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Abstract

The bunchgrass prairies of the Palouse region in eastern Washington state and adjacent Idaho were almost completely converted to agriculture in the past century. Today, prairie habitat exists only on small remnants scattered across the landscape. The invertebrate fauna of these habitat remnants is poorly known, both in terms of species diversity and community composition. Pitfall traps baited with carrion were used to sample carrion beetles (Coleoptera: Silphidae) during June and July of 2003. Prairie remnants were selected based on size to test whether habitat area influenced the diversity of this important insect community. Three size classes were identified; greater than ten hectares, between ten and two hectares, and less than two hectares. Only remnants of high habitat quality based on previously established floristic criteria were included in the study. Eight species of carrion beetles were collected, most of which were in the genus *Nicrophorus* (the burying beetles). Species richness and Shannon-Wiener diversity were not significantly correlated with habitat area or perimeter to area ratio. Beetle abundance was strongly correlated with soil parent material. The potential significance of soil type was explored with multivariate analyses. Soil characteristics appear to exert a strong influence on carrion beetle communities.

Keywords: Palouse prairie, Silphidae, carrion beetles, *Nicrophorus*, landscape fragmentation

Introduction

The Palouse region of southeastern Washington and adjacent Idaho is characterized by dune-like topography of loess hills overlying basalt and granitic outcroppings (Breckinridge 1986). The Palouse region lies between the Rocky Mountains and Columbia Basin, forming an ecotone between the arid sage-steppe and mesic coniferous forests (Daubenmire 1942). The moderate climate and rich soils once supported lush bunchgrass prairies, dominated by Idaho fescue (*Festuca idahoensis*) and bluebunch wheatgrass (*Pseduoregenaria spicata*). A diverse forb community and abundant shrub coverage, predominantly snowberry (*Symphoricarpus alba*) and wild roses (e.g. *Rosa woodsii*), are also characteristic of Palouse prairie.

As the region was settled by farming families from the eastern United States, the native prairies were quickly converted to agriculture (Tisdale 1961). Black and others (2000) estimate that over half of the Palouse was converted to farmland by the late 1890s. Agricultural conversion continued throughout the twentieth century, and today Palouse prairie may occupy as little as one-tenth of a percent of its former extent (Black and others 2000). Prairie remnants are found primarily on steep northern slopes of the loess hills or on rockier soils derived from granitic parent material (Aller and others 1981, Weddell and Lichthardt 1998), where farming was either impossible or unprofitable (Black and others 2000). Palouse prairie is currently considered a critically endangered ecosystem (Noss and others 1995), with remaining prairie habitat found in relatively small, isolated fragments throughout the region (Weddell and Lichthardt 1998).

Although two major universities are located on the Palouse (University of Idaho and Washington Sate University), the regional fauna has not been well described. Studies of Palouse prairie arthropods have been limited to the natural history and systematics of a few taxa (such as Green 1975). Arthropods are an important part of terrestrial ecosystems because of the many functional roles they fill in ecological communities, and because they represent the majority of species diversity. Arthropod communities in human dominated ecosystems can be surprisingly species rich, maintaining several populations in even very small habitat fragments (Tscharntke and others 2002a).

The fragmented nature of the remaining Palouse prairie may have a variety of negative consequences for the native arthropod biota. Habitat fragmentation increases exposure of arthropod populations to invasive species, disrupts community and population dynamics, and reduces genetic variation (Tscharntke and others 2002b). Managing remnant habitats in relict ecosystems requires applications of landscape ecology, metapopulation theory, and island biogeography. Island biogeography, developed to delineate the effects of isolation and size on species diversity of oceanic islands (MacArthur

Figure 1. The Palouse region, including the "core" area (the snowberry/Idaho fescue plant association) and various other proposed boundaries. Modified from Caldwell 1961.

and Wilson 1963), has been applied to terrestrial habitat "islands" within matrices of altered land use (Weins 1997). Despite some caveats (e.g. Fahrig 2001) the positive relationship between habitat size and species diversity described by island biogeography remains one of the most consistent patterns in biological diversity and ecology (Rosenzweig 2001), and continues to influence conservation planning, including on the Palouse (Weddell and Lichthardt 1998).

Currently, we are conducting inventories of the invertebrate fauna of Palouse prairie remnants. We are also examining how habitat fragmentation affects this fauna, with an emphasis on understanding how remnant size, shape, and the surrounding landscape effect invertebrate communities. This report describes one study of the carrion beetles (Coleoptera: Silphidae).

Beetles in the family Silphidae are obligate carrion feeders. Species in the genus *Nicrophorus* are known as burying beetles because they find and bury small dead animals (such as mice), laying their eggs on the carrion prior to burial (Anderson and Peck 1985, Scott 1998). Carrion beetles were selected for study because they have been documented to travel long distances (Creighton and Schnell 1998, Bedick and others 1999), and could potentially indicate the degree of connectivity between prairie fragments. In addition, carrion beetles may be relatively restricted to prairie remnants and other perennial systems in the region (e.g., land enrolled in the USDA Conservation Reserve Program), since intensive agriculture could limit their successful reproduction within fields (Duelli and others 1999). Habitat destruction and fragment size has been implicated in the endangerment of the American burying beetle (*Nicrophorus americanus*) (Lomolino and others 1995, Lomolino and Creighton 1996). However, relatively little empirical work has been employed to elucidate the impact of habitat fragmentation on carrion beetles. Trumbo and Bloch (2000) found that one carrion beetle species (*Nicrophorus marginatus*) was never trapped in cleared fields smaller than 5 ha (12.5 acres) within a forested landscape. Carrion beetle richness and abundance in New York forests was found to be significantly reduced in small forest fragments in urban and agricultural matrices by Gibbs and Stanton (2001). These results indicate that carrion beetles may be sensitive to habitat fragmentation in the Palouse, and that carrion beetle communities may differ between large and small prairie remnants.

To examine the relationship between prairie fragment size and carrion beetle diversity, twelve prairie remnants in three size classes were sampled for carrion beetles. We predicted that carrion beetle abundance, richness, and diversity would be greatest in the largest remnants. Because the Palouse is heterogeneous with respect to soil type, an important carrion beetle habitat characteristic (Lomolino and Creighton 1996, Scott 1998, Bishop and others 2002), we also compared populations captured on granitic and loessal soils.

Methods

Site Selection

Selection of prairie remnants was influenced by our knowledge of the location and size of extant remnants. To date, there is no comprehensive database that identifies the location and physical attributes of Palouse prairie remnants. Only remnants that contained high quality Palouse prairie communities, as defined by Daubenmire (1942), were selected. Remnants were also selected to comprise three size classes: less than 2 ha (5 acres), between 2 and 10 ha (5–27 acres), and greater than 10 ha (27 acres). Four remnants were sampled in each size class (Figure 1). Distance between remnants varies from approximately one km (0.62 mile) to more than 35 km (21.7 miles). Remnant area and perimeter were determined by walking the borders of each site with a Trimble GEO III GPS unit (Trimble Navigation Limited, Sunnyvale, California). All remnants had clearly delineated borders with the adjacent habitat types. Location points were logged every second. Area and perimeter length were obtained directly from the GPS unit.

Sampling

Beetles were sampled using baited pitfall traps over three one-week periods during June and July, 2003. Thirty-six attractive traps were placed in the 12 fragments. The number of traps employed was stratified with fragment size, with 2 traps in small fragments, 3 traps in medium fragments, and 4 traps in large fragments. Traps were constructed from two 1-quart deli containers, one inside the other and buried flush with the soil surface. A plastic culinary spice container (120 ml) with a perforated screw-cap lid was glued inside the trap and baited with uncooked chicken wings (approximately 90 g). During the first trapping period, the chicken wings were aged for two days. For subsequent collections, raw wings were placed in the

traps with no aging period; hot days and rapid putrescence obviated pre-aging. The quart container was partially filled a 1:1 mixture of propylene-glycol antifreeze (Sierra brand) and water, and covered with a course wire mesh to deter vertebrate scavengers. Traps were open for one week at a time, with a week between each sample (Creighton and others 1993, Gibbs and Stanton 2001). The chicken-wing baits were replaced at the beginning of each trapping period.

Traps were randomly placed within fragments with the proviso that they be at least 100 m (320 ft) apart. At the end of each trapping period, trap contents were collected and taken back to the lab for analysis. All adult beetles in the family Silphidae were identified to species using keys from Anderson and Peck (1985).

Analysis

Abundance and species richness were determined by counting the number of adult carrion beetles and total number of species in each trap. The Shannon-Wiener index was used as a measure of community diversity. The Shannon-Wiener index is calculated as:

$$H' = -\sum_{i=1}^{Sobs} p_i \ln p_i ,$$

where p_i = the proportion of individuals in the ith species (Southwood and Henderson 2000). Linear regression was used to test the hypothesis that abundance, species richness, and diversity are positively correlated with remnant area. Regression was also used to test the relationship of these parameters with the relative amount of edge (area/perimeter ratio). Average total abundance between sites based on soil type was compared with repeated measures ANOVA, assigning soil type as the main effect (two treatment levels, loess and granitic), week as the repeat variable, and pitfall trap as the subject variable upon which repeated observation were made. Soil type was determined from published soil surveys (Donaldson 1980, Barker 1981).

Species abundance data were analyzed separately based on summed total adult beetles for each sampling week in this analysis. *Necrodes surinamensis* was excluded from this analysis because of its infrequency in the data set, and *Nicrophorus investigator* was collapsed into *N. hybridus* because these two species were not reliably distinguished during the first sampling period. A square-root transformation of the abundance data for six beetle species used in the analysis gave the best fit to the assumption of a multivariate normal distribution. Principal components analysis (PCA) was performed on the transformed species abundance data from each sampling period and the entire period to determine the dimensionality of the data, and to detect whether communities differ between sites with granitic and loessal soils. Analyses were performed in SAS (Version 8.2, SAS Institute Inc., Cary, North Carolina).

Results

Adult carrion beetles (10,001 specimens) in eight species were collected during the study (*Nicrophorus guttula*, *N. marginatus*, *N. hybridus*, *N. defodiens*, *N. nigrata*, *N. investigator*, *Thanatopholis lapponicus*, and *Necrodes surinamensis*). According to species distributions noted in Anderson and Peck (1985), these eight species comprise all the carrion beetles likely to occur in the region. *Nicrophorus guttula* was collected in much higher numbers than all other species (Figure 2). *Nicrophorus nigrata*, *N. investigator* and *Necrodes surinamensis* were collected in small numbers in only a few traps.

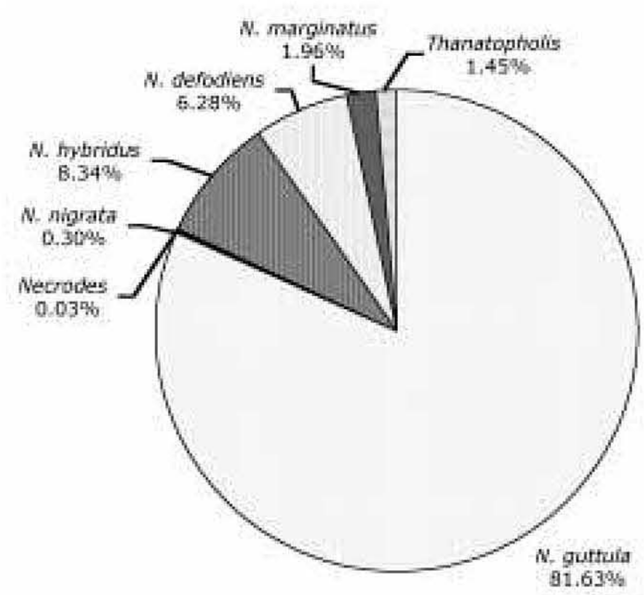

Figure 2. Pie chart of relative abundance of silphid species caught in 2003, given as percentages of the total catch.

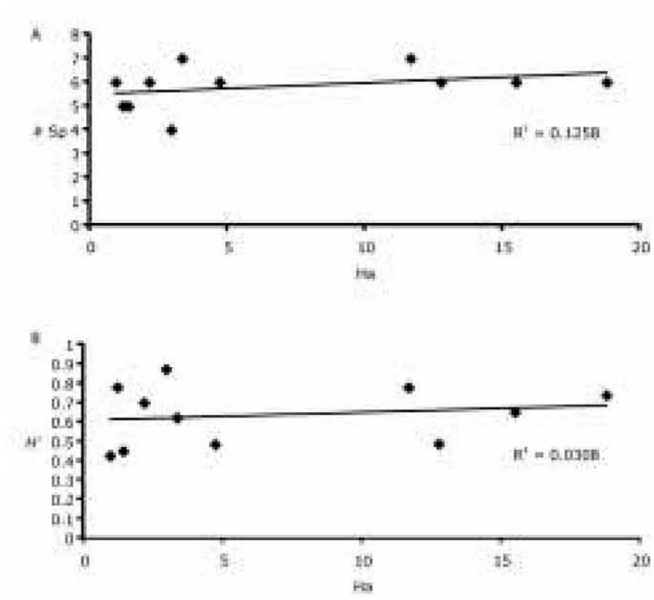

Figure 3. A) Regression of species richness against fragment area (P = 0.284). B) Regression of Shannon-Weiner diversity against fragment area (P = 0.605. Both graphs are based on the total 2003 silphid catch.

We found no significant relationships between fragment area or perimeter-area ratio and species richness or diversity, either by week or for the entire sampling period (Figure 3). By the end of the sampling period, most species had been trapped at least once at most sites, so cumulative species richness was approximately equal between sites. Beetle abundance varied by soil type (Table 1, Figure 4). This observation provided the basis for using ordination to examine the relationship between carrion beetle community and soil type.

Principal components analysis suggests that the structure of carrion beetle communities may vary with soil type within remnants (Figure 5). Traps from loessal soils tended to score higher on principle component one, while little structuring was evident along principle component two. Approximately 70% of the variation for the complete trapping period was explained by the first two Eigenvalues. Removing the infrequently trapped *Nicrophorus nigrita* from the data set improved the separation of these groups (greater than 75% variation explained by the first two Eigenvalues, data not shown).

Discussion

The lack of response of carrion beetle diversity metrics to remnant size may reflect several phenomena. The lack of relationship suggests that, contrary to expectations, the matrix in the Palouse system provides adequate carrion beetle habitat. Despite their distinct vegetation, prairie remnants may not constitute concentrated resource patches for these animals. In other studies (Hatten and others unpublished) carrion beetles were captured by un-baited pitfall traps in both prairie remnants and the surrounding matrix. Although these captures were too infrequent for statistical analysis, they suggest that carrion beetles are moving across the agricultural matrix and could colonize available carcasses. Baited traps in the matrix could help determine if carrion beetles are restricted to any degree to prairie fragments.

The high mobility of carrion beetles (Creighton and Schnell 1998) may reduce response to remnant size at the spatial scale we examined, and could indicate that habitat connectivity is relatively high for this taxon. Movement capabilities of individual carrion beetles in the Palouse have not been assessed; however, studies of the large-bodied American burying beetle, *N. americanus* indicate this species moves as much as 6 km in a single night (Bedick and others 1999).

Effects of remnant size on carrion beetle distribution may have been obscured by other factors. Soil texture is known to affect the ability of carrion beetles to secure carrion resources through rapid burial (Scott 1998, Trumbo and Bloch 2002). Bishop and others (2002) found strong affinities with soil type among several *Nicrophorus* species in Nebraska. Similarly, we found that trap-catch of beetles in remnants with loessal soils differed from trap-catch in remnants with granitic soils. *Nicrophorus guttula*, *N. hybridus*, and *N. marginatus* were much more abundant in loessal soils than in granitic soils. In contrast, *N. defodiens* and *N. nigrita* were most abundant in sites with granitic soils. This suggest that the three most abundant carrion beetle species captured during the study (*N. guttula*, *N. hybridus*, and *N. marginatus*) may be more competitive in the silt-loam soils of the Palouse, while *Nicrophorus nigrita* may be more competitive at burying carrion in coarser soils. *Nicrophorus defodiens* buries carrion beneath plant litter (Anderson and Peck 1985, Trumbo and Bloch 2002), so is unlikely to be affected by soil texture.

Landscape context may also have influenced carrion beetle abundance during the study. Granitic soils on the Palouse are typically associated with coniferous forests. Greater abundance of *N. nigrita* and *N. defodiens* in granitic prairie sites could reflect colonization by these species from nearby forests. *Nicrophorus defodiens* has been captured in

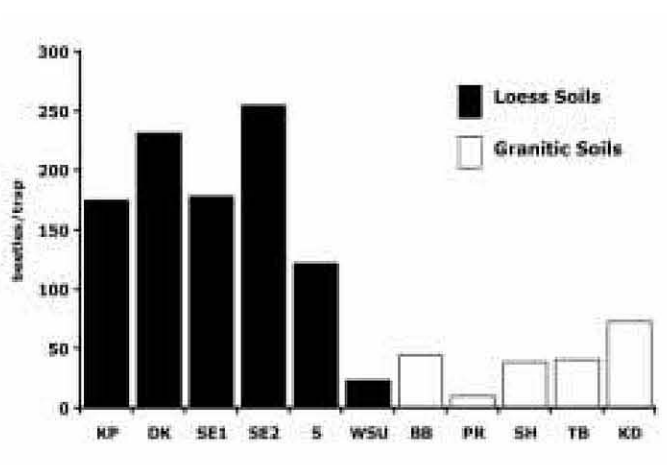

Figure 4. Average per trap adult beetle catch in loess and granitic sites. Average number of beetles per trap was 163 in loess sites, and 40 in granitic sites (P <0.007).

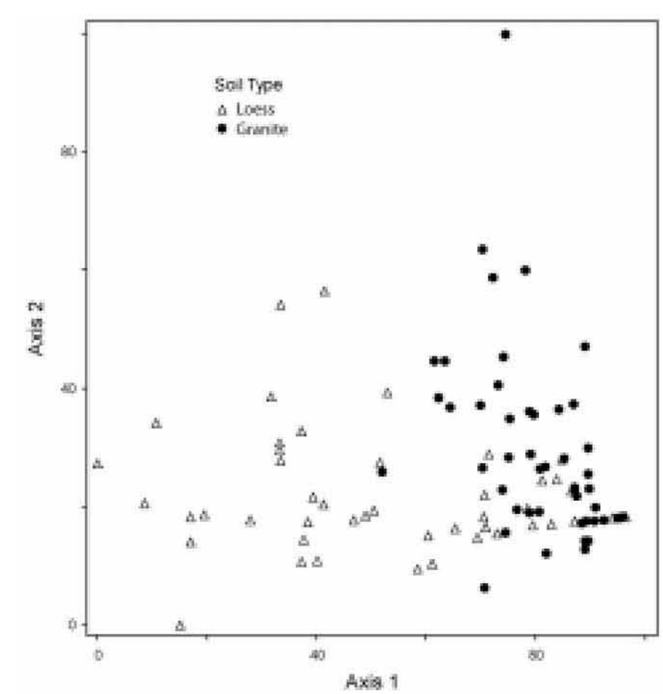

Figure 5. PCA ordination of square root transformed data over the entire study period. Each symbol represents a single trap.

greater numbers and shown to inter more carcasses in forest habitats (Trumbo and Block 2000). *Nicrophorus nigrita* has also been observed to have greater success at carcass burial in mesic coastal forests (Sikes 1996). Cooler conifer forests in the region may be the preferred habitat of these species.

Based on the patterns we have detected, species conservation efforts in the Palouse region should be based on considerations other than remnant size and presence of the Palouse prairie plant community. Rather, our data suggest that attention should be paid to ensuring that conserved areas capture the variability in soil type and associated factors in order to maximize habitat diversity. These factors appear to be important to the co-existence of competitive sympatric species, such as the Nicrophorine beetles discussed here.

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