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Influence of Matrix Elements on Prairie-inhabiting Curculionidae, Tenebrionidae, and Scarabaeidae in the Palouse

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Abstract

It is well established that the invertebrate community in cropland under conservation-tillage (consT) is often enriched relative to the community under conventional-tillage (CT) systems. The question posed in this research is whether consT contributes to the maintenance of regional biodiversity and to the conservation of prairie-inhabiting species in agriculturally dominated landscapes that contain prairie remnants. During 2002, we sampled the ground-dwelling beetle fauna of remnant Palouse prairie and surrounding cropland (under CT and consT) in the Palouse region of northwestern Idaho and southeastern Washington. Biological diversity of the representative taxa—Curculionidae (weevils), Tenebrionidae (darkling beetles) and Scarabaeidae (scarab beetles)—is significantly higher in the prairie than in agricultural fields, while diversity of these groups in fields under consT is intermediate to that found in the prairie and fields under CT. Faunal similarity (Bray-Curtis Index) is greater between consT and prairie than between CT and prairie. Together, these results indicate that ConsT potentially improves conservation and the preservation of prairie species in agriculturally dominated landscapes.

Keywords: Palouse prairie, habitat fragmentation, matrix, insect biodiversity, conservation-tillage, Coleoptera, Curculionidae, Tenebrionidae, Scarabaeidae

Introduction

The destruction and fragmentation of habitat is a leading contributor to biodiversity loss globally. Fragmentation results in a net reduction of native habitat for biota, a change in its spatial configuration, and a reduction in connectivity (Haila 2002). This in turn may alter ecological processes including plant and animal dispersal, movement, reproduction, and population dynamics (see Collinge 2000 for discussion and references). Nevertheless, relatively small native habitat remnants can be important repositories of regional species diversity (Panzer and DeMauro 1983, Daily and others 2001, Ricketts and others 2001, Rodger and Woodliffe 2001, Vidrine and others 2001, Tscharntke and others 2002a) and can be targets for conservation efforts.

While the human-dominated habitats surrounding remnant habitat (termed the 'matrix') have historically been viewed as uniformly hostile to the native biota, it is now understood that the varying quality and structure of the matrix influences 1) movement of biota across the matrix containing native habitat patches and 2) use by native biota of matrix habitats for foraging, reproducing, overwintering, and other activities (Turner and others 2001, Tscharntke and others 2002b). Assessing the distribution and abundance of native biota in matrix and native habitats of fragmented land-scapes has been dubbed "countryside biogeography" (Daily 1997, Ricketts and others 2001). Such a landscape-level analysis can guide conservation efforts that consider the role of the matrix in sustaining native biota.

Worldwide, grasslands are among the ecosystems most intensely impacted by human activity because of their rich potential for agriculture (Tscharntke and others 2002a). In many former grasslands, including the prairie grasslands of North America, the native habitat has been reduced to small, scattered patches isolated within vast matrices of cropland. Two questions arise: "Does the agricultural matrix provide resources or habitat for prairie faunae or is it largely hostile to these species?" and "Do specific agricultural practices influence the suitability of the agricultural matrix as habitat for prairie faunae, especially insects?"

Insects are an important component of biodiversity and perform a large number of ecological functions in ecosystems including herbivory, population regulation, pollination, and nutrient cycling (Samways 2005). Some low-disturbance tillage systems, for example conservation-tillage (consT), have enriched invertebrate faunae relative to high-disturbance tillage systems, such as conventional-tillage (CT), and hence might provide conservation benefits for prairie insects in grassland agro-ecosystems. Conservation-tillage reduces the intensity of tillage and thus maintains more crop residue

on the soil surface after planting than CT systems (greater than 30% compared to less than 15%, Uri 1999). Consequently, consT is also less disruptive to the soil strata than is CT, allowing soil organic matter (Stinner and House 1990), nutrients, and microbial activity (Doran 1980, House and Parmelee 1985) to be concentrated near the soil surface as occurs in undisturbed habitats. Conservation-tillage may also create greater vertical habitat structure in surface crop residue (Hendrix and others 1986), reduce moisture loss, and dampen temperature extremes and fluctuations (House and Parmelee 1985). Both soil biota (e.g., earthworms, mites and Collembola) and soil-surface biota (including many beetle taxa) have been shown to benefit from consT (see Stinner and House 1990 for references).

The Palouse region of southeastern Washington State and adjoining Idaho provides an ideal setting to test the hypothesis that consT increases the richness and diversity of the native faunae in agricultural fields, with potential benefits for conservation of prairie remnants in the landscape. Prior to settlement by Euroamericans, the Palouse supported grasslands and prairie with a rich flora of perennial grasses (Weaver 1917, Daubenmire 1942, Tisdale 1961), forbs and shrubs (Lichthardt and Moseley 1997). Since the 1830s, the region has been steadily developed and transformed. Today, the landscape is a mosaic comprised of cereal and legume crops, grazing lands, USDA Conservation Reserve Program lands, managed forests, urban areas, and isolated parcels of original prairies and grasslands (Dziedzic 1951, Weddell 2001). The remnants are scattered and typically only a few hectares in size. The extent of this conversion has made the Palouse prairie one of the most endangered ecosystems in the United States (Noss and others 1995).

The conditions in the Palouse region are similar to those in other American prairies converted for agriculture. Remnants of Palouse prairie are embedded in a matrix dominated by agriculture, with less than 0.1% of the prairie remaining (Noss and others 1995). In the tallgrass prairie of the midwestern United States, insects whose distribution is limited to remnants of fragmented ecosystems occur in prairie remnants as small as 2.5 ha (Panzer and others 1995). The dominant crop grown in the Palouse is wheat, as in much of the northern Great Plains and Canada. The percentage of cropland under consT in the Palouse is approximately 45%, as is true in other United States' agro-ecosystems (Uri 1999). The Palouse prairie remnants still contain a rich native flora, however. For example, 14 rare and sensitive plant taxa, several of which are listed as globally imperiled (Lichthardt and Moseley 1997), are associated with remnants of Palouse prairie (Weddell and Lichthardt 1998).

In this study we examine the distribution and diversity of selected beetle species across the Palouse landscape, specifically comparing such beetle fauna in consT, CT, and prairie habitats to determine whether faunae are more similar between consT and prairie than between CT and prairie.

Methods

During 2002, we surveyed the ground-dwelling (epigeal) beetle fauna in matrix and prairie habitats of the Palouse. We sampled six consT and six CT agricultural fields, located in Latah County and northern Nez Perce County, Idaho. We also sampled five prairie remnants located in Latah Co., and in Whitman Co., Washington. A large number of beetle families were collected. However, at the time of this publication only three families of Coleoptera-Curculionidae (weevils), Tenebrionidae (darkling beetles) and Scarabaeidae (scarab beetles)–were processed and fully analyzed (The remaining families will be reported at a later date.). Species belonging to these three families differ in feeding habits, vagility, and ecological function, providing an opportunity to assess matrix effects on a diverse subset of the epigeal fauna. Weevils are almost exclusively herbivorous, both in the adult and larval stages. Their host range tends to be narrow, although some are polyphagous (Anderson 2002). Scarab adults tend to be either dung feeders, herbivores, pollenivores or carrion feeders (Ratcliffe and others 2002). In contrast, darkling beetles tend to be vagile generalist detritivores (Wiens and Milne 1989).

Site Selection and Sampling

The agricultural fields sampled were selected based upon rainfall zone, soil type, topography, grower participation, type of crop rotation, and tillage system. Operations that use moldboard plows or extensive tillage, including cultipackers, were classified as CT, whereas operations that used alternative tillage practices, such as light chiseling or harrowing, and drills to insert seed through the preceding years' crop residue were classified as consT. This latter method is also referred to as "direct seeding" (Veseth and Karow 1999). Crop rotations used in the Palouse have two- to five-year cycles. Wheat is the dominant cash crop and hence grown in these rotations as frequently as possible. Legume crops are included to provide nutrients and to break-up disease cycles. Both winter and spring wheat are grown in the region. For this study we sampled only spring wheat (SW) and spring pea (SP) grown in three-year rotations. These crops were chosen because: 1) only two crops could be efficiently sampled during the study; 2) they could be sampled together over the same growing season, and 3) sampling a cereal and a legume provided a better opportunity to assess average tillage effects across crops than by sampling two wheat crops in the rotation. We then identified growers using CT or consT systems, selecting three fields from each crop-tillage system in the rotation (i.e., three CT-SP, three consT-SP, three CT-SW and three consT-SW), for a total of 12 fields.

To capture the arthropods, pitfall traps were placed 50 m apart along transects. Each field received two transects with five traps/transect. Traps consisted of 6-cm diameter, 9 oz. plastic drink cups (70 mm top diameter, 45 mm bottom, and a depth of 95 mm) set in plastic liners flush with the soil surface (Hatten and others 2003). Each trap was filled weekly with 1 to 2 oz. of low-toxicity antifreeze (Sierra brand) and

left open for seven days at a time. Arthropods that fell into the traps were preserved by the antifreeze and subsequently collected. Samples were collected weekly for eight weeks. Trap contents were processed by transferring all specimens into 70% ethanol. Adult beetles of the selected families were then identified to the lowest taxonomic level, or pending identification, sorted to morphospecies (i.e., individuals that are very similar based upon size, shape and color).

The selection of remnant prairies was based largely upon their floral integrity (Weddell and Lichthardt 1998) and size. Intact native plant communities support a greater diversity of native faunae than do disturbed, native plant communities. Larger "habitat islands" support greater species richness of many taxa than do smaller habitat islands (MacArthur and Wilson 1967, Brown 1991). Because we were interested in character-izing as much of the extant prairie-inhabiting beetle fauna as possible, we sampled only the largest Palouse prairie remnants available to us during the 2002 field season. To capture the arthropods, we used a sampling method similar to that employed in the agricultural fields. Differences included: 1) a three-week earlier start date in the fields than in the prairie; 2) a four-week later stop date in the prairie than in the fields; 3) bi-monthly sampling in the prairie as opposed to weekly sampling in the fields; 4) closer spacing between pitfall traps in Rose Creek (the smallest remnant) than in the other remnants and fields (i.e., 15-m intervals in Rose Creek as opposed to 50-m intervals in the other sites); and 5) greater trap densities in each prairie remnant (n = 18) than in each field (n = 10 traps).

In all habitats, traps were left open for one week at a time. Prior to analysis, sample sizes among habitats were standard-ized by randomly deleting from the data set one sample from the consT data set, and 43 samples from the prairie data set, so that each habitat was described by 477 traps collected during the study.

Analytical Methods

The distribution of selected beetles was calculated by noting presence-absence of species by habitat type (prairie, CT, and consT). Beetle diversity for each habitat type was calculated using the following non-parametric indices: richness (S); evenness (E); and Shannon-Wiener (H'):

Richness, $S = \Sigma\ s$ (1)

where S = number of species (richness) and s = species.

Evenness, $E = H' - \ln S$ (2)

where E = evenness of species, ln = the natural logarithm, and H' = Shannon-Wiener index.

Shannon-Weiner index, $H' = -\Sigma\ p_i \ln p_i$ (3)

where H' = biological diversity, p_i = the observed relative abundance of species i, and ln= natural logarithm (indices according to Southwood and Henderson 2000, p.474).

The true number of species S^* for the three beetle fami-lies combined was estimated for each habitat with the first-order jackknife using EstimateS (Colwell 2000).

$$S^* = S_{obs} + L(n-1/n),$$

where n = the number of samples and L = the number of unique species occurring in only one sample (Heltshe and Forrester 1983). In this study, the data were randomly selected and mean S^* estimated 500 times for each cumulative sample. The confidence intervals for S^* was compared to determine whether S^* differed among habitats.

To test whether the diversity of the selected beetle taxa differed significantly among habitats, we used a randomization test. As described by Solow (1993), the prairie data and each matrix data set (CT and consT) used to calculate H' were combinedinto single data sets (CT-prairie, consT-prairie, and CT-consT). Each of these combined data sets was then randomly partitioned by shuffling the data (without replace-ment) into two subsets of size N (where N = number of indi-viduals trapped per habitat). The Shannon-Wiener index was then calculated for each subset and the difference recorded. This procedure was repeated 10,000 times utilizing Resampling Stats (Resampling Stats, Inc. 2001), and the p-value calculated as described by Manly (1991).

Faunal similarity among prairie remnants and fields was determined using the Bray-Curtis similarity index (Bray and Curtis 1957, see Southwood and Henderson 2000):

$$C_N = 2N_j/(N_a+N_b)$$

where C_N = faunal similarity, N_a = the total number of indi-viduals sampled in habitat a, N_b = the same in habitat b, and N_j = the sum of the lesser values common to both habitats.

Results

Composition, Richness and Distribution

The composition, distribution, and abundance of the weevils, darkling beetles, and scarab beetles captured during 2002 are presented in Table 1. Species richness, which is the total number of species per habitat type, is summarized in Table 2. Twelve (39%) of the 31 species captured during the study were exotics. If we exclude the two unidentified weevil species, the exotics accounted for 41% of all species captured. All the exotic species, except for one scarab, were weevils (Table 1). Composition, distribution and diversity patterns differed considerably with and without the inclusion of exotic species. For clarity and comparison purposes, we treat these as two separate analyses below.

All species

Twenty-three (74%) of the 31 species captured occurred in prairie, 13 (42%) occurred in consT, and 17 (55%) occurred in CT. Of the species captured, 10 (32%) occurred only in prairie, 13 (42%) occurred in both prairie and matrix habitats,

Table 1. Composition and abundance of weevils (Curculionidae), darkling beetles (Tenebrionidae), and scarab beetles (Scarabaeidae) across prairie and matrix habitats [conservation-tillage (ConsT) and conventional-tillage (CT) fields] of the Palouse during 2002. The status of each species indicates whether it is native (N) or exotic (Ex), a released biological control agent (BC), or a pest (P) species.

Family Species	Status	Prairie	ConsT	CT
Curculionidae				
Sitona lineatus (Linnaeus)	Ex, P	357	1479	8403
Hypera postica (Gyllenhal)	Ex	0	0	3
Spenophorus cicatristriatus Fahraeus	N	0	4	1
Otiorhynchus orvatus (Linnaeus)	Ex, P	6	1	0
Ceutorhyncus erysimi (Fabricius)	Ex	0	0	1
Ceutorhynchus rapae Gyllenhal	Ex, P	0	0	2
Ceutorhynchus assimilis (Paykull)	Ex, P	1	1	0
Barypeithes pellucidus Boheman	N	12	1	1
Cu11 (morphospecies)		0	0	2
Gymnetron tetrum (Fabricius)	Ex, BC	1	0	1
Eustenopus villosus (Boheman)	Ex, BC	3	1	2
Sibinia maculata (LeConte)	N	0	1	4
Larinus planus (Fabricius)	Ex, BC	0	0	1
Rhinocyllus conicus (Frölich)	Ex, BC	1	0	1
Tychius picirostris (Fabricius)	Ex	0	1	0
Mesagroicus elongatus Buchanan	N	3	0	0
Panscopus squamosas Pierce	N	3	0	0
Anthonomus spp.	N	2	0	0
Cunose (morphospecies)		2	0	0
Lixus perforatus LeConte	N	1	0	0
Tenebrionidae				
Eleodes nigrina LeConte	N	44	13	5
Blapstinus substriatus Champion	N	83	64	2
Eleodes novoverrucula Boddy	N	47	1	0
Coniontis ovalis (LeConte)	N	18	0	0
Coelocnomis californicus Mannerheim	N	2	0	0
Scarabaeidae				
Euphoria inda rufobrunnea (Casey)	N	300	1	2
Onthophagus nuchicurnius (Linneus)	Ex	2	5	14
Serica curvata LeConte	N	9	0	1
Bolboceras obesus (LeConte)	N	1	0	0
Aphodius militaris LeConte	N	1	0	0
Aphodius cribratulus (Schmidt)	N	3	0	0

Table 2. Richness (S), evenness (E), and diversity (H') of all species (native + exotics) (a) and natives species (b) of weevils (Curculionidae), darkling beetles (Tenebrionidae), and scarab beetles (Scarabaeidae) by family across prairie and matrix habitats [conservation-tillage (ConsT) and conventional-tillage (CT) fields] captured during 2002 in the Palouse. Here S = Σ s, where S = number of species (richness) and s = species; E = H' – ln S, where E = eveness of species, ln = the natural logarithm; and H' = -Σ p_i ln p_i, where H' = Shannon-Weiner index of biological diversity, p_i = the observed relative abundance of species i, and ln = natural logarithm; D = 1/C, where D = the Simpson index of biological diversity, C = Σ p_i^2 , with parameters as described above (see Southwood and Henderson 2000, p. 474).

a Habitat	Family	*S*	*E*	*H'*
Prairie	Curculionidae	12	0.194	0.483
ConsT		8	0.025	0.052
CT		12	0.008	0.021
Prairie	Tenebrionidae	5	0.815	1.311
ConsT		3	0.470	0.517
CT		2	0.863	0.598
Prairie	Scarabaeidae	6	0.147	0.263
ConsT		2	0.650	0.451
CT		3	0.526	0.578
Prairie	Combined	23	1.644	0.524
ConsT		13	0.299	0.116
CT		17	0.044	0.016

b Habitat	Family	*S*	*E*	*H'*
Prairie	Curculionidae	6	0.836	1.498
consT		4	0.832	1.154
CT		3	0.790	0.868
Prairie	Tenebrionidae	5	0.815	1.311
consT		3	0.470	0.517
CT		2	0.863	0.598
Prairie	Scarabaeidae	5	0.141	0.226
consT		1	0.000	0.000
CT		2	0.918	0.637
Prairie	Combined	16	0.546	1.515
consT		8	0.436	0.907
CT		7	0.899	1.750

and eight (26%) occurred only in the matrix. Of the species found across habitats, ten occurred in prairie and consT, and ten occurred in prairie and CT. Of the species found only in the matrix, three occurred in consT, while seven occurred in CT. By family, 20 (65%) of the 31 species captured were weevils, five (16%) were darkling beetles, and six (19%) were scarabs. Of the 'prairie only' subgroup, five were weevils, two were darkling beetles, and three were scarabs. All of these are native species, excluding the unidentified weevils. Of the "across habitat subgroup," eight were weevils, three were darkling beetles, and two were scarabs. There was little difference in the composition or distribution of species found among prairie and each matrix habitat (see Native species). Concerning the species found only in the matrix, all eight

were weevils. Of this group, seven occurred in CT, while only three occurred in consT.

Native species

Excluding theexotic species and the two unidentified weevil species, we captured 18 species. Eight of these (44%) were weevils, five (28%) were darkling beetles, and five (28%) were scarabs. Sixteen of these occurred in prairie, nine occurred only in prairie, seven occurred across prairie and matrix habitats, while two occurred only in the matrix. Within the matrix, eight species occurred in consT, while seven species occurred in CT. With respect to the "prairie only" subgroup, four were weevils, two were darkling beetles, and three were scarabs. Of the "across habitat subgroup," one was a weevil, three were darkling beetles, and two were

scarabs. The distribution of species was similar between prairie and each matrix habitat, though one darkling beetle species was found in consT, but not in CT. The two species detected only in the matrix were weevils and occurred in both consT and CT fields.

Abundance

All species

By habitat, abundance of natives and exotics combined was greatest in CT (8,446), lowest in prairie (902), and intermediate in consT (1,573). By species, the weevils were the most abundant group with 10,303 individuals captured, compared to 279 and 339 darkling beetle and scarab individuals, respectively. However, the exotic weevil *Sitona lineatus* (Linnaeus) accounted for more than 99.3% of all weevils collected, and 94% of all beetles. Of *S. lineatus* individuals, 85% occurred in CT fields, while only 14% and 1% occurred in consT and prairie, respectively. Similarly, the native scarab species, *Euphoria inda rufobrunnea* (Casey), accounted for 89% of all scarabs collected, while a native *Blapstinus* species accounted for 53% of all darkling beetles collected. Relative to these species, the other species had low abundance patterns, with the exception of the native *Eleodes nigrina* (LeConte) and *Eleodes novoverrucula* (Boddy), which made up an additional 22% and 17% of the darkling beetles, respectively.

The relative abundance pattern of communities, or species by habitat, can be expressed as evenness (*E*). More evenly structured communities within and across habitats result in higher *E* values compared to less evenly structured communities. The dominance of *S. lineatus* among the weevils, especially in the CT fields, is reflected by low *E* values within CT and among all habitats (Table 2). Similarly, the low *E* value for the scarab community in prairie habit compared to other habitats reflects the dominance of *Euphoria inda rufobrunnea* in prairie habitat. In contrast, the *E* values for the darkling beetles are quite similar for each habitat, reflecting the more even abundance patterns of these beetles among habitats.

Native species

By habitat, abundance of native beetles was greatest in the prairie (535), lowest in CT (16), and intermediate in consT (86). Excluding the exotics, the scarabs were the most abundant group with 315 individuals, compared to 279 darkling beetle and 40 weevil individuals captured, respectively (Table 1). Scarabs had the most uneven abundance pattern of the three families, owing to the high number of *Euphoria inda rufobrunnea* individuals captured in the prairie relative to the other habitats or relative to other scarab species captured. The relative abundance pattern of the native

darkling beetles was no different than that of the entire community, given that all the darkling beetles captured are natives. If *S. lineatus* is not included, the relative abundance pattern of native weevils was even among and across habitats, with species abundance being low.

Diversity (with and without exotics)

The true number of species (*S**) in each habitat type was extrapolated by jackknifing the 31 species data set. With this procedure, *S** was greatest in prairie (28.99 ± 0.11), intermediate in CT (25.98 ± 0.14), and lowest in consT (20.98 ± 0.13). The same analysis, excluding the exotic species, hence resampling an 18-species data set, yielded a different richness pattern with *S** greatest in prairie (19.99 ± 0.08), lowest in CT (9.99 ± 0.08), and intermediate in consT (12.99 ± 0.1). As none of the confidence intervals for *S** overlapped, differences in *S** for all pairwise comparisons are significant ($P < 0.05$). The relative values of *S** with and without exotic species is consistent with the relative values of observed number of species (Table 2). Species diversity as described by *H'* of the three beetle families with and without exotics are presented in Table 2a, and Table 2b, respectively. For the entire data set, *H'* was greatest in the prairie, lowest in CT, and intermediate in consT. Pairwise comparisons using a randomization test indicate these differences are highly significant (Table 3).

For the data set without exotics, the diversity patterns were very different, with *H'* greatest in CT, least in consT, and intermediate in prairie. The strong contrasts in *H'* for the weevil data sets with and without the abundant *S. lineatus* illustrate the sensitivity of *H'* to species numbers and their relative abundance patterns. For this reason, the observed number of species (*S*) may provide the most straightforward
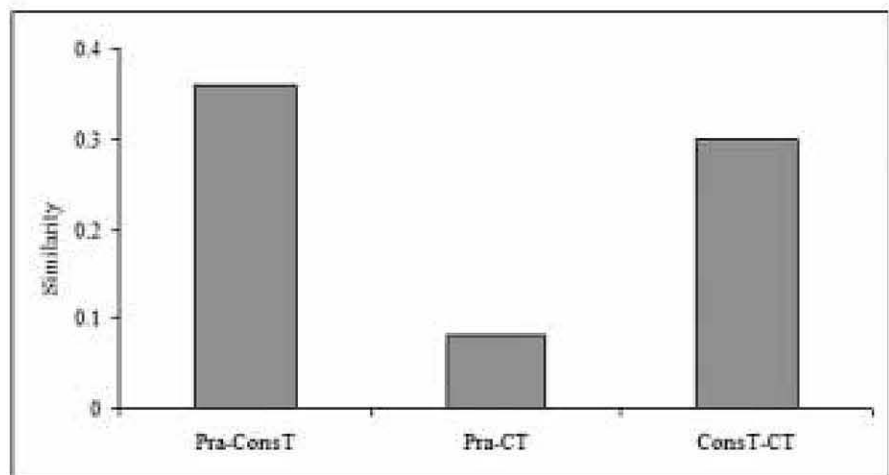

Figure 1. Similarity of weevils, darkling beetles, and scarab beetles among prairie (Pra) and matrix habitats [conventional-tillage (CT) and conservation-tillage (ConsT) fields] during 2002 across the Palouse. Similarity was measured with the Bray-Curtis index $C_N = 2jN/(aN+bN)$, where C_N = faunal similarity, aN = the total number of individuals sampled in habitat *a*, bN = the same in habitat *b*, and jN = the sum of the lesser values common to both habitats (see Southwood and Henderson 2000).

Table 3. Results from a randomization test using 1,000 partitions to determine whether the overall diversity (H') of weevils, darkling beetles, and scarab beetles differed among prairie and matrix habitats [conservation-tillage (ConsT) and conventional-tillage (CT) fields] during 2002 across the Palouse. The notation δ equals the difference in diversity, or community structure, observed among habitats. In this case δ was so large for each paired comparison that the simulated δ used in one-tailed tests and $|\delta|$ used in two-tailed tests never exceeded the observed δ, indicating that diversity among habitats differed significantly ($P < 0.001$) (Solow 1993).

Shannon-Wiener H'	
Observed Prairie	0.524
Observed CT	0.016
Difference δ	0.508
Number simulated $|\delta| > |\delta|$	0.000
Number simulated $\delta >$ observed δ	0.000
Observed Prairie	0.524
Observed consT	0.116
Difference δ	0.408
Number simulated $|\delta| > |\delta|$	0.000
Number simulated $\delta >$ observed δ	0.000
Observed consT	0.116
Observed CT	0.016
Difference δ	0.100
Number simulated $|\delta| > |\delta|$	0.000
Number simulated $\delta >$ observed δ	0.000

measure for comparing diversity among habitats with the proviso that sample sizes are equivalent among habitats (Southwood and Henderson 2000). In our study, sample data were adjusted to standardize sample size among habitats (n = 477 for each habitat).

Faunal similarity (with and without exotics)

Faunal similarity among habitats as measured by the Bray-Curtis (C_N) index is both a function of the number of species in common to both habitats and the abundance of species in common. Habitats with a greater number of species shared among them exhibit greater faunal similarity than those with fewer species shared among them, assuming that abundance patterns for each comparison are the same. Habitats with the same number of species in common but with different abundance patterns will differ in similarity. Those with similar abundance patterns among shared species will exhibit greater faunal similarity than those with less similar abundance patterns.

In our study, faunal similarity was greatest among prairie and consT, least among prairie and CT, and intermediate among CT and consT (Figure 1). We observed the same similarity patterns when the exotic species were excluded from the analysis, with C_N greatest among prairie and consT (0.26), least among prairie and CT (0.039), and intermediate among CT and consT (0.215). Analysis of faunal similarity by taxonomic family (Table 4) clearly indicates that the darkling beetle faunae are much more similar among prairie and consT

than among prairie and CT, and contributes significantly to overall similarity patterns observed during this study.

Discussion

The first question we posed in this study was whether the agricultural matrix provides resources or habitat for prairie faunae, or is it largely hostile to these species. Our study clearly indicates that native prairie-inhabiting weevils, darkling beetles, and scarabs use matrix habitats of the Palouse. For instance, within these three families we found that as many as 39% of the native species occurred in both prairie and matrix habitats. An additional 11% occurred only in the matrix, while the remaining 50% occurred exclusively in prairie remnants. Other studies have found similar insect distribution patterns in fragmented ecosystems, suggesting matrix support for native biota. For example, Ricketts and others (2001) documented that 42% of forest-inhabiting moth species occurred across a variety of agricultural habitats, while 58% were restricted to forest remnants. Similarly, bird studies in tropical agro-ecosystems have also shown that many forest bird species commonly use matrix habitats (Estrada and others 1997, Daily and others 2001), indicating the potential for matrix management to improve conservation of these and perhaps other species (Daily and others 2001).

Our data indicate that weevils, darkling beetles, and scarabs respond in a differential manner to habitat fragmentation. The mechanisms contributing to the observed distribution and abundance patterns are not known, and the scope of our study limits our ability to detect underlying mechanisms. Nonetheless, we offer the following observations. Of the native species found only in the remnants, four were weevils, three were scarabs, and two were darkling beetles. In contrast, of the native species found across habitats, one was a weevil, two were scarabs, and three were darkling beetles. Hence, the distribution patterns of the taxa found during our study follow a gradient, with a greater proportion of probable specialists, such as weevils, restricted to the remnants, and a greater proportion of generalists, such as darkling beetles, occurring across habitats. Vagility and polyphagy have been identified as important characteristics of biota using fragmented ecosystems (Thomas 2000). Polyphagous species are more likely to find resources in highly fragmented ecosystems than are monophagous or specialist feeders. For the generalist, remnant habitat may be connected by useable, lower quality habitat patches across the landscape (Tscharntke and others 2002b). Thus, it is not unexpected that the most widely distributed native species found during this study are darkling beetles. Nor is it unexpected that a higher proportion of specialist feeders are restricted to prairie remnants. For the specialist, resources are inherently more isolated. Specialists, especially those with poor dispersal capabilities, are more vulnerable to fragmentation effects and extinction than generalists (Steffan-Dewenter and Tscharntke 2000). Remnant-dependent species tend to be specialists or poor dispersers.

The second question we asked is whether specific agricultural practices influence the suitability of the agricultural

Table 4. Similarity of weevils, darkling beetles, and scarabs among prairie and matrix habitats [conservation-tillage (ConsT) and conventional-tillage (CT) fields] captured during 2002 across the Palouse. Similarity was measured with the Bray-Curtis index C_N = $2jN/(aN+bN)$, where C_N = faunal similarity, aN = the total number of individuals sampled in habitat a, bN = the same in habitat b, and jN = the sum of the lesser values common to both habitats (see Southwood and Henderson 2000). Higher C_N values reflect greater faunal similarity among habitats. Similarity estimates for the entire weevil community (natives + exotics) was not feasible due to extreme differences in relative abundance patterns.

Data set	Compared habitats	Weevils	Darkling beetles	Scarabs
Natives + exotics	Prairie - consT	**	0.57	0.02
	Prairie - CT	**	0.07	0.03
	CT - consT	**	0.16	0.52
Natives only	Prairie - consT	0.12	0.57	0.01
	Prairie - CT	0.06	0.07	0.02
	CT - consT	0.46	0.16	0.50

matrix as habitat for prairie faunae. Our results showing greater similarity in the native beetle faunae between consT and prairie than between CT and prairie, suggest that low-disturbance tillage is conducive to prairie species in the landscape. The response pattern of these faunae to tillage also indicates that species and taxa respond differentially to tillage on the Palouse, perhaps owing to the influence of tillage on environmental or ecological factors. Our study indicates the native darkling beetle community in consT, as opposed to CT fields, is more similar to the native darkling beetle community in prairie. Three species of darkling beetles were found in consT fields compared to two in CT fields, and the abundance patterns were more similar between these species in consT and prairie than between those found in CT fields and prairie. This clearly suggests that adults of these vagile generalist detritivores, which are known to forage on the soil surface across large areas (Wiens and Milne 1989), benefit from consT. More research is required to elucidate the mechanisms contributing to their conservation under low-disturbance tillage regimes.

We hypothesized that consT should increase the richness and diversity of native prairie faunae relative to CT systems across the matrix. Our results yield unexpected findings. First, we found that diversity as measured by H' is greatest in prairie, least in CT and intermediate in consT, as hypothesized. These diversity patterns include, however, 12 exotic species (39% of the overall faunae), 11 of them weevils, collected during the study. Five of these species are biocontrol agents, and at least one species, *S. lineatus*, feeds broadly on legumes, and is a key pest of spring peas in the Palouse. Of these 12 exotics, we found five in prairie remnants. Diversity patterns for the native faunae differed depending on the analysis method applied. Observed richness yielded the most straightforward index of diversity for both overall faunae and native faunae. With this metric, the number of observed species was lower in consT than CT fields when both native and exotic species were considered, but slightly higher in consT than CT when exotic species were excluded from the analysis. In contrast, observed richness was always greater in prairie than in matrix habitats. Extrapolation methods confirm these richness patterns, and indicate these differences to be significant. Our findings underscore the importance of small remnant habitats

for biodiversity conservation. Fifty percent of prairie species were found only in remnant habitats, suggesting that the matrix is hostile for a large proportion of prairie species, but, perhaps, not as hostile for other prairie species.

The implications for management are twofold: 1) because species respond differently, management strategies may differ depending on which species are of concern; and 2) discovering more broadly applicable principles for management will require a better understanding of mechanisms that lead to idiosyncratic responses by species.

Acknowledgments

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