



Comparative biogeography of grasshoppers (Orthoptera: Acrididae) in North America and Siberia: Applications to the conservation of biodiversity

Jeffrey A. Lockwood^{1,*} & Michael G. Sergeev²

¹*Entomology Section, Department of Renewable Resources, University of Wyoming, Laramie, WY 82071-3354, USA*

²*Department of General Biology, Novosibirsk State University, 2, Pirogova St., Novosibirsk, 630090, Russia*

**Author for correspondence (e-mail: lockwood@uwyo.edu; fax: (307)766-5025; phone: (307)766-4260)*

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Abstract

The objective of this study was to apply knowledge of holarctic grasshopper biogeography in representative, temperate ecosystems (Russia, South Siberia, Sayans region; 685,000 km² and USA, Wyoming; 272,000 km²) to develop a comparative basis for understanding and conserving insect biodiversity. Maps of species distributions and vegetation zones were digitized, and a Geographic Information System was used to identify habitats with the greatest biodiversity and to characterize this diversity as a function of selected attributes. With respect to subfamilies, the greatest differences were in cold, mesic zones, where gomphocerines and melanoplinae were dominant in Sayans and Wyoming, respectively. In terms of mobility, the Sayans has more flightless species and individuals, with the taiga supporting the greatest frequency of flightless acridids in both countries. With regard to feeding types, the diversity and richness of graminivores and forbivores were similar in the two regions, but mixed feeders were much more frequent in Wyoming. In the Sayans and Wyoming, pest species were most common in boreal and prairie zones, respectively. Ecoregions with a high diversity of pests also supported a high diversity of rare species. Shrub and desert zones supported many rare species in both countries. Thus, in terms of conservation, the Sayans' acridofauna appears to be at greater risk in terms of ecological vulnerability; acridid biodiversity is dispersed among habitats, with high frequencies of flightless and oligophagous species. The acridofauna of Wyoming could be conserved in fewer habitats than in the Sayans, but these habitats are subject to considerable human disturbance.

Introduction

Knowing the insect fauna of rangelands (i.e., lands that are grazed by livestock, including grasslands, shrublands, and forest understory) is vital to sustaining biological diversity on a global basis. There are at least three compelling reasons to seriously consider the role of rangelands in biodiversity. First, with 60% of the entire landmass of the world classified as rangeland (USDA 1996), its contribution to global biodiversity is substantial. More than 500 million ha of the U.S. is comprised of grass- or shrublands, so the future of biodiversity in the U.S. is intimately tied to these ecosystems.

Second, although rangelands clearly have been altered from their pristine states (Wilson 1988) much of these lands are still dominated by native species. As opposed to croplands which are almost exclusively dedicated to nonindigenous species in Russia and the U.S., extensive agriculture depends on the continuing production of primarily native ecosystems. A largely intact steppe dominates the landscapes of southern Siberia and the U.S.

Third, because of the dependence of extensive agriculture on self-sustaining native ecosystems, it is, in principle, possible to harvest these lands indefinitely. Indeed, the grasslands of central Asia have been grazed by livestock for 3000 years without any apparent



decline in productivity (Mordkovich *et al.* 1997). Of course it is possible to harvest biomass at a rate that exceeds replacement, and such overgrazing caused serious damage to the grasslands of the U.S. in the last century and continues today in some locations (Busby 1994). However, the potential sustainability of agricultural production through the preservation of native species creates a particularly valuable opportunity with respect to biodiversity. It is essential to recognize that the vastness of the Asian and North American steppes is not sufficient to afford protection of their biodiversity. A range of factors continues to endanger the world's rangelands.

Perhaps the greatest threats to rangelands are inappropriate grazing and land conversion. A wide range of studies have demonstrated that mammalian grazing at rates markedly above or below those in which a grassland system evolved have negative consequences to biodiversity (Watts *et al.* 1988; Usher 1995). Although overgrazing is clearly the more frequent and serious threat to sustain these lands and their biodiversity, it is interesting to note that an absence of grazing can also be detrimental (Risser 1988). In a parallel fashion, there is also evidence that fire (mis)management can have serious consequences for the well-being of extensive agroecosystems (Risser 1988; Watts *et al.* 1988; Samways 1995).

As with most ecosystems, wholesale habitat destruction of rangelands is devastating for biodiversity. Plowing is the most common form of physical destruction, and one need only realize that the tallgrass prairies of the U.S. were reduced from 1.1 million km² to a few hundred km² (Duncan 1978) and that cropland conversions destroyed 80% of eastern Siberian grasslands in the 1950s (Popov 1987) to understand the potential of human destruction. In Illinois, less than 1500 ha remains of the original 15 million ha of tallgrass prairie. Perhaps the most striking and well-documented case of damage to an environment impacting a native species of the steppe is the extinction of the Rocky Mountain grasshopper, *Melanoplus spretus*, at the turn of this century (Lockwood & DeBrey 1990).

In terms of biodiversity on landscapes dominated by rangelands, Wyoming may serve as a representative case, having 113 species of acridids compared with 117 species of mammals, 84 species of birds (as year-long residents; 227 species have been documented as nesting in the State), 22 species of reptiles, and 12 species of amphibians (Lockwood 1999). Grasshoppers are an ideal indicator of grassland biodiversity because: (1) they are easy and cost-effective to collect, (2) they rely

on a wide range of plants and, in turn, a broad spectrum of organisms rely upon grasshoppers as food, and (3) their taxonomy and biogeography are relatively well-resolved (Sergeev 1986; 1992; Lockwood *et al.* 1993 (see Hawksworth and Ritchie (1993) for a more complete description of the desired qualities of a biodiversity indicator taxon)). Thus, the Acrididae are perhaps the most biologically diverse and ecologically integral aboveground herbivores on the world's rangelands (Wilson 1998; Pfadt 1994; Lockwood 1993; Chapman & Joern 1990; Watts *et al.* 1988; Hewitt & Onsager 1983; Stebaev 1968; Lavigne & Pfadt 1966).

In developing conservation approaches for orthopteran, a comparative ecological approach has been advocated by Samways and Lockwood (1998). Given apparent similarities among the acridofauna of temperate rangeland (Lockwood *et al.* 1994) and the limited resources available for developing conservation plans and implementing appropriate tactics, comparative studies have at least two advantages. Where there are similarities between ecosystems, the practices and knowledge of one locale may be extrapolated to another, thereby enriching the available information and allowing an internationalization of both policies and practices. Where there are differences between ecosystems, the unique aspects of a locale become of particular conservation importance from a global perspective, thereby allowing allocation of resources to those systems that represent rare or uncommon biological systems. Although the available data have not been synthesized in any rangeland system with regard to an assessment of acridid biodiversity, knowledge of where species richness is highest, what ecoregions support high diversity, and which of these areas are most threatened (or least protected, as indicated by Gap Analysis) should provide vital insights into grassland management and biodiversity conservation. As such, we undertook a comparative ecological analysis of the biogeography of acridid diversity in similar vegetation zones of rangelands in Russia (southern Siberia) and the U.S. (Wyoming).

In terms of a comparative approach to conservation of acridids on rangelands, we focused on four essential parameters. First, **taxonomic similarities** provide an essential perspective in any orthopteran conservation strategy (Green 1998). Next, the **mobility of the organisms is critically related to their distribution, (re)colonization potential, and sensitivity to localized disturbances** (Steward 1998). Third, the **feeding behavior of the acridids is intimately linked to their vulnerability to the effects of livestock grazing, invasive weeds,**



and other alterations to the plant community (Pfadt 1994; Lockwood 1993; Kemp 1992). Finally, the status of a species as pestiferous or rare is an important consideration, as the management practices of each must be integrated to allow for the maintenance of biodiversity in agroecosystems (Lockwood 1998; Samways & Lockwood 1998).

Methods

Spatial data

The study was focused on two northern, temperate grasslands: the Sayans region of Siberia, Russia and Wyoming, U.S.A. (each region being ca. 270,000 km² and lying between 40°N and 55°N latitude). These two areas are representative of the Asian and North American steppes and montane zones, and they provided an ideal range of scales and conditions for ecological comparisons between continents.

The data on grasshopper biogeography in the Sayans region were derived from two sources. Field data were collected during several expeditions, in which sampling within a region was conducted using transects ranging from hundreds of meters to several kilometers with the choice of the distance depending on environmental conditions and habitat types. Grasshoppers were captured by sweep netting for a fixed period of time. These collections yielded 24,886 individual records which were used to generate digitized, species range maps (Sergeev 1986; 1992). In addition, data from museum collections (850 records) were integrated into the database derived from the field expeditions. From these two sources of information, 25,736 distribution records representing 62 species were obtained.

The grasshopper biogeography data from Wyoming were obtained from field surveys conducted by US Department of Agriculture's Animal and Plant Health Inspection Service in cooperation with the University of Wyoming using collecting methods similar to those adopted in Russia (i.e., fixed-effort sweep net sampling across a range of habitat types). From these collections, we developed a database of 35,164 individual collection records representing 103 species in the state from 1988 to 1998 (Lockwood *et al.* 1993; 1999). These records served as the basis for the North American analysis.

The major vegetation types (ecoregions) in both countries were digitized from available maps using the process described in Schell and Lockwood (1997).

These ecoregions conformed to those described by Shelford (1978), Roberts (1989) and the US Environmental Protection Agency (1993) for the U.S. and by Buks *et al.* (1977), Sotchava (1979) and Kuminova *et al.* (1985) for southern Siberia. Using quantitative (elevation and annual precipitation and temperature) and qualitative (dominant plant taxa and vegetative architecture), we generated a common set of vegetation zones representing ecologically homologous habitats between the two regions (only the shortgrass prairie of Wyoming lacked an ecological equivalent in Siberia). We note that while the ecoregions are characterized by a primary type of vegetation (Table 1), these lands are not homogeneous and vegetation and abiotic factors overlap between ecoregions.

Geographic information system analyses

For the US data, individual observation locations were converted from the database to DIG files and then placed within a raster format using ERDAS, PC-VGA, version 7.5, geographic information system. Raster-based systems assign numeric class values to individual map areas, called grid cells, which make up the total map area (ERDAS 1991). The grid cell size chosen was 1000 m², which is a coarser resolution than the actual survey data, which were recorded to the nearest second of latitude/longitude via a geographic positioning system. However, the memory limitations of our computer system precluded any finer spatial resolution over the geographic scale of the dataset (263,139 grid cells comprise the state of Wyoming), and 1000-m resolution is a reasonable approximation given the smallest ecoregion comprised 331,000 ha (tundra; Table 1).

For the Siberian data, individual survey maps were digitized and stored in a raster format. The grid cell size chosen was 2000 m², a scale which represents a compromise between the resolution of the data and the ability to represent vectors (e.g., political and ecological borders). This is perhaps a finer resolution than the actual annual survey maps would allow because the yearly maps were hand-drawn with only political borders for reference marks. However, 2000-m resolution is not an egregious overestimate of the accuracy of the data, and this scaling allowed reasonable comparability with the U.S. data. The smallest ecoregion in Siberia comprised 597,000 ha (montane, which included nearly 1500 grid cells; Table 1).

We used ERDAS (1991) Imagine software, for the spatial analyses of the biological data. For each country, we overlaid and indexed all of the species distribution



Table 1. Vegetation zones (ecoregions) in Wyoming (U.S.A.) and the Sayans region of Siberia (Russia) for which grasshopper biodiversity was assessed.

Vegetation zone	Description		% of geographic area	
	Wyoming	Sayans	Wyoming	Sayans
Tundra	<p>Elevation >3400 m</p> <p>Yearly mean temperature <0°C</p> <p>Precipitation 1000–1500 mm per year</p> <p>Vegetation mosaic of herbaceous vegetation dominated by alpine avens, bistort, and timothy; trees formed as krummholz; willow thickets in depressions</p>	<p>Elevation >2000 m</p> <p>Yearly mean temperature –8°C to –10°C</p> <p>Precipitation 400–800 mm per year</p> <p>Vegetation high montane tundras with small shrubs (<i>Salix</i>, <i>Betula</i>, <i>Rhododendron</i>), <i>Dryas</i>, mosses, lichens; including stone-fields, alpine meadows, insular open woodlands</p>	1.3	6.2
Boreal	<p>Elevation 3200–3400 m</p> <p>Yearly mean temperature –3°C to 3°C</p> <p>Precipitation 500–1000 mm per year</p> <p>Vegetation forests dominated by Engelmann spruce and subalpine fir, interspersed with aspen groves, lodgepole pine or mountain meadows; understory of dwarf huckleberry, grasses, herbs, and low shrubs</p>	<p>Elevation 1200–2000 m</p> <p>Yearly mean temperature –6°C to –8°C</p> <p>Precipitation 400–800 mm per year</p> <p>Vegetation high montane open coniferous forests (<i>Larix sibirica</i>, <i>Pinus sibirica</i>, <i>Abies</i> spp.) with low grasses and green mosses; including meadows and steppes on the southern slopes</p>	4.8	28.2
Montane	<p>Elevation 1800–3300 m</p> <p>Yearly mean temperature 0–4°C</p> <p>Precipitation 350–1500 mm per year</p> <p>Vegetation dense to open forests dominated by lodgepole pine, with an understory (sometimes sparse) of grasses, herbs, and shrubs; common associates subalpine fir, Engelmann spruce, and aspen</p>	<p>Elevation 800–1700 m</p> <p>Yearly mean temperature –6°C</p> <p>Precipitation 340–800 mm per year</p> <p>Vegetation montane taiga from <i>Larix sibirica</i> and <i>Pinus sibirica</i> with bushes; including openings, forest–steppes intermountain basins, meadows and steppes on the southern slopes</p>	10.2	2.3
Taiga	<p>Elevation 2400–3000 m</p> <p>Yearly mean temperature 3–6°C</p> <p>Precipitation 400–1000 mm per year</p> <p>Vegetation dense forests to open woodlands (interspersed with foothills grasslands) dominated by Douglas fir or oak (bur or Gambel); other pines may be present</p>	<p>Elevation 400–1200 m</p> <p>Yearly mean temperature –5°C to 6°C</p> <p>Precipitation 400–800 mm per year</p> <p>Vegetation Plain and low montane taiga from <i>Picea</i> spp., <i>Abies</i> spp., <i>Pinus sibirica</i> with birches, aspens, grasses; including swamps, birch–aspen forests, meadows</p>	3.2	19.2
Woodland	<p>Elevation 1200–2400 m</p> <p>Yearly mean temperature 2–8°C</p> <p>Precipitation 350–500 mm per year</p> <p>Vegetation forests to open woodlands or savannas dominated by ponderosa pine, with an understory of grasses, herbs, and shrubs; limber pine, Douglas fir, white spruce and aspen are common associates</p>	<p>Elevation 200–800 m</p> <p>Yearly mean temperature –2°C to 0°C</p> <p>Precipitation 400–800 mm per year</p> <p>Vegetation plain southern pine (<i>Pinus silvestris</i>) forests with <i>Larix</i> spp., bushes, <i>Vaccinium vitis-idea</i>, sometimes with steppe grasses; including openings, meadow and typical steppe plots</p>	8.1	21.0
Shrub	<p>Elevation 1500–2700 m</p> <p>Yearly mean temperature 4–8°C</p> <p>Precipitation 150–250 mm per year</p> <p>Vegetation steppes dominated by big sagebrush, black sagebrush (shallow soils), or silver sagebrush (mesic soils); interspersed with grasses</p>	<p>Elevation 200–600 m</p> <p>Yearly mean temperature –2°C to 0°C</p> <p>Precipitation 300–400 mm per year</p> <p>Vegetation plain and low montane shrub steppes with <i>Caragana</i> spp., <i>Spiraea</i> spp., and <i>Pentaphylloides fruticosa</i></p>	45.6	8.8
Desert	<p>Elevation 900–1800 m</p> <p>Yearly mean temperature 6–8°C</p> <p>Precipitation 150–200 mm per year</p> <p>Vegetation dry, often saline, soils dominated by greasewood, Gardner saltbush, shadscale, birdfoot sagebrush, bud sage, or big sagebrush; some sand dunes with sparse herbaceous vegetation</p>	<p>Elevation 400–1600 m</p> <p>Yearly mean temperature –3°C to 6°C</p> <p>Precipitation 150–300 mm per year</p> <p>Vegetation dry steppes and semi-deserts from xerophilous plants (e.g., <i>Stipa glareosa</i>, <i>Carex duriuscula</i>, <i>Potentilla acaulis</i>, <i>Artemisia frigida</i>) with <i>Caragana</i> scrubs, petrophilous groups and desert plots</p>	4.6	14.3
Prairie	<p>Elevation 900–2100 m</p> <p>Yearly mean temperature 7–8°C</p> <p>Precipitation 300–400 mm per year</p> <p>Vegetation grasslands dominated by blue grama, western wheatgrass, junegrass, Sandberg bluegrass, needle-and-thread grass, rabbitbrush, and fringed sage</p>	Absent	22.2	0.0



maps to generate a single, synthetic map. This map differentially identified the number and types of grasshopper species within each grid cell. By overlaying these faunal maps with the ecoregions, we were able to assess acridid community structure from the perspectives of diversity, evenness, and richness. As with all sampling methods, sweep netting (the primary method by which sampling occurred) is biased with respect to the groups that are collected. However, the application of diversity indices to selected portions of a biotic community (e.g., Kappelle *et al.* 1995) is appropriate as long as the results are interpreted in the context of the constraints of the sampling methodology (Southwood 1978). Sampling was generally uniform throughout each geographic area (Sergeev 1986; 1992; Lockwood *et al.* 1993; 1999), so that sampling intensity in each ecoregion was roughly proportional to the area of that region.

Diversity (a measure of both the abundance and equitability of species) was expressed using the Shannon–Wiener index (H , base 2) (Southwood 1978). The number of occurrences of a species was expressed as the number of sites from which it was collected, rather than the total number of specimens, as the latter data values could not be reliably obtained. This diversity index was chosen because it is: (1) normally distributed (Taylor 1978), (2) more appropriate than the Simpson–Yule index, which is strongly influenced by the underlying distribution for samples with more than ten species (May 1975), (3) more appropriate than the Berger–Parker index because there were several cases of co-dominant species, (4) dependent on both evenness and richness (Magurran 1988), and (5) perhaps the most commonly encountered index in the literature (Magurran 1988; Spellerberg 1991). The disadvantages of using H are that the index is a purely relative measure, without absolute meaning (as opposed to the Simpson–Yule index (Southwood 1978)), but we were particularly interested in comparisons between ecoregions, so the relativity of this index was not problematical. In addition, H is not sensitive to the character of the ratio of species to individuals and it is dominated by the abundant species (May 1975), but these qualities did not constitute serious disadvantages in the context of our application.

Having chosen H as the measure of diversity, we used the Shannon–Wiener index of evenness. This measure is the ratio of the maximum value of H (assuming that the individuals were evenly distributed among the species) to the realized value of H . As such, this measure of evenness ranges from 0.0 to 1.0.

We expressed the species richness as the number of species. Although this measure has the clear advantage of simplicity, it has the disadvantage of insensitivity to numerically rare species (i.e., rare species are not collected if the sample size is too small). Findley (1973) and Hendrickson and Ehrlich (1971) have criticized restricting expressions of diversity to the number of species present while failing to consider the forms and functions of the species. However, our assessment of species richness avoids this pitfall in that we employed concomitant analyses of diversity and we have a good understanding of the ecological functions of the species in the taxon of interest. Given the sampling constraints, the use of numerical species richness is appropriate (Magurran 1988). Chi-squared analysis was used to compare the frequencies of species in the Wyoming and Sayans biomes across vegetation classes (Lund 1986); differences were considered significant at $P < 0.05$.

To facilitate conservation and ecological interpretations, we conducted our analyses of diversity, evenness, richness, and frequency using all species and selected categorizations of the acridofauna, including: subfamilies (Gomphocerinae, Melanoplinae, and Oedipodinae), flight abilities (both sexes fly, only males fly, neither sex flies), feeding preferences (graminivores, forbivores, and mixed feeders), pest status (ten most damaging species), and rarity (ten most uncommon species). These biological attributes were derived from available literature (Berezhkov 1956; Mulhern *et al.* 1964; Capinera & Sechrist 1982; Stebaev & Pshenitsina 1984; Sergeev 1986; Storozhenko 1991; Pfadt 1994), our unpublished observations (J.A.L. and M.G.S.), and consultation with other experts (R. Pfadt, pers. comm.).

Results

Analysis of Acrididae and major subfamilies

The ecological analysis of all acridids revealed striking similarity in diversity of the Sayans and Wyoming (Table 2). However, it is important to note that a single zone (e.g., shrub or woodland) in Wyoming can account for 90% of all species, while the richest zone in the Sayans region (desert) only accounts for 74% of all species. Despite the similarity in diversities, Wyoming has about 50% higher species richness than the Sayans. In terms of all acridids, the greatest species richness in Wyoming is found in woodland and shrub, but the greatest richness in southern Siberia is in desert and



Table 2. Biogeography of Acrididae: subfamily biodiversity in the Sayans and Wyoming as a function of vegetation zone.

Group	Biome	Measure	Vegetation class									
			Tundra	Boreal	Montane	Taiga	Woodland	Shrub	Desert	Prairie	All	
All	Wyoming	Diversity	3.093	4.413	5.101	4.950	5.514	5.549	5.051	5.260	5.668	
		Evenness	0.463	0.660	0.763	0.740	0.825	0.830	0.755	0.787	0.848	
		Richness	20	42	76	50	92	93	60	83	103	
		Frequency	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Sayans	Diversity	1.000	4.907	4.700	3.577	4.930	4.837	5.180	NA	5.635	
		Evenness	0.168	0.824	0.789	0.601	0.828	0.812	0.870	NA	0.946	
		Richness	11	38	31	19	36	34	46	NA	62	
		Frequency	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Gomphocerinae	Wyoming	Diversity	1.922	1.936	3.117	3.415	3.877	3.719	3.084	3.689	3.881
			Evenness	0.404	0.407	0.655	0.718	0.815	0.782	0.649	0.776	0.818
			Richness	9	11	21	16	26	25	17	25	27
			Frequency	0.357	0.228	0.233	0.396	0.376	0.302	0.290	0.468	0.370
Sayans		Diversity	0.000	4.470	4.248	3.236	4.486	4.176	4.484	NA	5.022	
		Evenness	0.000	0.840	0.798	0.608	0.843	0.785	0.843	NA	0.944	
		Richness	1	26	22	14	25	22	28	NA	40	
		Frequency	0.500	0.794	0.731	0.737	0.698	0.639	0.580	NA	0.659	
Melanoplinae		Wyoming	Diversity	1.252	3.366	3.858	3.346	3.924	3.767	3.064	3.577	3.994
			Evenness	0.244	0.656	0.752	0.652	0.765	0.734	0.597	0.697	0.779
			Richness	9	19	27	18	32	31	18	27	35
			Frequency	0.429	0.472	0.423	0.347	0.387	0.311	0.306	0.289	0.329
	Sayans	Diversity	0.000	1.906	0.000	1.371	0.000	0.000	1.459	NA	2.204	
		Evenness	0.000	0.179	0.000	0.300	0.000	0.000	0.267	NA	0.949	
		Richness	0	4	1	4	1	1	3	NA	5	
		Frequency	0.000	0.127	0.038	0.263	0.019	0.028	0.037	NA	0.061	
	Oedipodinae	Wyoming	Diversity	1.000	2.722	3.356	3.281	4.031	4.257	3.998	3.898	4.335
			Evenness	0.189	0.515	0.635	0.621	0.763	0.805	0.756	0.738	0.820
			Richness	10	15	29	17	33	35	26	31	39
			Frequency	0.143	0.233	0.306	0.188	0.217	0.365	0.383	0.236	0.283
Sayans		Diversity	0.000	2.322	2.000	0.000	2.661	2.522	3.105	NA	3.174	
		Evenness	0.000	0.648	0.558	0.000	0.742	0.703	0.866	NA	0.885	
		Richness	0	7	7	0	9	8	11	NA	12	
		Frequency	0.000	0.079	0.154	0.000	0.245	0.194	0.309	NA	0.219	

boreal habitats. The distribution of species across vegetation classes differed significantly between Wyoming and the Sayans ($df = 6$; $\chi^2 = 18.14$; $P = 0.0065$).

With respect to the Gomphocerinae, it is evident that southern Siberia has markedly greater diversity and richness overall. Furthermore, the vegetation zones with the greatest richness in the Sayans (desert, woodland, boreal) are different than the richest zones in Wyoming (prairie, shrub, and woodland). Wyoming has greater richness of tundra gomphocerines, while Siberia has much greater richness of boreal gomphocerines. Finally, it is clear that gomphocerines account for a much greater proportion of the acridofauna in the Sayans region, where 58–79% of acridids belong to this subfamily, compared to just 22–47% in Wyoming. The distribution of gomphocerines across vegetation classes differed significantly between Wyoming and the Sayans ($df = 6$; $\chi^2 = 14.93$; $P = 0.0212$).

The ecological situation is reversed with regard to the Melanoplinae. That is, Wyoming has markedly greater diversity and richness overall. In all habitats except tundra, the diversity in Wyoming was remarkably consistent and high (3.0–3.9) relative to Siberian diversity. Melanoplinae are also numerically dominant in Wyoming, accounting for 29–47% of acridids caught, compared to 2–26% in the Sayans. The distribution of melanoplinae across vegetation classes did not differ significantly between Wyoming and the Sayans ($df = 6$; $\chi^2 = 10.24$; $P = 0.1154$).

The overall diversity and frequency of Oedipodinae is rather similar in southern Siberia and Wyoming. Despite the similarity in these two ecological measures, Wyoming has more than three-times as many species. In both Wyoming and the Sayans region, the greatest richness and frequency of oedipodinae are associated with drier vegetation zones (woodland, shrub,



and desert). The distribution of oedipodines across vegetation classes did not differ significantly between Wyoming and the Sayans ($df = 6; \chi^2 = 10.84; P = 0.0938$).

Analysis of flight (mobility)

Across all vegetation zones, macropterous grasshoppers are much more frequent in Wyoming than in the Sayans region (Table 3). The greatest richness of macropterous species in Wyoming is in woodland and shrub, while shrub and desert support the most species in southern Siberia. Thus, lower, dryer, and warmer habitats are associated with greater numbers of species capable of flight. It should be noted in terms of acridid conservation that while macropterous forms account for no less than 77% of the individuals in any vegetation zone in Wyoming, such species account for no more than 69% of the taxonomic richness. The distribution of macropterous grasshoppers across vegetation classes differed significantly between Wyoming and the Sayans ($df = 6; \chi^2 = 17.29; P = 0.0088$).

With respect to those species in which only the male is capable of flight, the Sayans has six-times more species and ten-times greater frequency than Wyoming. Indeed, the highest frequency in Wyoming (7%) is

lower than the lowest frequency in the Sayans (8%). In Wyoming, higher frequencies are found in high, cold vegetation zones, but lower, warmer zones support higher frequencies in the Sayans. In both countries low frequencies are found in shrublands. The distribution of these grasshoppers across vegetation classes did not differ significantly between Wyoming and the Sayans ($df = 5; \chi^2 = 0.83; P = 0.9729$).

Flightless species were evenly distributed across all vegetation classes in the sayans (except tundra). A similar pattern was evident in Wyoming, with the most evident difference being that only a single flightless species occurs in the desert (compared to eight such species in the sayans). However, the distribution of flightless grasshoppers across vegetation classes differed significantly between Wyoming and the Sayans ($df = 5; \chi^2 = 7.58; P = 17.02$). The Sayans region generally had higher diversity and frequency of flightless grasshoppers across vegetation classes.

Analysis of feeding habits

Across all vegetation zones, it is apparent that both countries have similar diversity and richness of graminivorous species; the Sayans region has 25% greater frequency of these acridids (Table 4). Indeed,

Table 3. Biogeography of Acrididae: biodiversity of mobile and immobile taxa in the Sayans and Wyoming as a function of vegetation zone.

Group	Biome	Measure	Vegetation class								
			Tundra	Boreal	Montane	Taiga	Woodland	Shrub	Desert	Prairie	All
Both sexes fly	Wyoming	Diversity	2.752	4.081	4.827	4.554	5.268	5.396	4.943	5.099	5.469
		Evenness	0.428	0.635	0.751	0.709	0.802	0.840	0.769	0.794	0.851
		Richness	17	35	65	40	78	79	54	73	86
	Sayans	Frequency	0.857	0.817	0.873	0.772	0.858	0.934	0.963	0.942	0.915
		Diversity	0.000	4.027	3.585	2.236	3.814	4.324	4.452	NA	4.739
		Evenness	0.000	0.779	0.693	0.432	0.738	0.836	0.861	NA	0.917
		Richness	1	22	16	10	18	23	28	NA	36
		Frequency	0.500	0.571	0.462	0.368	0.547	0.694	0.549	NA	0.551
		Diversity	0.000	0.000	0.000	0.000	0.493	0.782	0.649	0.776	0.818
Only males fly	Wyoming	Evenness	0.000	0.000	0.000	0.000	0.493	0.782	0.649	0.776	0.818
		Richness	1	1	1	1	2	2	2	2	2
		Frequency	0.071	0.033	0.032	0.040	0.047	0.025	0.012	0.024	0.029
	Sayans	Diversity	0.000	2.722	2.807	1.500	3.239	1.585	3.085	NA	3.418
		Evenness	0.000	0.759	0.783	0.418	0.903	0.442	0.861	NA	0.953
		Richness	0	8	8	6	10	6	10	NA	12
		Frequency	0.000	0.159	0.269	0.211	0.245	0.083	0.302	NA	0.238
		Diversity	0.000	1.426	2.738	2.624	2.431	2.583	0.000	2.043	2.827
		Evenness	0.000	0.374	0.719	0.689	0.638	0.678	0.000	0.537	0.743
Non flying	Wyoming	Richness	0	7	10	9	11	11	1	8	14
		Frequency	0.000	0.083	0.062	0.129	0.079	0.021	0.014	0.031	0.040
		Diversity	0.000	2.895	2.807	2.156	2.914	2.500	2.678	NA	3.652
	Sayans	Evenness	0.000	0.760	0.737	0.566	0.765	0.657	0.703	NA	0.959
		Richness	1	8	7	6	8	7	8	NA	14
		Frequency	0.500	0.270	0.269	0.421	0.208	0.222	0.148	NA	0.211



Table 4. Biogeography of Acrididae: biodiversity as a function of feeding preferences in the Sayans and Wyoming with respect to vegetation zones.

Group	Biome	Measure	Vegetation class								
			Tundra	Boreal	Montane	Taiga	Woodland	Shrub	Desert	Prairie	All
Graminivore	Wyoming	Diversity	1.922	2.540	3.422	3.880	4.302	4.240	3.912	4.010	4.342
		Evenness	0.364	0.481	0.648	0.734	0.814	0.802	0.704	0.759	0.822
		Richness	10	15	28	22	35	36	26	34	39
		Frequency	0.357	0.350	0.403	0.515	0.496	0.442	0.408	0.572	0.494
	Sayans	Diversity	1.000	4.335	4.170	2.914	4.561	4.513	4.356	NA	4.976
		Evenness	0.191	0.826	0.795	0.555	0.869	0.860	0.830	NA	0.948
		Richness	9	24	20	12	25	24	25	NA	38
Forbivore	Wyoming	Frequency	1.000	0.730	0.692	0.579	0.698	0.806	0.512	NA	0.626
		Diversity	0.000	0.439	2.670	1.500	2.499	3.040	2.429	2.837	3.186
		Evenness	0.000	0.100	0.608	0.342	0.569	0.692	0.553	0.646	0.725
		Richness	0	8	13	8	17	18	13	14	21
	Sayans	Frequency	0.071	0.033	0.032	0.040	0.047	0.025	0.012	0.024	0.029
		Diversity	0.000	2.664	2.322	1.371	2.413	2.522	3.597	NA	3.751
		Evenness	0.000	0.639	0.557	0.329	0.579	0.605	0.863	NA	0.899
		Richness	0	10	9	8	9	9	16	NA	18
		Frequency	0.000	0.175	0.192	0.263	0.208	0.194	0.377	NA	0.277
		Diversity	2.000	3.774	4.264	3.737	4.345	4.403	3.581	4.235	4.571
Mixed	Wyoming	Evenness	0.371	0.700	0.791	0.693	0.806	0.817	0.664	0.785	0.848
		Richness	11	25	36	24	40	39	23	36	42
		Frequency	0.571	0.522	0.509	0.386	0.421	0.476	0.374	0.373	0.428
		Diversity	0.000	1.918	1.585	0.918	0.971	0.000	1.952	NA	2.255
	Sayans	Evenness	0.000	0.742	0.613	0.355	0.376	0.000	0.755	NA	0.873
		Richness	0	5	4	5	5	0	5	NA	6
		Frequency	0.000	0.094	0.115	0.158	0.093	0.000	0.111	NA	0.096

the lowest frequency in the Sayans was 51% – nearly as high as the highest frequency in Wyoming. The greatest diversity and richness of graminivores in both countries is found in woodlands and shrublands. The habitats with the highest frequency of these grasshoppers in Wyoming (52–57% in taiga and prairie) are not the same as in the Sayans (73–81% in shrubland and boreal).

As with graminivores, both countries (overall) have similar diversity and richness of forbivores. However, the Sayans region has nearly a ten-fold greater frequency of graminivorous grasshoppers than Wyoming. The greatest frequency in both countries is found in xeric conditions. However, in south Siberia the greatest frequency is in desert while in Wyoming it is in tundra. Even so, the greatest frequency in Wyoming is less than the lowest frequency in the Sayans (boreal, 18%). In Wyoming the habitats with the greatest richness are woodlands and shrublands, while in the Sayans desert and boreal have the greatest richness.

With respect to mixed (forb and grass) feeders, Wyoming has a greater diversity, richness, and frequency across all vegetation zones. It is interesting to note that one of the two richest habitats in Wyoming

(shrubland – the other being woodland) supports no species of mixed-feeders in the Sayans region. The greatest frequencies of grasshoppers with this feeding style in Wyoming are in tundra and boreal habitats. In the Sayans they are in montane and taiga zones, which have less than one-half the frequency of the lowest values in Wyoming (prairie, 37%).

None of the distributions of species with respect to feeding types differed significantly across vegetation classes in Wyoming and the Sayans ($df = 6$; $\chi^2 \leq 9.84$; $P \geq 0.1318$).

Analysis with respect to pestiferous and rare species

The pestiferous species exhibited very similar diversities in Wyoming and the Sayans region across all vegetation zones (Table 5). However, the overall frequency of individuals within the pest species is much higher in Wyoming than in the Sayans. Habitat types generated markedly different patterns in terms of pest frequency. For example, pest species were very frequent in Siberian boreal zones but infrequent in Wyoming boreal habitats, but they were frequent in Wyoming



Table 5. Biogeography of Acrididae: biodiversity of pestiferous and rare species in the Sayans and Wyoming as a function of vegetation zone.

Group	Biome	Measure	Vegetation class								
			Tundra	Boreal	Montane	Taiga	Woodland	Shrub	Desert	Prairie	All
Pest	Wyoming	Diversity	1.000	1.575	2.407	2.512	3.167	3.205	2.993	3.172	3.246
		Evenness	0.301	0.474	0.725	0.756	0.953	0.965	0.901	0.955	0.977
		Richness	7	7	10	8	10	10	10	10	10
	Sayans	Frequency	0.143	0.150	0.279	0.317	0.389	0.396	0.323	0.454	0.401
		Diversity	0.000	2.839	2.585	0.918	3.102	2.252	3.226	NA	3.255
		Evenness	0.000	0.855	0.778	0.276	0.934	0.678	0.971	NA	0.980
		Richness	0	9	8	7	9	7	10	NA	10
		Frequency	0.000	0.317	0.231	0.158	0.321	0.167	0.321	NA	0.288
		Diversity	0.000	0.000	1.530	0.000	1.846	2.117	0.811	0.722	3.209
Rare	Wyoming	Evenness	0.000	0.000	0.461	0.000	0.556	0.637	0.244	0.217	0.966
		Richness	0	1	4	0	5	5	5	5	10
		Frequency	0.000	0.006	0.007	0.000	0.003	0.004	0.009	0.001	0.003
	Sayans	Diversity	0.000	1.459	0.000	0.000	0.000	1.500	2.355	NA	3.038
		Evenness	0.000	0.439	0.000	0.000	0.000	0.452	0.709	NA	0.915
		Richness	0	5	0	0	1	5	6	NA	10
		Frequency	0.000	0.095	0.000	0.000	0.038	0.111	0.074	NA	0.066

taiga and woodland but infrequent in these habitats in southern Siberia.

With respect to rare species, the overall diversity was similar in Wyoming and southern Siberia, but the greatest diversity in Wyoming was in shrub habitats while in the Sayans it was in the desert (which had low diversity in Wyoming). The overall frequency of rare species in the Sayans was > 20-fold higher than in Wyoming. Desert had the greatest frequency in Wyoming (which was still less than many of the Siberian habitats), and shrub zones had more rare individuals than other habitats in the Sayans. Species richness was consistent between the Sayans and Wyoming in tundra and taiga (no rare species) and shrub and desert (5–6 rare species). However, markedly more rare species were found in southern Siberian versus Wyoming boreal habitats, but there were more rare species in Wyoming versus southern Siberian montane and woodland zones.

None of the distributions of species with respect to pest ($df = 6$; $\chi^2 = 6.92$; $P = 0.3292$) or rarity ($df = 4$; $\chi^2 = 9.24$; $P = 0.0552$) status differed significantly across vegetation classes in Wyoming and the Sayans.

Discussion

Analysis of Acrididae and major subfamilies

Although the ecological analysis of all acridids revealed striking similarity in diversity of the Sayans

and Wyoming, the biogeographic contexts suggest potentially different approaches to conservation of acridid biodiversity. In Wyoming, a single zone can account for a markedly higher proportion of species that in the Sayans region. Hence, acridid biodiversity in North America may be more effectively conserved within fewer habitats than in Russia. Other differences may also be important with respect to conservation. For example, the greatest species richness in Wyoming is found in woodland and shrub, but the greatest richness in southern Siberia is in desert and boreal habitats. As such, we might expect that North American biodiversity is at somewhat greater risk given that the most speciose habitats are those under the greatest anthropogenic pressure via grazing, land conversion, and related impacts.

Three trends emerged from the analyses of subfamily biogeography. First, the frequency of acridid subfamilies in the Sayans region and Wyoming differs most markedly in cold and mesic vegetation zones, where gomphocerines dominate in southern Siberia and melanoplinae dominate in Wyoming. In more xeric zones, oedipodinae are common but subdominant in both countries. Next, in both countries, the frequency of the major subfamily does not appear to be related to its richness within a vegetation zone (e.g., in the Sayans, gomphocerines are most common in boreal, taiga, and montane but desert, boreal, and woodland have the greatest richness; in Wyoming, melanoplinae are most common in boreal, tundra, and montane but woodland, shrubland, and prairie/montane



have the greatest richness). Finally, the species distribution across subfamilies is much more even in Wyoming (26% Gomphocerinae, 34% Melanoplinae, 38% Oedipodinae, and 2% others) than in the Sayans region (65% Gomphocerinae, 8% Melanoplinae, 19% Oedipodinae, and 8% others).

Analysis of flight (mobility)

Given that micropterous and brachypterous species are incapable of flight, they represent a category a particular concern with respect to conservation. The two countries have identical richnesses and similar diversities of flightless species, but the Sayans region has a five-fold greater frequency of such individuals. The greatest diversity of these species in Wyoming is found in montane and taiga zones, which is similar to the Sayans (where they are also highly diverse in woodland), although deserts support eight species in the Sayans region and only one in Wyoming. It should be noted in terms of relative sensitivity to habitat degradation that the highest frequency in Wyoming (13%) is lower than the lowest frequency in the Sayans (15%).

In summary, flightless acridids are represented by many more species and individuals within a community in southern Siberia, compared to Wyoming. The taiga supports the greatest frequency of flightless acridids in both countries, but frequency is not strongly related to richness. It should also be noted that diversity and richness of flightless species do not generally track moisture, elevation, and temperature. Given this ubiquity, conservation of particular habitats may not consistently protect these poorly mobile, and consequently susceptible, species of acridids.

Analysis of feeding habits

Although the diversity and richness of graminivores and forbivores in the Sayans region and Wyoming are similar, the frequencies of these restricted feeding types are much higher in the Sayans. Such specialization suggests particular concern with regard to conservation. If feeding habits are more specialized in southern Siberia, then the possibility that localized or otherwise concentrated anthropogenic disturbances could have significant conservation impacts is increased. Wyoming has much higher frequencies of mixed feeders, as well as greater richness and diversity of this feeding type. Such a pattern may indicate a potentially more robust fauna, as the diet breadth appears to be more generalized. Of

course, species with more specialized feeding behaviors also exist in Wyoming, and these may need to be a focus of conservation concern.

Analysis of pestiferous and rare species

The Sayans region has fewer pest species and they are most common in boreal vegetation (31% of grasshoppers), while Wyoming has a much more frequent occurrence of pests and they are most often in prairie (45% of grasshoppers). In terms of potential conflicts between pest management and conservation, it should be noted that habitats with high pest-species diversity tend to have high rare-species diversity, but this trend is not seen with respect to frequency. Finally, it is important to consider that while rare species have higher frequencies in the Sayans region than in Wyoming, in the Sayans they are primarily concentrated into just three vegetation zones (versus five in Wyoming, including woodland and montane); shrub and desert support high richnesses of rare species in both countries.

Conclusion

This study revealed a strong, general similarity in acridid diversity of the Sayans and Wyoming, which suggests that a continuing dialogue and flow of information regarding conservation practices in Siberia and the U.S. would be mutually beneficial. In particular, efforts to protect grasshoppers in the shrub and desert zones would be most important, as these habitats appear to support the highest number of rare species in both ecosystems. However, there are also some intriguing differences that could give rise to divergent strategies. In general, the Sayans' acridofauna appears to be at greater risk in terms of ecological vulnerability. The acridid biodiversity is more dispersed among habitats than in Wyoming, with particular challenges in conserving the numerous species that are incapable of flight and that have restricted feeding habits. Conversely, the acridofauna of Wyoming could potentially be conserved in fewer habitats than in the Sayans, but it is at relatively greater risk in terms of ecological disturbance. That is, the greatest species richness in Wyoming is associated with vegetation classes that are most severely impacted by human activity. In summary, the analyses suggest that the acridid fauna is more vulnerable 'in principle' in the Sayans, but grasshopper species may be at greater risk 'in practice' in Wyoming.



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