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Authors: VanDyke, Kirk A., Latchininsky, Alexandre V., and Schell, Scott P.

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Importance of ecological scale in montane grasshopper (Orthoptera: Acrididae) species structure in similar habitat between differing soil textures and dominant vegetative canopy coverage

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KIRK A. VANDYKE, ALEXANDRE V. LATCHININSKY, SCOTT P. SCHELL

Dept. of Renewable Resources, University of Wyoming, Laramie WY 82071. Email: kirkv30@uwyo.edu; Latchini@uwyo.edu

Abstract

Discrepancies in scale dynamics often make cohesive structural conclusions difficult, especially when dealing with ecological variance. We studied presence and abundance of grasshopper species in similar, yet distinct, montane habitat of southeast Wyoming and northern Colorado, USA. By limiting ecological variance, grasshopper species structure at two behavioral scales (grouped species dynamics and individual species interactions) was maximized with regard to soil texture and vegetative canopy coverage. Combining univariate and multivariate statistical methods, we note montane grasshopper species interactions to be scale dependent.

Key words

ecology, grasshopper, community, scale, structure, habitat

Introduction

As acridologists, we struggle to define cohesive grasshopper species interactions in relation to biotic and abiotic habitat requirements. Simplifying these ecological interactions proves important in both management practices and evolutionary understanding. With this though, we run the risk of adhering to dichotomous conclusions (*i.e.*, either community or facultative assemblage) without incorporating scale dynamics into the analysis.

North American grasshopper outbreaks, especially in the central Rocky Mountain region and adjoining steppe, typically consist of numerous species, some of which are historically abundant (dominant) and others historically not abundant (subdominant). This species diversity also exists in nonoutbreak scenarios. How these species are structured among habitats is behaviorally associated with feeding preferences, flight capacity, and reproductive potential (Pfadt 1996).

Regarding grasshopper species structure among habitats, conflicting information emerged between species behavior akin to communities (Kemp *et al.* 1990a) or facultative assemblages of species (Kemp 1992). Habitat requirements for grasshopper species behavior have emphasized the relationship to vegetation (Joern 1979, Joern & Lawlor 1980, Kemp *et al.* 1990a, 1992, Ritchie & Tilman 1993) and soil (Johnson 1989, Skinner & Child 2000, Latchininsky 2001, Schell & Lockwood 1997). In montane systems however, vegetative habitat requirements along a precipitation/elevation gradient, while significant (Kemp *et al.* 1990a), may be complicated by the effects of varied minimum threshold temperatures and developmental rates between grasshopper species along such a gradient (Watcher *et al.* 1998).

Kemp *et al.* (1990 b) noted the importance of spatial scale in

rangeland grasshopper studies with regard to pest management issues, but assumptions about temporal scale in rangeland and montane studies are also worth noting. Past studies cited in this area of ecology, while informative, are plagued with confounding variables of scale which influence quantitative interpretation of results.

Soil, in relation to vegetation, incorporates greater temporal scales regarding grasshopper species than vegetation alone, due to its direct influence on grasshopper oviposition (Uvarov 1977), embryonic development (Hewitt 1985), and hatching success (Isley 1938), and its indirect influence on vegetative composition. Vegetation changes annually, while soil texture changes over periods of 100 to 1,000 years, or greater. Precipitation and evaporation change annually, but elevation captures ecological dynamics that change over periods of 100 to 10,000 years, or greater (VanDyke *et al.* 2004).

To account for this, we created a narrowly-defined ecological region to address confounding scale variables (elevation, precipitation, temperature, vegetation type) and isolate scale variables of interest (canopy coverage, soil texture) with regard to diverse species scale dynamics (group interactions versus individual species interactions). We incorporated the scales of time with regard to grasshopper habitat: the present (canopy coverage only) and hundreds of years (soil), while removing confounding temporal and spatial variables by studying distinct, disjunct meadows of the same elevation, precipitation, temperature, and vegetative species composition.

The Medicine Bow Mountains of southeast Wyoming and northern Colorado provide the necessary similarity in habitat within a localized region, while exhibiting variation in soil types and vegetative canopy coverage (USDA-FS 1985).

In the central Rocky Mountains of North America, a montane system is an elevational zone characterized by lodgepole pine, limber pine, and ponderosa pine forests, with isolated mixed grass-forb meadows. It resides below a subalpine elevational zone, which is characterized by Engelmann spruce and subalpine fir forests interspersed with tundra. The alpine zone is the tundra elevational ecosystem (Barbour *et al.* 1987). We studied select, disjunct, montane meadows, to limit environmental variance from multiple elevational ecosystems.

We looked at grasshopper species presence and abundance as a function of select soil textures and vegetative canopy coverages, combining univariate and multivariate analysis, to determine at what structural scale, if any, these montane species behaved as cohesive communities or relatively independent assemblages. If scale dependence in a narrowed study doesn't exist, with grasshopper habitat

addressed, then both total and individual species interactions will be either 1) cohesive communities or 2) independent assemblages at all levels (group or individual) with regard to narrowly-defined habitat differences.

Methods

Sites.—In July, 2006, 15 montane meadows in an elevation range from 2636 to 2690 m in the Laramie River drainage of the Medicine Bow/Routt National Forest, Wyoming and Colorado, were surveyed for similar dominant plant coverage and differing soil textures. Selected meadows were bordered by mixed limber and lodgepole pine stands, with some aspen and ponderosa pine. The closest of the 15 meadows were 322 m apart; the most distant of the 15 meadows were 8529 m apart. The meadows ranged in area from 1 to 5 ha.

A qualitative classification of vegetative and bare-ground coverage

was based on species dominance types (Whittaker 1962, Grossman *et al* 1998). Percentages of bare ground and canopy coverage of the five most prominent plant species were visually estimated at each meadow along a transect and classified into 5 coverage groups: 1 = 1 to 20% coverage, 2 = 31 to 40%, 3 = 41 to 60%, 4 = 61 to 80%, and 5 = 81 to 100% (VanDyke *et al.* 2004). The percentage of bare ground or plant species was based on the median of the appropriate coverage classification. The plant specimens were collected, pressed and later identified to genus.

Soil subsamples were taken every 40 paces along a transect, starting at a random location of the meadow edge, by removing the top 8 cm of a 10-cm² area. Subsample sizes ranged from 2 to 5, depending on the size of the meadow. Meadow subsamples were later hand textured for consistency throughout the meadow, and differing subsamples were analyzed for soil texture using a LaMotte Chemical Soil Analysis Outfit, Model AM-31 (Chestertown, MD, 21620). Soil texture classifications based on USDA (1950) standards were obtained from the percentage composition.

Table 1. Grasshopper species abundance per 10 selected meadows; meadow locations (GPS).

Meadow	GPS (N) Latitude	GPS (W) Longitude	#/ m ²	% sand	soil	Plant Group	<i>Arphia</i> <i>conspersa</i>	<i>Camnula</i> <i>pellucida</i>	<i>Circotettix</i> <i>rabula</i>	<i>Pardalophora</i> <i>haldemani</i>	<i>Spharagemon</i> <i>equale</i>
1	41.02.264	106.06.429	1.0	50	L	2	0	5	0	1	2
2	41.03.247	106.04.922	1.75	60	S	2	0	17	0	0	0
3	41.03.114	106.04.135	0.25	47	L	2	1	3	1	4	5
4	41.03.143	106.03.821	1.0	67	S	1	0	0	1	2	5
6	41.02.539	106.04.739	0.75	67	S	2	0	10	0	0	0
9	41.01.718	106.04.580	0.75	44.3	L	2	0	4	1	0	0
12	41.01.134	106.06.134	0.5	56.5	S	2	0	14	0	0	0
13	40.59.972	106.07.774	0.75	53	L	1	0	0	0	0	10
14	40.59.617	106.07.702	0.25	43	L	2	0	5	0	0	1
15	40.59.826	106.06.901	0.25	62	S	1	0	2	0	0	0

Table 1. (contin.)

Meadow	<i>Trimerotropis</i> <i>campestris</i>	<i>Trimerotropis</i> <i>latifasciata</i>	<i>Trimerotropis</i> <i>pallidipennis</i>	<i>Trimerotropis</i> <i>verruculatus</i>	bandwing nymph	<i>Aeropedellus</i> <i>clavatus</i>	<i>Bruneria</i> <i>brunea</i>	<i>Chorthippus</i> <i>curtipennis</i>	slant-faced nymph
1	2	0	0	1	4	0	0	2	0
2	1	0	0	6	0	1	0	3	1
3	1	0	0	1	0	0	0	2	0
4	2	0	0	0	0	0	2	3	2
6	0	3	1	2	0	0	0	1	2
9	0	0	1	0	0	0	1	1	0
12	0	0	0	1	0	0	0	0	0
13	0	0	0	0	1	0	4	1	0
14	0	0	0	0	0	0	0	0	0
15	0	0	0	4	1	0	4	0	0

Table 1. (contin.)

Meadow	<i>Melanoplus</i> <i>alpinus</i>	<i>Melanoplus</i> <i>bruneri</i>	<i>Melanoplus</i> <i>dawsoni</i>	<i>Melanoplus</i> <i>femurrubrum</i>	<i>Melanoplus</i> <i>infantilis</i>	<i>Melanoplus</i> <i>kennicotti</i>	<i>Melanoplus</i> <i>occidentalis</i>
1	4	0	0	0	0	1	1
2	0	0	0	0	0	3	0
3	2	0	0	0	0	2	0
4	1	0	1	0	1	3	0
6	0	0	0	0	0	0	0
9	0	1	0	1	0	2	0
12	1	1	0	0	0	0	0
13	0	0	0	0	0	2	1
14	0	0	0	0	4	0	0
15	0	0	1	0	0	1	0

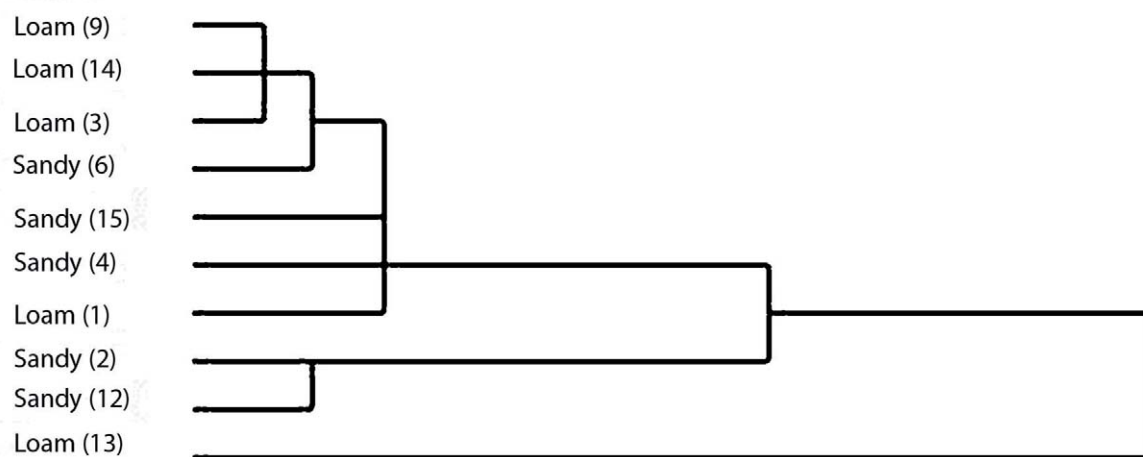


Fig. 1. Dendrogram of hierarchical cluster analysis for grasshopper species by meadow (meadow #).

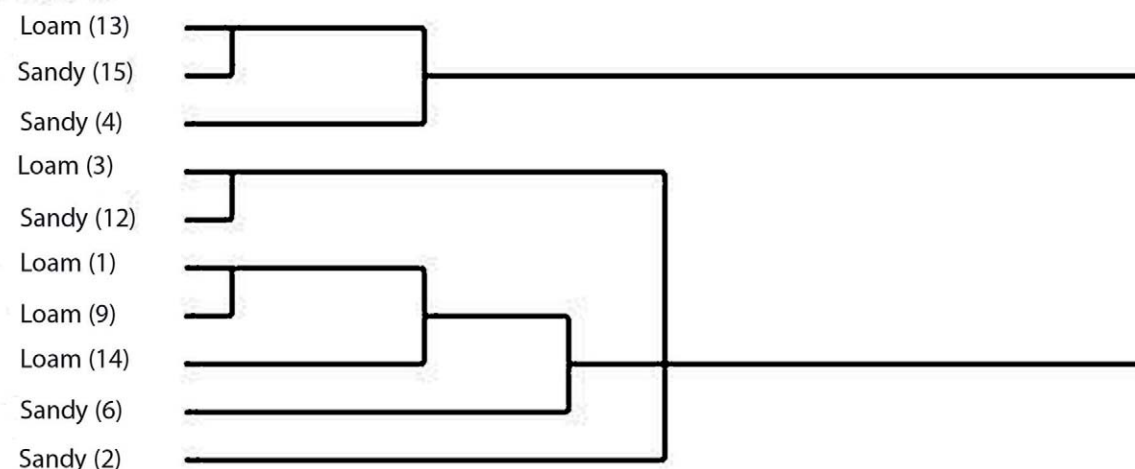


Fig. 2. Dendrogram of hierarchical cluster analysis for vegetation by meadow (meadow #). Group 1 comprises meadows 13, 15, 4 and Group 2 comprises meadows 3, 12, 1, 9, 14, 6, 2— with significant ($p < 0.05$) differences between groups for *Artemisia*, *Antennaria*, bare ground, and *Eriogonum* coverage.

Of the original 15 meadows surveyed, ten were chosen based on similarity of dominant plant coverage and differences in soil texture. These included five meadows of sandy loam soil, three of loam, one changing from loam to silt loam, and one predominantly silt loam. The resulting ten meadows were grouped according to their sand composition as follows: the five sandy loam meadows (with 57 to 67% sand composition) comprised group 1, and the other five selected meadows (with 40 to 50% sand composition) comprised group 2.

Geographic coordinates of approximate centers of the ten selected meadows were defined using Garmin GPS (Table 1).

Grasshopper composition.—On August 10, 2006 and August 30, 2006, the ten chosen meadows were surveyed for grasshopper species presence and abundance. The choice of the sampling dates was based on the phenology of montane grasshoppers in the Rocky Mountain region, where mid-to-late August usually corresponds to maximum species diversity and abundance (Pfadt 1996). Grasshopper density per m^2 was assessed on August 10, 2006 by 40 counts of grasshoppers in a visualized $0.1 m^2$ -area (Pfadt 1977, Legg *et al.* 1996). Grasshoppers were collected using 38-cm diameter sweep nets with 100 low and slow sweeps (bottom of net near the ground;

one sweep per step), and 100 high and fast sweeps (bottom of net at top of vegetation; two sweeps per step). Due to low grasshopper densities, sweep-net sampling was followed by 30 min of hand sampling per meadow. Collections were later analyzed for species composition and abundance at the University of Wyoming, using the guides of Pfadt (1996), Capinera & Sechrist (1982), Otte (1984), and by comparing insects with identified specimens from the Robert E. Pfadt Grasshopper Collection (Department of Renewable Resources, University of Wyoming). All adults were identified to species. Nymphs were grouped at subfamily level, as so-called “bandwing” nymphs (Oedipodinae) and “slant-faced” nymphs (Gomphocerinae).

Data Analysis.—All data analysis was conducted in SPSS v.14. Hierarchical cluster analysis was conducted on grasshopper species composition with regard to soil type, as well as vegetative canopy coverage with regard to soil type, using Squared Euclidean Distance and Centroid linkage. Discriminant analysis was conducted on grasshopper species composition between vegetative canopy coverage and soil texture groupings: sandy loam and loam-to-silt loam. Partial correlations were conducted between grasshopper species and vegetation, controlling for per cent sand in soil. Multi-

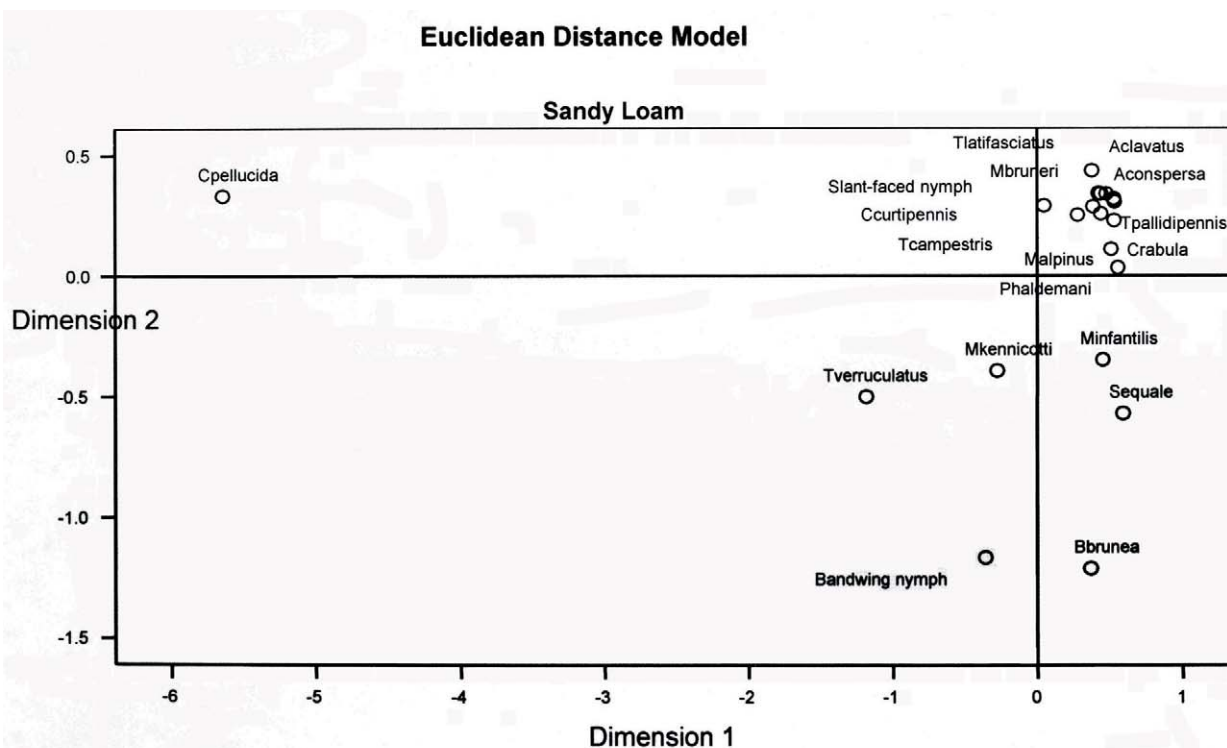


Fig. 3. Results of multidimensional scaling using 2-dimensional Euclidean distance scaling model of grasshopper species in sandy loam meadows.

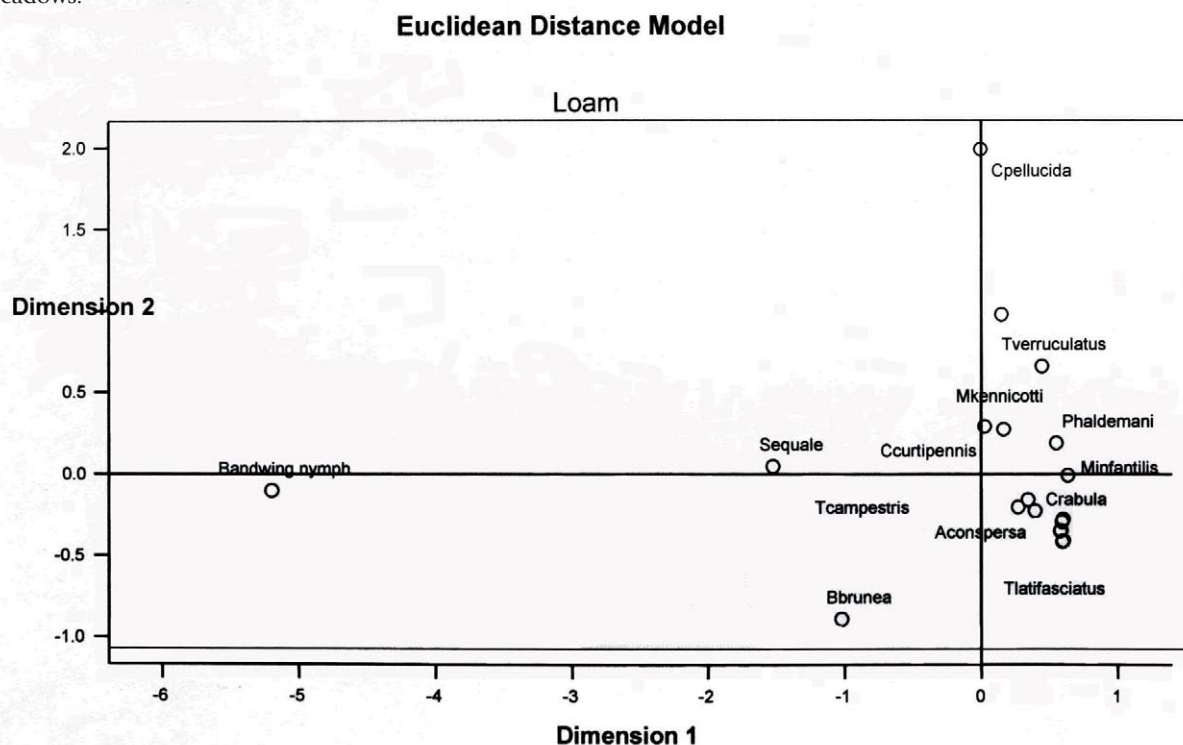


Fig. 4. Results of multidimensional scaling using a 2-dimensional Euclidean-distance scaling model of grasshopper species in loam to silt meadows.

dimensional scaling was conducted for grasshopper species for each canopy coverage and soil group. We performed t-tests for each species between soil groups and plant groups, as well as overall grasshopper densities between soil groups. Linear regression was performed for grasshopper density in relation to per cent sand in soil.

Results

A total of 190 specimens belonging to 19 identified grasshopper species was collected. The number of species per meadow varied from 3 to 10 (Table 1).

Table 2. Partial correlations ($p < 0.05$) of grasshopper species regardless of soil texture.

	A. <i>conspersa</i>	C. <i>pellucida</i>	C. <i>rabula</i>	P. <i>haldemani</i>	S. <i>equale</i>	T. <i>campestris</i>	T. <i>latifasciatus</i>	T. <i>pallidipennis</i>	Bandwing nymph	A. <i>clavatus</i>	C. <i>curtipennis</i>	M. <i>bruneri</i>
<i>P. haldemani</i>	0.67											
<i>T. pallidipennis</i>							0.71					
<i>B. brunnea</i>		-0.75			0.67				0.71			
<i>C. curtipennis</i>												
Slant-faced nymph						0.82	0.79					
<i>M. alpinus</i>			-0.67									
<i>M. dawsoni</i>				0.77								
<i>M. femurrubrum</i>			0.71					0.71				0.71
<i>M. kennicotti</i>										0.70	0.79	
<i>M. occidentalis</i>	0.80											

Table 3. Partial correlations ($p < 0.05$) of grasshopper species regardless of dominant plant group.

	A. <i>conspersa</i>	C. <i>pellucida</i>	C. <i>rabula</i>	P. <i>haldemani</i>	S. <i>equale</i>	T. <i>campestris</i>	T. <i>latifasciatus</i>	T. <i>verruculatus</i>	Bandwing nymph	A. <i>clavatus</i>	C. <i>curtipennis</i>
<i>P. haldemani</i>	0.72										
<i>A. clavatus</i>		0.67						0.69			
<i>B. brunnea</i>									0.70		
Slant-faced nymph						0.81	0.86				
<i>M. dawsoni</i>	0.75			0.76					-0.68		
<i>M. femurrubrum</i>			0.81								
<i>M. kennicotti</i>										0.77	0.81
<i>M. occidentalis</i>	0.81				0.69						

Hierarchical cluster analysis for grasshopper species composition by meadow resulted in no clear clustering (Fig. 1), but the same analysis for vegetative composition by meadow, resulted in two final clusters (cluster 1 with three meadows, cluster 2 with seven meadows), with a distance of 2.181 (Fig. 2). Descriptive F-tests showed significant ($p < 0.05$) differences between two clusters for *Artemisia*, *Antennaria*, bare ground, and *Eriogonum* plant-genera coverage. As anticipated after the results of hierarchical cluster analysis for grasshopper species, discriminant analysis for grasshopper species composition between the two soil groupings was insignificant. The resulting first function had a Wilks' $\lambda = 0.095$, $p = 0.309$. Discriminant analysis for grasshopper species composition between the plant groupings was also insignificant. The resulting 1 function had a Wilks' $\lambda = 0.109$, $p = 0.354$.

With grasshopper species not discriminating in a community manner with regard to soil texture or variation in canopy coverage, the question became whether or not species behaved independently to one another with regard to habitat variation, thereby acting as facultative assemblages. Partial correlations between grasshopper species and vegetation revealed clear relationships ($p < 0.05$) among

select grasshopper species, despite variation in habitat (Tables 2 and 3). Additionally, some species showed clear relationships ($p < 0.05$) with plant genera and bare ground when corrected for the per cent sand composition in soil (Table 4).

These correlations can be more readily observed using Multidimensional Scaling for soil type (Figs 3 and 4) and dominant plant groups (Figs 5 and 6). These analyses used a two-dimensional Euclidean distance scaling model with s-stress convergence = 0.001, minimum s-stress value = 0.005 and maximum iterations = 30. Correlated grasshopper species can be found in close proximity in two dimensional space, with notable exceptions being *Camnula pellucida*, *Bruneria brunnea*, *Spharagemon equale*, and the 'bandwing nymphs' (subfamily: Oedipodinae). Species lists and descriptive statistics for both soil types and plant groups (Table 5) suggest that dimension 1 in the 4 multidimensional scaling figures is a trend toward sub-dominance. Dimension 2, however, is not clearly interpretable, a limitation common to multidimensional scaling. The t-tests revealed significant differences ($p < 0.05$) between plant groupings for *B. brunnea*, and a trend toward significance ($p < 0.10$) between plant groupings for *C. pellucida* and *S. equale*. No linear relationship ($p > 0.05$) existed between grasshopper densities and per cent sand in soil, suggesting densities did not influence scale results with regard to soil.

Table 4. Partial Correlations between grasshoppers and vegetation ($p < 0.05$).

Species	Plant Genus or Bare Ground	Correlation
<i>A. clavatus</i>	<i>Festuca</i>	0.930
<i>B. brunnea</i>	<i>Eriogonum</i>	-0.743
<i>C. curtipennis</i>	Bare ground	-0.654
	<i>Carex</i>	-0.731
<i>M. dawsoni</i>	<i>Antennaria</i>	0.679
<i>M. infantilis</i>	<i>Carex</i>	0.732
<i>M. kennicotti</i>	<i>Festuca</i>	0.815
<i>T. campestris</i>	<i>Carex</i>	-0.726

Discussion

The scale at which the interaction takes place among and between grasshopper species greatly influences what type of conclusion we draw: community or facultative assemblage. With confounding variables of elevation, precipitation, temperature, and movement-overlap addressed, montane grasshopper species do not represent cohesive communities structured among select soil textures or varia-

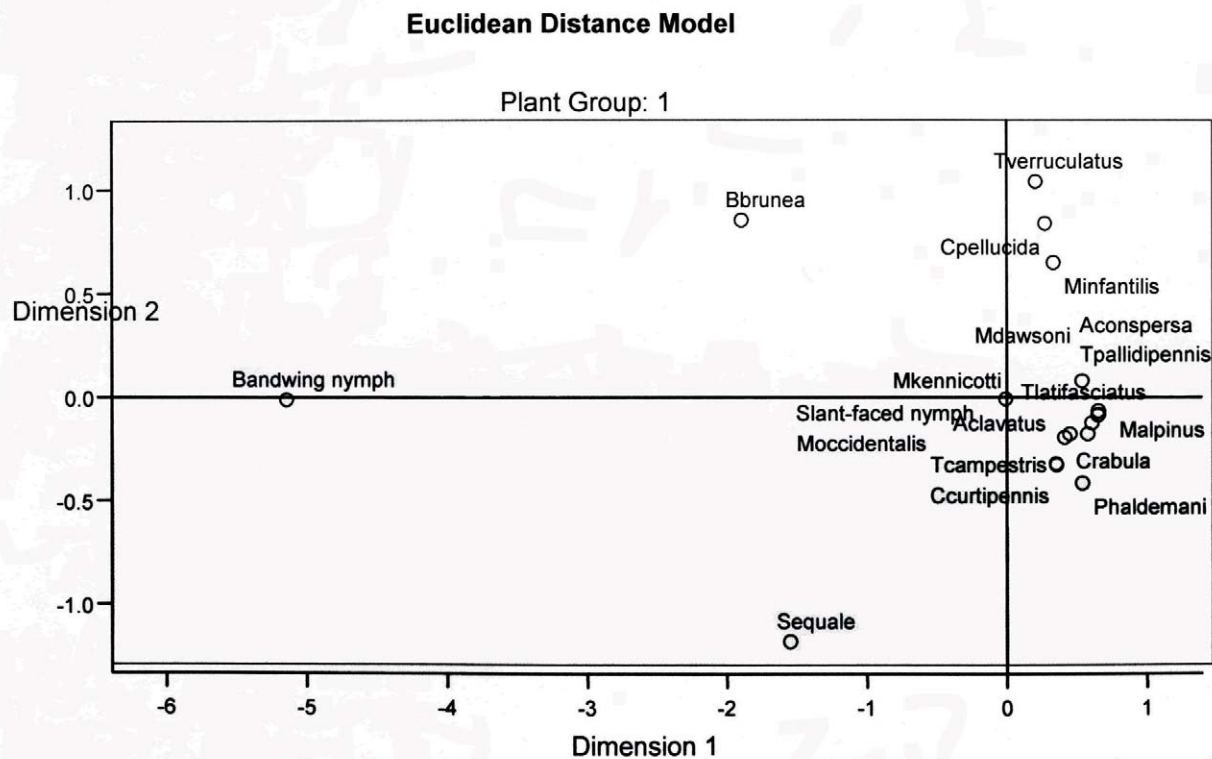


Fig. 5. Results of multidimensional scaling using a 2-dimensional Euclidean distance scaling model of grasshopper species in meadows of plant group 1, as defined by hierarchical cluster analysis.

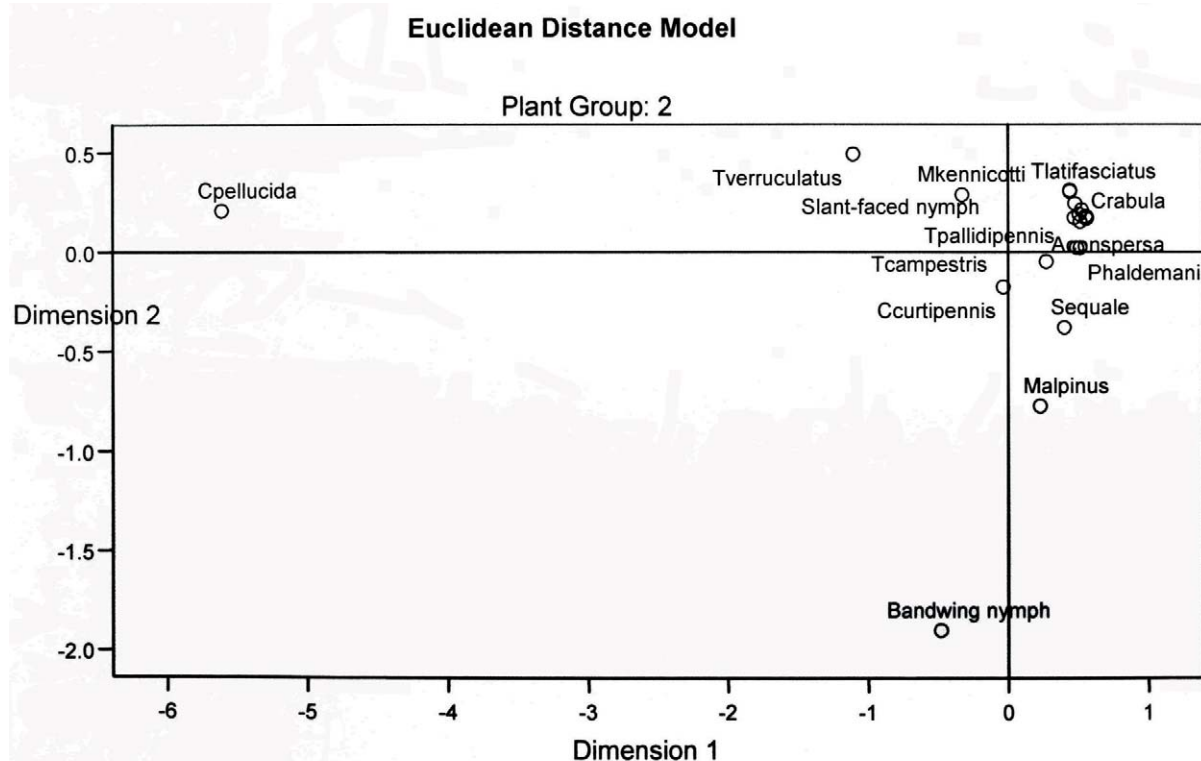


Fig. 6. Results of multidimensional scaling using a 2-dimensional Euclidean distance scaling model of grasshopper species in meadows of plant group 2, as defined by hierarchical cluster analysis.

Table 5. Descriptive statistics for grasshopper species between soil and plant groups.

Species	Soil	N	$\bar{x} \pm \text{SEM}$	Plantgroup	N	$\bar{x} \pm \text{SEM}$
<i>A. conspersa</i>	Sandyloam	5	0.0+0.0	1	3	0.0±0.0
	Loam	5	0.2+0.2	2	7	0.1±0.1
<i>C. pellucida</i>	Sandyloam	5	14.6+5.3	1	3	2.0±1.5
	Loam	5	5.0+1.3	2	7	13.1±3.6
<i>C. rabula</i>	Sandyloam	5	0.2+0.2	1	3	0.7±0.3
	Loam	5	0.8+0.4	2	7	0.4±0.3
<i>P. haldemani</i>	Sandyloam	5	0.8+0.8	1	3	1.3±1.3
	Loam	5	1.0+0.8	2	7	0.7±0.6
<i>S. equale</i>	Sandyloam	5	1.4+1.4	1	3	5.7±3.0
	Loam	5	3.8+1.7	2	7	1.3±0.7
<i>T. campestris</i>	Sandyloam	5	1.4+0.7	1	3	1.3±0.9
	Loam	5	0.8+0.4	2	7	1.0±0.4
<i>T. latifasciatus</i>	Sandyloam	5	0.6+0.6	1	3	0.0±0.0
	Loam	5	0.0+0.0	2	7	0.4±0.4
<i>T. pallidipennis</i>	Sandyloam	5	0.2+0.2	1	3	0.0±0.0
	Loam	5	0.2+0.2	2	7	0.3±0.2
<i>T. verruculatus</i>	Sandyloam	5	4.8+1.4	1	3	2.3±1.9
	Loam	5	2.0+0.8	2	7	3.9±1.0
Bandwing nymph	Sandyloam	5	3.8+1.5	1	3	12.3±7.1
	Loam	5	9.2+4.8	2	7	4.0±1.8
<i>A. clavatus</i>	Sandyloam	5	0.2+0.2	1	3	0.0±0.0
	Loam	5	0.0+0.0	2	7	0.1±0.1
<i>B. brunnea</i>	Sandyloam	5	2.8+1.7	1	3	7.7±0.9
	Loam	5	2.0+1.8	2	7	0.1±0.1
<i>C. curtippennis</i>	Sandyloam	5	1.6+0.8	1	3	1.3±0.9
	Loam	5	1.6+0.6	2	7	1.2±0.6
Slant-faced nymph	Sandyloam	5	1.0+0.6	1	3	0.7±0.7
	Loam	5	0.0+0.0	2	7	0.4±0.4
<i>M. alpinus</i>	Sandyloam	5	0.4+0.2	1	3	0.3±0.3
	Loam	5	2.4+1.0	2	7	1.9±0.8
<i>M. bruneri</i>	Sandyloam	5	0.2+0.2	1	3	0.0±0.0
	Loam	5	0.2+0.2	2	7	0.3±0.2
<i>M. dawsoni</i>	Sandyloam	5	0.4+0.2	1	3	0.7±0.3
	Loam	5	0.2+0.2	2	7	0.1±0.1
<i>M. femurrubrum</i>	Sandyloam	5	0.0+0.0	1	3	0.0±0.0
	Loam	5	0.2+0.2	2	7	0.1±0.1
<i>M. infantilis</i>	Sandyloam	5	1.0+0.8	1	3	1.7±1.2
	Loam	5	0.8+0.8	2	7	0.6±0.6
<i>M. kennicotti</i>	Sandyloam	5	2.6+1.1	1	3	2.7±0.7
	Loam	5	2.0+0.5	2	7	2.1±0.8
<i>M. occidentalis</i>	Sandyloam	5	0.0+0.0	1	3	0.3±0.3
	Loam	5	0.8+0.4	2	7	0.4±0.3

tions in vegetative canopy coverage. However, these species groups are not purely independent assemblages either. Some species are highly correlated with one another, despite landscape variations. And a select few species show such correlation while displaying a trend toward significant dependence on slight habitat variation. The study suggests grasshopper species are structured in a correlative, or community, manner between select species, but that overall species structure is largely an independent, or facultative, assemblage with regard to select habitat. Despite the discrepancies in scale dynamics, no single species behaves independently of the entire structure of species.

In a technical sense, we could define these small-scale species interactions as communities, but only relatively so. The exact nature of such species interactions cannot be resolved through mere correlation. Certainly, one could attribute some of these interactions

to proven models of mutualism and competition, but from an evolutionary standpoint, high correlations between select species do not necessarily imply dependency — rather similar habitat exploitation.

Furthermore, the quantitative analysis of this question is hampered by low abundance in some species, thereby violating assumptions of correlative properties. By addressing in a practical way the more obscure issues of confounding scale assumptions, we ran into more apparent issues of sample size. To increase the sample size by extending it into multiple years obscures the question with precipitation and temperature. Likewise, to increase the sample size by greater space, obscures the question with elevation and extreme vegetative, precipitation and temperature shifts therein. Ecological and evolutionary models are often complicated by violations at some level, some seen (sample size) and some not seen (scale).

This quandary to a logical model once again shows the issue of scale dependence in the question. An assumption of scale independence fails to attain desired sample size, and fails again regarding species interaction if the assumptions of sample size are relaxed.

We felt the data's strong divergence from a pure probability (a third significantly negative, a third significantly positive, and a third insignificant) merited continuance. In continuance, we strengthened the statistical relationship requirements beyond those often reported in imaging, modeling, and systematic studies hampered by low abundance. The study has no great strength in its quantitative approach. But it has enough quantitative analysis to demonstrate the theoretic point of the less obvious confounding effects of scale dependence. These effects complicate the strength of our ecological and pest management models over years and landscape.

Acknowledging the limitations within size, it is worth noting the extreme diversity between and among species interactions and behavior sampled herein. The cases potentially adhere to various proven models of cooperation and competition.

These correlations may be facultative in some cases, such as the possible one between *Pardolophora haldemani* and *Arphia conspersa*, both subdominant strong fliers preferring open habitat regardless of variations in soil texture and canopy coverage. Another correlation of this possible nature exists between *Melanoplus femurrubrum* and *Circotettix rabula*. Both are mixed grass/forb feeders and strong fliers with wide distributions. These facultative correlations can exist between subdominant species, such as *Trimerotropis pallidipennis* and *Trimerotropis latifasciatus*, or between potentially dominant migratory pest species, such as *T. pallidipennis* and *M. femurrubrum* (Pfadt 1996, Otte 1984, Capinera & Sechrist 1982).

However, in select positive correlations in which the diet of one species may actually enhance a differing diet in another species, with both species benefitting as a result, Consumer-Resource Theory may offer an explanation of some small-scale grasshopper species interactions (Ritchie & Tilman 1993). Such a relationship could exist between *Aeropedellus clavatus* and *Melanoplus kennicotti*, both dominant montane pests with short-range dispersal abilities but with differing diets. Another such relationship, regardless of soil texture and canopy coverage, could exist between *Arphia conspersa* and *Melanoplus occidentalis*, both nonpest species with differing diets that have strong dispersal capabilities (Pfadt 1996).

Not all the observed correlations are positive, however. Select correlations are negative between grasshopper species regardless of soil texture or plant canopy coverage. *B. brunnea* and *C. pellucida* both prefer grasses and are negatively correlated regardless of soil texture. *Melanoplus alpinus* and *C. rabula* are both subdominant montane-to-alpine species with good dispersal capabilities, that feed on grasses and forbs. Such negative correlations between similar dietary niches might be explained by Exploitative Competition, a condition previously noted in *Melanoplus sanguinipes* (Branson 2003). With regard to negative correlations between grasshoppers of differing behavior, Interference Competition in the form of territoriality (Amarasekare 2002) could explain the interaction between *Melanoplus dawsoni* (a nonpest, short winged forb feeder) and bandwing nymphs of the subfamily Oedipodinae (which are mixed grass/forb feeders, and include some potential pest species) (Pfadt 1996, Capinera & Sechrist 1982).

A few species, although not entirely independent of the overall species structure, exhibit some form of presence and abundance response to select soil textures and vegetative canopy coverage. These species do not necessarily exhibit similar behavioral characteristics. *C. pellucida* is a severe pest of grains and grasses with

a wide distribution in North America, often displaying migratory tendencies at high densities. *B. brunnea*, while also a pest of grasses, is nonmigratory and more limited to foothills and mountains of the northwest United States. *S. equale*, on the other hand, is a subdominant, nonpest, accidental in montane ecosystems, with a diverse diet of grasses and forbs (Pfadt 1996).

Therefore, multiple forms of competition may exist between select grasshopper species in the overall facultative assemblage of species. Correlations within these competitive dynamics do not adhere to a single behavioral adaptation. Differing behaviors may have evolved in a similar selective framework, making any structural large-scale grasshopper species generalizations difficult.

These conditions and correlations are, of course, reported here under low density grasshopper species presence and abundance. The fact that no single species behaves independently of the overall assemblage of species, but that these interactions are not uniform, suggests that grasshopper species behave in both communal and assemblage ways, depending on the scale at which the data are analyzed. Furthermore, most species appear to behave relatively independently of moderate changes in a montane environment, but not all species do so collectively. Select species appear to be primarily dependent on variations in canopy coverage and secondarily dependent on soil texture. Any beneficial feeding activity one species might impart to another is bound to saturate at certain population or species densities (Bascompte *et al.* 2006).

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