beetles sharing similar soil texture preferences and response to land use have high degrees of co-occurrence. For example, the niches based on soil texture and land use for *Necrophila americana*, *O. inequale*, *O. novaboracense*, *Nicrophorus pustulatus*, and *Nicrophorus orbicollis* overlap almost entirely (see Plate 4). Plates 2 and 4 show habitat specialists that do not overlap in distribution with one another and which also have niche overlap indices of less than 0.3 (Table 3). Likewise, *Nicrophorus marginatus* can be identified from Plate 3 as a habitat generalist, with approximately equal probability of occurrence in three land use/soil combinations, and it has four EcoSim niche overlap indices above 0.8 (Table 3).

4 Discussion

We found that spatial probability maps and the EcoSim model of niche segregation produced very similar results (Plates 2–4 and Tables 1 and 2). The EcoSim model calculates the likelihood of species sharing the resources under investigation. Spatial probability maps produced with GIS provide several important elements that are unavailable with the EcoSim software. GIS allows examination of which habitats beetles have in common, while EcoSim only calculates the degree to which habitats are shared. Additionally, GIS indicates where to find these habitats. A third potential use of GIS is the creation of maps that allow analysis of where species distributions do not overlap. These areas suggest the possibility of niche partitioning and could lead to further ecological investigation. Thus, GIS may play a critical role in identifying and describing niche partitioning when species subdivide habitat based on physical characteristics that can be spatially referenced, such as soil attributes.

Previous studies have shown that soil texture may be important to *Nicrophorus* species (e.g. Muths 1991, Scott 1998), suggesting that geographic information technologies can play a role in examining niche partitioning among carrion beetles. For Nicrophorinae, the unique burial of carcasses requires specific soil characteristics, while the Silphinae utilize larger carcasses and are presumably less dependent upon soil features. As expected, this study found soil textures to be important in determining habitat use for several species of burying beetles. Surprisingly, we also found strong differences in habitat use among members of the Silphinae. Nine of the 11 species collected showed affinity for a particular soil texture, suggesting that soil texture can be useful in predicting the occurrence of carrion beetle species (Table 1). The association of Silphinae with particular soil textures may be explained by the fact that these species burrow into the substrate during periods of inactivity (Hoback 2002, pers. obs.). These results demonstrate the usefulness of GIS in ecological research aimed at characterizing community interactions, specifically niche partitioning among competing species.

Table 3 EcoSim probability of niche overlap. Index values are between 0 and 1. Low numbers show lack of shared habitat use, higher numbers show great niche overlap. N.s. = *Necrodes surinamensis*, N.a. = *Necrophila americana*, O.i. = *Oiceoptoma inequale*, O.n. = *Oiceoptoma novaboracense*, T.l. = *Thanatophilus lapponicus*, T.t. = *Thanatophilus truncatus*, N.c. = *Nicrophorus carolinus*, N.m. = *Nicrophorus marginatus*, N.o. = *Nicrophorus orbicollis*, N.p. = *Nicrophorus pustulatus*, and N.t. = *Nicrophorus tomentosus*

	N.s.	N.a.	O.i.	O.n.	T.l.	T.t.	N.c.	N.m.	N.o.	N.p.	N.t.
N.s.		0.53	0.52	0.55	0.71	0.88	0.72	0.81	0.54	0.54	0.81
N.a.			0.96	0.99	0.055	0.26	0.03	0.04	0.94	0.97	0.47
O.i.				0.98	0.03	0.27	0.01	0.01	0.87	0.95	0.43
O.n.					0.08	0.26	0.04	0.03	0.95	0.99	0.46
T.l.						0.89	0.97	0.89	0.07	0.03	0.87
T.t.							0.93	0.92	0.20	0.21	0.87
N.c.								0.88	0.04	0.00	0.81
N.m.									0.03	0.01	0.83
N.o.										0.98	0.42
N.p.											0.40

For *Nicrophorus* species, the EcoSim model showed that some carrion beetles (e.g. *N. tomentosus*) share habitat with many other species, while others overlap with few species. Ecologically, this result is likely explained by differences in activity period or carcass size preference (Shubeck 1971, Scott 1998). For *N. pustulatus*, the high degree of overlap with *N. orbicollis* is probably a result of the reported brood parasitism by *N. pustulatus* on *N. orbicollis* (Anderson and Peck 1985, Trumbo 1992). Niche partitioning among Nicrophorinae by latitudinal distribution (Anderson and Peck 1985), seasonal and diurnal activity patterns (Shubeck 1971, 1983), and mass of carrion resource (Anderson 1982) has been documented. In addition, burying beetle habitat preference has been repeatedly tested for niche partitioning (Anderson 1982, Shubeck 1983, Peck and Kaulbars 1987, Creighton et al. 1993, Lingafelter 1995) and to explain declines in the American burying beetle (Lomolino and Creighton 1996). However, these studies based habitat preferences on vegetation or statewide physiographic regions. Because data on soil characteristics are important to habitat use by carrion beetles, are readily available at relatively fine resolution, and are less dynamic than either vegetation or land use, our approach results in maps that can be used immediately for predicting beetle distributions and over the long term for monitoring.

Land use appeared to impact carrion beetle occurrence. However, because land use is not independent of physiography, several combinations of soil texture and land use (e.g. alluvial agriculture) do not exist and therefore could not be directly tested through sampling and statistical analysis. Despite these limitations, we found that three species favored rangeland habitats and five species occurred more often in habitats that have alluvial soils and are riparian. It is unclear from these results whether the species found near the river prefer these characteristics because of their biology or because these areas provide a spatial refuge from the impacts of agricultural land use. Agricultural activities are likely to affect carrion beetles through the use of pesticides, tilling, and irrigation in cropland and soil compaction in grazed rangeland. As anticipated, we found that no species preferred agricultural areas over other land uses (Table 2).

A logical extension of this work is to use GIS to examine the occurrence of the American burying beetle, *Nicrophorus americanus*, in habitats with differing soil textures and land uses. Incorporating geographic information technologies into research on the habitat preferences of this endangered species would aid in recovery efforts in two ways. First, display and manipulation of digital data layers may aid in the efficient discovery of new populations of the beetle by narrowing sampling efforts to suitable habitat (Creighton et al. 1993, Lomolino and Creighton 1995). Second, precise measures of soil characteristics (Hoback et al. 2000) may be overlaid with species distributions to reveal subtle differences in habitat use that explain the co-existence of apparent competitors. Moreover, spatial analysis of carrion beetle occurrence across the species' range may enhance the success of re-introduction efforts for *N. americanus* by avoiding habitats where competition is likely. GIS may thus play a role in saving this species from extinction.

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