

## Chapter G

# Influence of Habitat and Region on Spider Communities Along Two Elevation Gradients in the Southwestern U.S.

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## Abstract

There has been little research examining the changes in community composition of ground-dwelling arthropods along elevation gradients, and yet, understanding how species are distributed along elevation gradients is critical for understanding how such communities may respond to climate change. This report is one of few comparative studies of spider communities along elevation gradients in the Southwest U.S. We examined the abundance and community composition of ground-dwelling spiders along elevation gradients in northern Arizona (San Francisco Peaks) and New Mexico (Bandelier National Monument), respectively. Our questions were (1) how are spider species distributed across elevation gradients that span piñon-juniper, ponderosa pine, and mixed-conifer habitats, and are there fundamental changes in community composition, or degree of habitat specialization from low to high elevations; (2) how do these patterns compare between similar habitats in two regions of the Southwest; and (3) what is the importance of habitat structure versus geographic distance in terms of community structure and abundance. Key findings from this study were (1) species composition was distinct among habitats for both elevation gradients, despite no consistent differences in overall abundance and species richness; (2) species displayed a strong affinity for specific habitats, 59 percent of the 79 taxa were found in only one habitat type; (3) there was also a strong degree of regionalization, where 77 percent of the 79 species were only found in northern Arizona or northern New Mexico; and (4) habitat affinity was more important than geographic distance, in that spider communities were more similar among the same habitats in different states than communities in adjacent but different habitats in the same area.

## Introduction

Many arthropod groups in the southwestern U.S., including spiders, are still poorly described (Parmenter and others, 1995). Ground-dwelling spiders are dominant predators in the region, typically composing 16–38 percent of ground-dwelling arthropod species in some habitats (Crawford, 1989; Ellis and others, 2000, 2001). Although scores of species may occupy a single habitat, many spiders are locally rare, although wolf spiders (Lycosidae) and ground spiders (Gnaphosidae) can be abundant (Bradley, 2013). Spiders are defined as generalist predators (Wise, 1993), but their distributions may reflect more specialized preferences for climate and habitat structure, such as the amount of precipitation, canopy cover, or litter depth (Uetz, 1991). Spider community composition may change dramatically over meters in response to changes in habitat structure, suggesting that they can be extremely sensitive to microhabitat changes (Higgins and others, 2014).

Because the southwestern U.S. is characterized by varied topography and gradients (Brown, 1982), spider communities can vary dramatically over short distances in response to changing habitat types (Chatzaki and others, 2005; Bowden and Buddle, 2010; Higgins and others, 2014). Additionally, directional habitat change over elevation gradients provides a proxy for climate change, replacing space for time and allows us to better understand how climate change impacts may affect species and communities. Since higher elevation habitats are often restricted to isolated areas throughout most of the Colorado Plateau, they are considered “at-risk” habitats under rapid climate change (Rehfeldt and others, 2006, 2009). At a larger geographic scale, higher elevation habitats can be separated by more than 50 kilometers (km), creating an archipelago of fragmented habitats. It is unclear how consistently these changes are reflected between these isolated mountain habitats.

During the past 13,000 years, vegetation zones in the Southwest, including the Colorado Plateau, have moved up in elevation and migrated northward as the climate has warmed (Vankat, 2013). In the process, it is likely that ecosystems ranging from mixed conifer forests to subalpine have become fragmented in a sea of lower elevation ecosystems. Concomitantly, species that are adapted to warmer and drier environments, for example, piñon pine (*Pinus edulis*), juniper

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(*Juniperus* sp.), and ponderosa pine (*Pinus ponderosa*), that have come to define southwestern woodlands, have radiated northward. There has been considerable interest in documenting the biogeography of species and communities associated with isolated mountains in southern Arizona, otherwise referred to as sky islands (Masta, 2000). However, there has been virtually no research examining community patterns on elevation gradients throughout the Colorado Plateau, which also contains complex gradients (Vankat, 2013).

An example of recent work on gradients in the region is Lightfoot and others (2008), which compared orthopterans and spiders along a latitudinal gradient that spanned from the Jornada Long-Term Research Program site in southern New Mexico to Bandelier National Monument in northern New Mexico. One of the most interesting results from that study was that spider assemblages were more similar to adjacent but different vegetation types, than they were to spider assemblages in the same vegetation type in different ecoregions. However, the only tree-dominated vegetation type represented in more than one area was piñon-juniper

woodland. It is unclear whether these patterns would be apparent in higher-elevation forests. Because higher elevation forests are more fragmented regionally, we expect that spider communities at higher elevations would show even stronger patterns in regional differences than was reported in Lightfoot and others (2008).

In this paper, we compare spider communities from two elevation gradients that are separated longitudinally from each other, one in the San Francisco Peaks (SFP) in northern Arizona, and the other in the Jemez Mountains (Bandelier National Monument [BAND]) in northern New Mexico. We address the following questions: (1) which species make up the ground-dwelling spider communities and do they show preferences for a given habitat type or do they occur in multiple habitats; (2) how do species composition and habitat preference compare between two widely separated locations with the same designated habitat types; and (3) from this comparison can we show the strength of habitat type versus ecoregion (in other words, adjacent but different vegetation types) in structuring these communities?



**EXPLANATION**

San Francisco Peaks habitats	Bandelier National Monument
● Piñon-juniper	■ Piñon-juniper
● Ponderosa pine	■ Ponderosa pine
● Mixed conifer	■ Mixed conifer

**Figure 1.** Map of the southern Colorado Plateau including the San Francisco Peaks (circles) and Bandelier National Monument (squares) study areas. Darker green areas between the two study areas typically represent ponderosa pine forests and mixed conifer vegetation types, as well as higher elevation forests. Piñon-juniper woodlands are nearly continuous between the two areas, whereas higher elevation forests are more fragmented.

**Table 1.** Habitat and climate characteristics at the two study locations, San Francisco Peaks (SFP), AZ and Bandelier National Monument (BAND), NM. Mean annual precipitation, maximum temperature, and minimum temperature are based on modeled 800 m PRISM data, which are not specific enough for each line of traps.

[°C, degrees Celsius; m, meters; cm, centimeters]

Area	Elevation (m)	Latitude	Longitude	Habitat	Dominant trees	Annual precipitation (cm)	Annual temperature, (°C)	
							Maximum	Minimum
SFP	2,011	35.5143	-111.6235	Piñon-juniper	<i>Pinus edulis, Juniperus monosperma</i>	39.6	19.0	2.5
BAND	1,948	35.7618	-106.2654	Piñon-juniper		39.6	18.1	0.9
SFP	2,285	35.3726	-111.5875	Ponderosa pine	<i>Pinus ponderosa</i>	52.7	15.5	0.6
BAND	2,454	35.8296	-106.3683	Ponderosa pine		55.7	16.5	-1.0
SFP	2,633	35.3624	-111.7413	Mixed-conifer	<i>Pinus strobiformis, Pseudotsuga menziesii, Abies concolor, Populus tremuloides</i>	67.7	12.4	-0.7
BAND	2,712	35.8511	-106.4102	Mixed-conifer		71.5	13.6	-0.4

## Sites and Methods

The San Francisco Peaks are located in Coconino County, Arizona; Bandelier National Monument is located in Sandoval County, New Mexico (fig. 1). Both areas are of volcanic origin with volcanic activity beginning about 6 Ma for SFP (Priest and others, 2001) and 18 Ma for BAND (Goff, 2009).

In both studies we compared three vegetation types, piñon-juniper woodland (PJ; low elevation), ponderosa pine (PIPO; medium elevation), and mixed-conifer/aspen forest (MC; higher elevation). The areas are at a similar latitude and approximately 475 km apart. SFP is part of the Arizona mountains forests ecoregion, BAND is part of the Southern Rockies forests ecoregion, and both are part of the broader temperate coniferous forest major habitat type (Ricketts and others, 1999). The data used for these comparisons were collected in 2009–11. We restricted the analysis to the three vegetation types where we had comparable data from each of the two gradients. The BAND study has been ongoing for more than 20 years (1992–present), sampling continuously during the growing season for many ground-dwelling arthropod taxa from piñon-juniper woodlands through mixed conifer (Lightfoot and others, 2008). The SFP study was initiated in 2010 and focused on ants, beetles, and spiders.

The three habitats studied at SFP and BAND are comparable with regard to elevation, dominant tree species, and climate (table 1). Temperature and precipitation data are based on modeled 30-year mean data using an 800-m pixel size (PRISM Climate Group, 2014), and are similar between sites. We established meteorological stations for all three habitats in the SFP since 2002 (Merriam-Powell Center for Environmental Research, 2014). The meteorological data do vary 2–8 centimeters (cm) in precipitation and 3–5 °C in temperature from PRISM data, indicating that modeled PRISM values do not precisely reflect climate at our scale of interest. We do not have comparable meteorological station data available for all of the BAND habitats.

To sample ground-dwelling spiders we used pitfall traps, which differed in trap type and sample duration between BAND and SFP studies. The SFP pitfalls consisted of 32 × 200 millimeters (mm) lipped borosilicate test tubes inserted in polyvinyl chloride (PVC) sleeves with a PVC cover, and filled with diluted ethylene glycol (Higgins and others, 2014). Pitfalls were placed in 2 lines of 10 traps in PJ; the lines in PIPO and MC were arranged with one set in the open and one set in forested areas to sample these two very distinct microhabitats that do not occur in the more open woodlands. Traps within a line and between lines were 10 meters (m) apart. We had 20 total traps per site for PJ, and 40 traps per site for PIPO and MC. Sampling occurred at three sites for each of the three vegetation types. Samples were collected after one month (approximately late August to late September) in 2010 and 2011.

The pitfall traps at BAND were somewhat larger (plastic cups inside tin cans, 7.5 cm top diameter and 10 cm deep) and placed in 5 lines of 6 traps, for a total of 30 traps per site. Within a line, traps were 10 m apart; the lines were at least 100 m apart. Propylene glycol was used as the preservative. Although we did not directly compare trap types, the smaller pitfall traps used for the SFP study were probably more efficient at collecting smaller individuals as reflected by the relatively high number of immature spiders. We also suggest they were more effective in sampling a larger number of species, as most of the species found in the SFP study and not found at BAND during the same time period have been recorded at BAND in other years. The open areas and closed canopy areas of PIPO sites at SFP were sampled separately and then combined. At BAND, the PIPO site was sampled continuously through open and closed canopy areas without separating them. More detail about the sampling can be found in Lightfoot and others (2008).

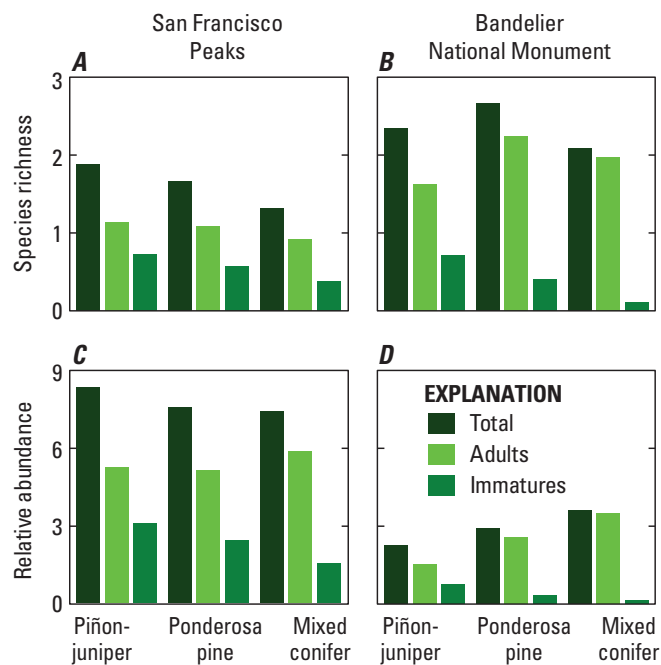
Samples were collected after two months (approximately late July to late September) in 2010 and 2011. In summer 2011, the Las Conchas wildfire burned most of the trap areas at BAND in the PIPO and MC habitats; therefore we used



pre-fire data from the fall of 2009 and 2010 for comparison. In order to compare results from both studies, we standardized the metric for spider catches that reflected the number of spiders captured per 10-cm pitfall trap perimeter per 30 days. Specimens from both studies were collected into 70 percent ethanol, sorted, and identified at the University of New Mexico (UNM) or Northern Arizona University (NAU). For both studies, the primary reference collection was deposited at UNM Museum of Southwestern Biology and a second reference at the NAU Colorado Plateau Museum of Arthropod Biodiversity.

## Data Analysis

To address our first and second research questions, we focused on five metrics that describe the spider communities at both locations and in the three habitats: (1) species richness and total abundance, (2) species composition, (3) family-level patterns, (4) dominant species, and (5) indicator species. These metrics then allowed us to address our third question



**Figure 2.** Graph of species richness (A, B) and relative abundance (C, D) in three habitat types: piñon-juniper, ponderosa pine, and mixed-conifer at the San Francisco Peaks (SFP) and Bandelier National Monument (BAND) study sites. Species richness in mean number of species per standardized trap/day of ground-dwelling spider species and relative abundance per standardized trap/day. Standardized trap size explained in Methods section. Significance values between SFP and BAND given in Results section.

concerning the strength of habitat type or ecoregion on structuring the communities.

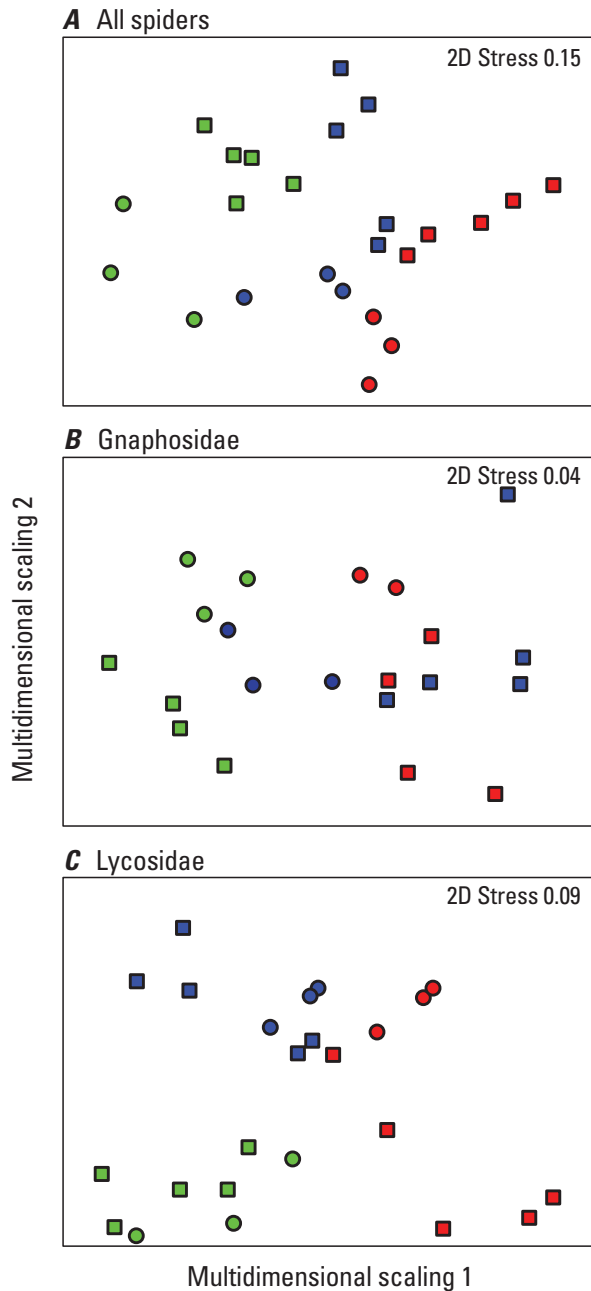
We combined data from the open and closed canopy SFP sites in PIPO and MC to more closely match the sampling at BAND. We defined spider species as generalists if they occurred in more than one habitat type and as specialists if they occurred in one habitat only. Single representatives of a given species were removed from all analyses. We analyzed the data two ways: (1) with immature spiders included in the analysis because they make up a large part of the active life stages and biomass (Norris, 1999; Jimenez-Valverde and Lobo, 2006), and (2) with adult stages only. To minimize the differences in sampling technique (trap design and placement) between SFP and BAND, we standardized the spider abundance values to reflect number of individuals per 10-cm length of the pitfall circumference per day of sampling.

For both locations, we compared spider species composition, species richness, and relative abundance in the habitats. To analyze differences in species richness and abundance between SFP and BAND, we used a two-factor analysis of variance (ANOVA): the factors were location (SFP and BAND) and habitat type (PJ, PIPO, and MC) nested within each location. We used species composition and the relative abundance of adults to analyze habitat and location effects (IBM Corp., 2013) for mean trap numbers, and Primer-6 software for multidimensional scaling (MDS) and an unweighted Bray-Curtis cluster analysis (Clarke and Gorley, 2006). Because samples were collected multiple times from the same traps, we used the PERMANOVA software (Anderson and others, 2008a) to analyze differences between locations and habitats. Data were square root transformed before analysis. Indicator species analysis was performed using PC-ORD software (McCune and others, 2002). The analysis is based on (1) the relative frequency of species and (2) the concentration of their abundance within groups, called fidelity and exclusivity, respectively, by McCune and others (2002). Species that are consistently found in only one habitat, even if they are rare, are strong indicators for that habitat.

## Results

### Species Richness and Abundance

A total of 1,741 individuals were collected in 79 taxa identified at the genus or species level (appendix). For all habitats at both SFP and BAND, Lycosidae and Gnaphosidae were the dominant families, as is common for ground-dwelling spiders throughout North America (Bradley, 2013). For both SFP and BAND, total species richness decreased with increasing elevation between PJ (38 species) and PIPO (24 species) habitats but increased again in MC (30 species), with no mid-elevation increase in richness, as seen in some other groups (Rahbeck, 1995). Examining species richness on



**EXPLANATION**

- |                     |                             |
|---------------------|-----------------------------|
| San Francisco Peaks | Bandelier National Monument |
| ● Piñon-juniper     | ■ Piñon-juniper             |
| ● Ponderosa pine    | ■ Ponderosa pine            |
| ● Mixed conifer     | ■ Mixed conifer             |

**Figure 3.** Multidimensional scaling ordination of ground-dwelling spider species (immature spider population removed). *A*, All spider taxa; *B*, Gnaphosid species only; *C*, Lycosid species only. Each symbol represents a line of traps. San Francisco Peaks site, circles; Bandelier National Monument site, squares; piñon-juniper habitat, green; ponderosa pine habitat, blue; mixed-conifer habitat, red.

**Table 2.** Number of species occurring in single and multiple habitats at San Francisco Peaks (SFP) and Bandelier National Monument (BAND) sites. Piñon-juniper habitat, PJ; ponderosa pine habitat, PIPO; and mixed-conifer habitat, MC.

Habitat	SFP only	BAND only	SFP and BAND	Total
PJ	14	6	0	20
PIPO	5	5	0	10
MC	8	7	2	17
PJ and PIPO	7	5	7	19
PIPO and MC	0	2	4	6
PJ, PIPO, and MC	1	1	5	7
<b>Totals</b>	<b>35</b>	<b>26</b>	<b>18</b>	<b>79</b>

a per sample basis indicated overall differences among habitats ( $df=2$ ,  $F=4.789$ ,  $P=0.009$ ) with a weak trend in decreasing species richness with increasing elevation at SFP and no significant differences at BAND (fig. 2). As was the case for most of the analyses, taxa dominated by adults (rather than immature individuals) showed differences within and between study areas. There were no differences in abundance among habitats ( $df=2$ ,  $F=0.068$ ,  $P=0.934$ ). Differences for location \* habitat were not significant for richness ( $df=2$ ,  $F=1.469$ ,  $P=0.231$ ) nor for abundance ( $df=2$ ,  $F=1.280$ ,  $P=0.279$ ). Species richness was significantly greater at BAND ( $df=1$ ,  $F=31.698$ ,  $P<0.001$ ), but significantly more individuals were collected at SFP ( $df=1$ ,  $F=75.821$ ,  $P<0.001$ ) (fig. 2). More species that occurred at BAND also occurred at SFP, while more unique species were collected at SFP (table 2, appendix).

**Spider Communities Among Habitats and Locations**

We found strong differences in the composition of spider communities among habitats and less so between locations; this clarified the ANOVA results, which looked only at number of species (richness) and abundance (table 2, appendix). In agreement with these values, the results of PERMANOVA tests showed the effect of location (SFP versus BAND) was not significant for all spiders combined (pseudo- $F=1.9918$ ,  $P=0.231$ ), for gnaphosids (pseudo- $F=1.4559$ ,  $P=0.299$ ), or for lycosids (pseudo- $F=1.8578$ ,  $P=0.322$ ). However, the effect of habitat was significant for all spiders combined (pseudo- $F=5.9398$ ,  $P=0.001$ ), for gnaphosids (pseudo- $F=3.7594$ ,  $P=0.001$ ) and for lycosids (pseudo- $F=10.697$ ,  $P=0.001$ ).

We used multidimensional scaling ordination (without including the immature stages) to visualize differences (fig. 3A–C) among habitats and locations. Spiders in the SFP habitats showed less scatter than BAND; PJ habitat was well separated from the other two habitats. Some of the trap lines in PIPO and MC sites overlapped at both locations. The Gnaphosidae showed less separation by habitat or location (fig. 3B) than the

Lycosidae, which were important contributors to the separation of habitats (fig. 3C). Analysis at the family level indicated that lycosids, gnaphosids, and linyphiids showed significant trends in abundance as elevation increased; lycosids ( $df=2$ ,  $F=10.786$ ,  $P<0.001$ ) and linyphiids ( $df=2$ ,  $F=8.305$ ,  $P<0.001$ ) increased, and gnaphosids ( $df=2$ ,  $F=20.380$ ,  $P<0.001$ ) decreased.

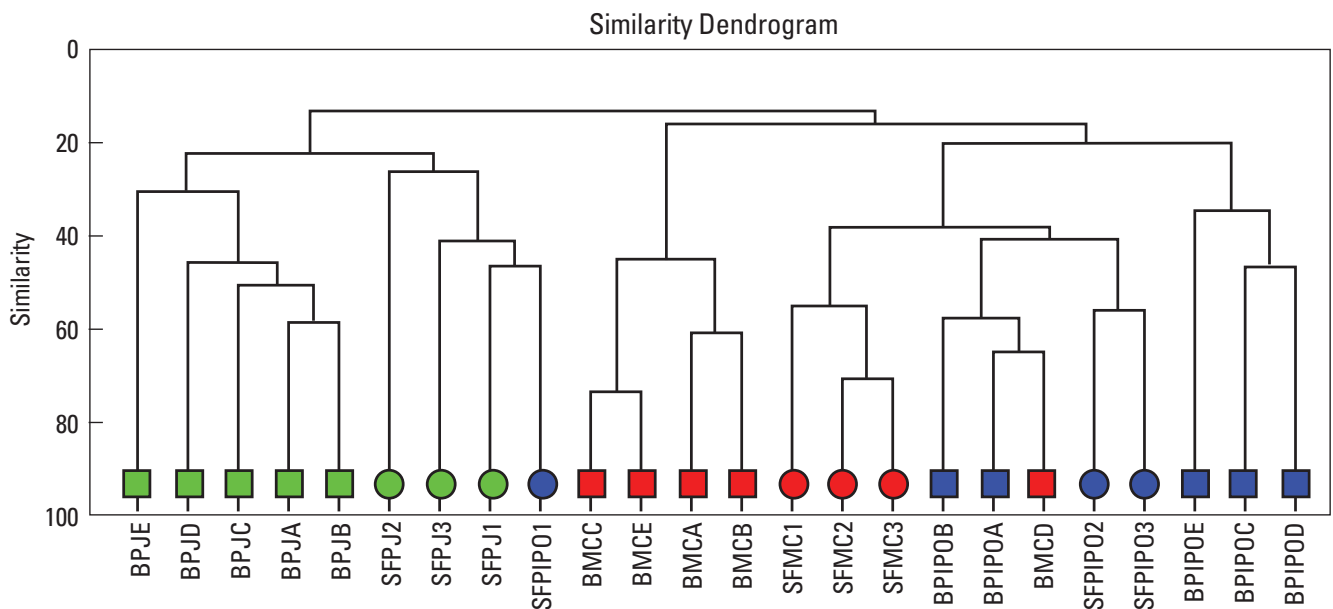
The cluster analysis (fig. 4) provided more resolution for the patterns seen in the MDS (fig. 3). The main division in the dendrogram is between PJ sites and combined PIPO and MC sites, with about a 20 percent similarity. Later divisions separated along location and habitat, with some mixing of both. The similarity levels among these sites never exceeded 70 percent, showing that there was a large amount of variation in both habitat and location.

The five most abundant species at each location and habitat type showed little overlap among locations (table 3A–C). The top five species made up about 50 percent of the abundance in PJ at SFP and BAND, but for the other two habitats, the proportion increased, as expected with fewer species at higher elevations (with the exception of SFP PIPO), but the proportion increased more at BAND (61.6 percent at PIPO and 82.6 percent at MC) than at SFP (48.4 percent and 76.6 percent at MC). The numbers of immature stages were high enough in most habitats to make up a large proportion of total spider numbers. Families contributing the most immature stages were Gnaphosidae and Lycosidae.

### Indicator Species Analysis

Another way of looking at habitat specificity is through indicator species analysis (table 4), which detects more than just numerically dominant species occurring in a habitat, as described in the Data Analysis section. For SFP, two of the five dominant PJ species were also indicators; at PIPO one of the dominant five was an indicator; and at MC two of the five were indicators. For BAND, one of the dominant five species was an indicator, and two of the five were indicators in PIPO and MC. Species that were not numerically abundant but important in distinguishing habitat types were *Pardosa montgomeryi* at SFP and *Anyphaena hespar*, *Trochosa terricola*, *Varacosa gosiuta*, and *Zorocrates karli* at BAND. Lycosids were indicators in all habitats (fig. 3C). Gnaphosids were indicators in PJ and MC, although present in all habitats, often as immature stages of *Zelotes*.

In general, spider species were specialists in habitat preference, with 20 in PJ only, 10 in PIPO only, and 17 in MC only or 59 percent of the total (table 2). Nineteen occurred in PJ and PIPO, 6 in PIPO and MC, and 7 in all three habitats (including immature stages of *Callilepis*, which probably represent multiple species, and the genus *Cicurina*, whose taxonomy is unsettled at present but at our locations probably includes several species). Within location, the number of species occurring in only one habitat at SFP was 14 in PJ, 5 in



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**Figure 4.** Dendrogram from Bray-Curtis cluster analysis for the effect of habitat and location on spider communities.

- |                           |                                   |
|---------------------------|-----------------------------------|
| San Francisco Peaks sites | Bandelier National Monument sites |
| ● Piñon-juniper           | ■ Piñon-juniper                   |
| ● Ponderosa pine          | ■ Ponderosa pine                  |
| ● Mixed conifer           | ■ Mixed conifer                   |

**Table 3.** The top five taxa, in relative abundance, in each habitat type. A, piñon-juniper; B, ponderosa pine, and C, mixed-conifer.

[imm, immature individuals]

A) Piñon-juniper					
San Francisco Peaks			Bandelier National Monument		
Taxon	Percent of total abundance	Cumulative percent	Taxon	Percent of total abundance	Cumulative percent
<i>Zelotes anglo</i>	19.1	19.1	<i>Schizocosa mccooki</i>	14.4	14.4
<i>Drassyllus mexicanus</i>	9.9	29.0	<i>Drassodes gosiutus</i>	13.3	27.7
<i>Zelotes imm.</i>	8.9	37.9	<i>Zelotes imm.</i>	9.9	37.6
<i>Drassodes imm.</i>	5.7	43.6	<i>Cicurina spp.</i>	7.7	45.3
<i>Habronattus imm.</i>	5.7	49.3	<i>Alopecosa kochi</i>	6.1	51.4

B) Ponderosa pine					
San Francisco Peaks			Bandelier National Monument		
Taxon	Percent of total abundance	Cumulative percent	Taxon	Percent of total abundance	Cumulative percent
<i>Alopecosa kochi</i>	16.7	16.7	<i>Pardosa yavapa</i>	17.1	17.1
<i>Pardosa yavapa</i>	9.2	25.9	<i>Alopecosa kochi</i>	13.7	30.8
<i>Zelotes imm.</i>	8.1	34.0	<i>Varacosa gosiuta</i>	11.8	42.6
<i>Xysticus montanensis</i>	7.7	41.7	<i>Cicurina spp.</i>	11.4	54.0
<i>Pardosa imm.</i>	6.7	48.4	<i>Zelotes imm.</i>	7.6	61.6

C) Mixed-conifer					
San Francisco Peaks			Bandelier National Monument		
Taxon	Percent of total abundance	Cumulative percent	Taxon	Percent of total abundance	Cumulative percent
<i>Alopecosa kochi</i>	55.6	55.6	<i>Cicurina spp.</i>	50.5	50.5
<i>Pardosa imm.</i>	7.0	62.6	<i>Pardosa uncata</i>	11.1	61.6
<i>Zelotes fratris</i>	6.2	68.8	<i>Helophora orinoma</i>	9.2	70.8
<i>Zelotes imm.</i>	4.1	72.9	<i>Alopecosa kochi</i>	8.6	79.4
<i>Micaria pulicaria</i>	3.7	76.6	<i>Zelotes fratris</i>	3.2	82.6

PIPO, and 8 in MC, for a total of 27 out of 35 (77 percent); at BAND there were 6 in PJ, 5 in PIPO, and 7 in MC, for a total of 18 out of 26 species (69 percent).

## Discussion

A major pattern that emerged was a significant degree of partitioning of communities among habitats in a predictable transition from piñon-juniper woodlands to ponderosa forests and mixed-conifer forests. We also found differences in spider communities among the regions, but not nearly to the degree as reported by Lightfoot and others (2008) who found that

adjacent but different habitats were much more similar than the same habitats in two areas. MDS (fig. 3) clearly showed that both habitat and location influenced the spider communities; but cluster analysis (fig. 4) and PERMANOVA results showed that habitat was the stronger of the two. Our study differed in that both areas are located on the southern Colorado Plateau and there has been continuity of habitats between SFP and BAND in the last 20,000 years, although higher elevation habitats have become more fragmented in the last 10,000 years (Vankat, 2013). Both the SFP and BAND also share the same forested vegetation types, whereas the three areas studied in Lightfoot and others (2008) ranged along a latitudinal gradient from the southern Chihuahuan desert (Jornada) to the northernmost Chihuahuan desert (Sevilleta National Wildlife

**Table 4.** Indicator species by habitat for San Francisco Peaks (SFP) and Bandelier National Monument (BAND) sites. PJ, piñon-juniper habitat; PIPO, ponderosa pine habitat; and MC, mixed-conifer habitat; NC, species not collected, therefore could not contribute to indicator value for combined locations; NP, not performed since species did not occur at SFP and BAND; NS, species not statistically significant as an indicator; imm., immature individuals.

Habitat	Species	P-value		
		SFP & BAND	SFP	BAND
PJ	<i>Schizocosa mccooki</i>	0.0002	0.0342	0.0012
	<i>Habronattus</i> imm.	0.0004	NS	0.0134
	<i>Latrodectus hesperus</i>	0.0036	NS	0.011
	<i>Drassyllus mexicanus</i>	0.0066	NS	NS
	<i>Drassodes</i> imm.	NP	0.0342	NC
	<i>Zorocrates karli</i>	NP	NC	0.011
	<i>Zelotes anglo</i>	NP	0.0342	NC
	<i>Schizocosa</i> imm.	NP	NC	0.0134
	<i>Drassodes gosiutus</i>	NS	NS	0.0134
PIPO	<i>Pardosa yavapa</i>	0.0002	0.0372	0.0034
	<i>Phrurolithus camawhitae</i>	0.0092	NS	0.023
	<i>Varacosa gosiuta</i>	NP	NC	0.0106
	<i>Hololena hola</i>	0.0352	NS	0.0346
	<i>Xysticus</i> imm.	0.049	NS	NS
	<i>Anyphaena hespar</i>	NP	NC	0.0372
MC	<i>Pardosa uncata</i>	0.0006	NS	0.0016
	<i>Cicurina</i> spp.	0.0038	NS	0.0016
	<i>Trochosa terricola</i>	NP	NC	0.0116
	<i>Zelotes fratris</i>	0.0492	NS	NS
	<i>Alopecosa kochi</i>	NS	0.0084	NS
	<i>Pardosa montgomeryi</i>	NP	0.0322	NC

Refuge) and finally to the southern Colorado Plateau (BAND). This suggests that there has been a much longer period of separation or fragmentation of habitats among the three areas.

A possible methodological reason explaining the different results between our study and that of Lightfoot and others (2008) may be the length of sampling time: two years and only the fall season for our study and seven years of year-round sampling for Lightfoot and others (2008). It is possible that short-term sampling collects mainly the more widespread or dominant species within habitats while longer-term sampling picks up more rare species (which might include more geographically restricted species), leading to a pattern of greater regional influence on species composition. A way to test this idea with the data from Lightfoot and others (2008) is to analyze the data for a few years only, and then add subsequent years to see if the pattern changes or not, and if so, determine how many years of sampling are needed before a change is detected. Even with our smaller dataset there were indications

that location influenced spider richness and abundance, but probably not as strongly as habitat type (fig. 3A–C). There were more unique species at SFP (35) than BAND (28) (appendix), which was driving some of the location difference. This may be due to regional distribution differences of species, such as *Calilena* spp., which occur westward from Arizona, Utah, and Nevada, but some of the species are widespread in the western U.S. (*A. utahana*, *M. pulicaria*, and *Z. lasalana*, so at least a part of the difference was likely due to undersampling. The three species just mentioned occurred at BAND, but not during the years used in this study (S. Brantley, unpub. data, 2015). Long-term studies may help us differentiate how habitat type and region organize spider communities.

We found the common pattern of decreasing species number with increasing elevation to be more pronounced at SFP (33 species in PJ, 28 in PIPO, and 18 in MC) with no mid-elevation increase, while at BAND richness changed little over the 3 habitats (22 species in PJ, 24 in PIPO, and 20 in MC), with only a slight mid-elevation increase (appendix). In mountain ranges in Canada, Bowden and Buddle (2010) did not show consistent changes in spider species numbers with elevation, in part because habitat structure did not always change (for example, forested sites occurred at different elevations). From this, we expected that species occurring in two of our habitats would be more likely to occur in PIPO and MC, because of similar canopy cover and litter. Instead, our results showed that species occurring in two habitats were more likely to be in PJ and PIPO at SFP, and at BAND were as likely to be in PJ and PIPO as PIPO and MC. Elevation changes cover a mixture of abiotic and biotic factors, which can confound explanation of species patterns (Körner, 2007); Bowden and Buddle's (2010) study design was able to separate abiotic elevation factors from vegetation and other habitat factors on their species distribution. In our study, we may be seeing the increasing importance of abiotic features at high-elevation besides forest cover (table 1 and Methods section), such as lower temperatures and higher precipitation (Rahbeck, 1995). Gnaphosids on Crete (Chatzaki and others, 2005) included many species that were widely tolerant of elevation changes. The gnaphosids at SFP and BAND were also somewhat less restricted by elevation (fig. 3B), showing less distinction between habitats compared with the lycosids (fig. 3C).

Otto and Svensson (1982) found different patterns in spider occurrence on an elevation gradient in Norway. At their sites, spiders at the highest elevation were widely distributed and occurred at some lower elevations, while the lowest elevation species were more restricted. An explanation they proposed is that high-elevation species disperse widely (referred to as fugitive species) and therefore occupy large areas. Spider species found in this high-latitude location may have already overcome the harsh abiotic conditions (compared to the southwestern US), where our mixed-conifer species were restricted perhaps by relatively hot and dry conditions at lower elevations and by less area where cooler conditions occur. The Linyphiidae at our sites were generally restricted to mixed-conifer habitat (appendix).



Although spiders are typically described as generalists in prey choice (Wise, 1993), they are often more specialized in their habitat preferences (Uetz, 1991). Of the 79 species collected over 3 habitats and 2 locations in this study, 59 percent were found in 1 habitat only (table 2, appendix). Within the dominant families Lycosidae and Gnaphosidae, which are speciose, there were examples of both habitat specialists and generalists. In the Lycosidae, specialists included *P. montgomeryi*, *P. uncatata*, and *T. terricola* in MC only, *P. orophila*, *P. yavapa*, and *S. mccooki* in PJ and PIPO; an example of a generalist is *A. kochi*, found in all habitats at both locations. In the Gnaphosidae, lower-elevation species included those in the genera *Drassodes*, *Herpyllus*, and *Micaria*, while MC genera included *Gnaphosa* and *Haplodrassus*. In the large gnaphosid genus *Zelotes*, *Z. anglo*, and *Z. lasalanus* occurred in PJ and PIPO, while *Z. fratris* occurred in PIPO and MC. Mallis and Hurd (2005), working on spider communities in six successional habitats in Virginia, found 50 percent were specialists (occurring in only one habitat) and no species was found in more than four habitats. *Pardosa* species were important there, and the widespread *T. terricola* also occurred in two habitats (the authors' disturbance recovery site and old field), whereas in our study it occurred only in mixed-conifer. Chatzaki and others (2005) sampled gnaphosids in five habitats on elevation gradients on Crete, finding that 14 (26 percent) of 54 species were found in only one habitat, and that the highest elevation sites had the fewest species and very little overlap with species from the other four habitats.

All habitats were strongly dominated by 4–6 species. The five most abundant taxa in each habitat were often different between locations (table 3A–C); when the habitats shared species, they were in different rank order. In contrast Roughley and others (2006) found four out of five of the most abundant spider species were shared between tallgrass prairie and forest in an ecotone setting in Manitoba, Canada. In fact, the dominant spider, *Pardosa moesta*, occurred in both habitats. While these habitats appear very different to people, they may provide some common features, such as cover and soil moisture, which are likely important from the spiders' point of view. In a Colorado grassland and mixed-grass/shrub landscape, Weeks and Holtzer (2000) found virtually no species overlap among species of Lycosidae or Gnaphosidae between the two habitats. Though the area is described broadly as shortgrass steppe, the two habitats were very different in the amount of ground cover (much less in the grass/shrub habitat), which probably influenced the microhabitat tolerances and mobility of the spiders.

Examples of species that were significant indicator species but were not among the dominant taxa (tables 3, 4) include *L. hesperus* and *Z. karli* in PJ, *P. camawhitae* and *H. hola* in PIPO, and *T. terricola* in MC. Useful indicator species for environmental categories (such as habitat type) can be overlooked if only the dominant taxa are examined. We do not yet have a complete understanding of the factors influencing spider habitat occurrences.

Consistent among habitats and locations in our study was the high relative abundance of immature-stage individuals,

which generally cannot be assigned to a species, but can be a large part of spider biomass in a given area (Weeks and Holtzer, 2000), creating difficulties in assessing richness and turnover (Norris, 1999; Jimenez-Valverde and Lobo, 2006). Immature stages were included in the lists of dominant taxa for each habitat type (table 3A–C) to show their importance in relative abundance, but were excluded from the MDS to clarify habitat associations (an MDS including immature stages did not alter the overall patterns; data not shown).

An interesting result from this study was the greater overlap in spider species between PJ and PIPO habitats, rather than between PIPO and MC (appendix), which appeared to be more similar in vegetation structure to each other than to PJ. A possible explanation is the shared geologic and climatic history of the PJ and PIPO habitat types in the southwestern U.S. About 14,000 yr. before present (B.P.) subalpine forests were found at elevations below 2,300 m (Anderson and others, 2008b) in parts of the southwestern U.S., so that these forests covered a much wider area than they do today (compare with our current habitat types, fig. 1, table 1). By 11,500 yr B.P. the climate had warmed, causing a retreat of mixed-conifer plant species; summer monsoon rains also increased, which allowed ponderosa pine, oaks, and piñon pine to move into some of the areas vacated by mixed-conifer species (Toney and Anderson, 2006; Anderson 2008b). Under these conditions the spider species from PJ and PIPO sites perhaps arrived in the area at about the same time, while the MC species were retreating with the wetter forests.

The southern Rocky Mountains and Colorado Plateau form an ideal landscape in which to study the distributions of higher-elevation arthropod species, as forested areas that are more connected in the Rockies become increasingly fragmented on the Colorado Plateau. Species may be “filtered” out by fragmentation (isolation) and (or) a warmer, drier climate (Wiescher and others, 2012). Such studies will allow us to predict distribution changes due to global warming, which is expected to increase temperatures and extreme climate events in the southwestern U.S. (Diffenbaugh and Ashfaq, 2010). While much work remains in understanding regional patterns in spider communities in the southwestern U.S., the cumulative results of this study and others (Lightfoot and others, 2008; Higgins and others, 2014) are steadily leading to a more complete picture.

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# Appendix

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**Appendix.** List of taxa and total specimen numbers collected at the San Francisco Peaks (SFP) and Bandelier National Monument (BAND) sites by habitat.

[PJ, piñon-juniper; PIPO, ponderosa pine; MC, mixed-conifer; imm., immature individuals]

Family	Species	Habitat Type									
		PJ		PIPO		MC		Total			
		SFP	BAND	SFP	BAND	SFP	BAND	SFP	BAND	BOTH	
<i>Agelenidae</i>	<i>Agelenopsis utahana</i>	0	0	0	0	1	0	1	0	1	
	<i>Novalena lutzi</i>	0	0	0	0	0	1	0	1	1	
	<i>Calilena arizonica</i>	3	0	1	0	0	0	4	0	4	
	<i>Calilena restricta</i>	0	0	0	0	1	0	1	0	1	
	<i>Hololena hola</i>	1	4	3	14	0	0	4	18	22	
<i>Anyphaenidae</i>	<i>Anyphaena hespar</i>	0	1	0	5	0	0	0	6	6	
<i>Clubionidae</i>	<i>Clubiona oteroana</i>	0	0	0	0	0	1	0	1	1	
<i>Corinnidae</i>	<i>Castianeira luctifera</i>	0	0	5	0	0	0	5	0	5	
	<i>Castianeira occidens</i>	1	1	13	3	0	1	14	5	19	
	<i>Phrurolithus camawhitae</i>	5	0	4	3	1	1	10	4	14	
	<i>Phrurolithus schwarzi</i>	1	0	0	0	0	0	1	0	1	
<i>Dictynidae</i>	<i>Phrurotimpus certus</i>	4	0	3	0	0	0	7	0	7	
	<i>Cicurina spp.</i>	0	14	19	24	6	159	25	197	222	
	<i>Dictyna apachea</i>	0	0	2	0	0	0	2	0	2	
	<i>Dictyna personata</i>	0	1	0	0	0	0	0	1	1	
<i>Euctenizidae</i>	<i>Lathys delicatula</i>	0	1	0	0	0	0	0	1	1	
	<i>Neoapachella rothi</i>	0	0	0	0	3	0	3	0	3	
<i>Filistatidae</i>	<i>Kukulcania imm.</i>	1	0	0	0	0	0	1	0	1	
<i>Gnaphosidae</i>	<i>Callilepis imm.</i>	9	0	2	0	1	0	12	0	12	
	<i>Drassodes gosiutus</i>	14	24	1	0	0	0	15	24	39	
	<i>Drassodes neglectus</i>	0	0	1	0	0	0	1	0	1	
	<i>Drassyllus dromeus</i>	0	0	0	5	0	0	0	5	5	
	<i>Drassyllus lepidus</i>	3	0	0	0	0	0	3	0	3	
	<i>Drassyllus mexicanus</i>	28	6	29	0	0	0	57	6	63	
	<i>Gnaphosa muscorum</i>	0	0	0	7	0	4	0	11	11	
	<i>Haplodrassus bicornis</i>	0	0	0	2	0	0	0	2	2	
	<i>Haplodrassus signifer</i>	0	0	0	0	0	8	0	8	8	
	<i>Herpyllus cockerelli</i>	1	0	0	0	0	0	1	0	1	
	<i>Herpyllus propinquus</i>	1	0	0	0	0	0	1	0	1	
	<i>Micaria longipes</i>	3	0	0	0	0	0	3	0	3	
	<i>Micaria pulicaria</i>	0	0	0	0	9	0	9	0	9	
	<i>Nodocion rufithoracicus</i>	1	0	0	0	0	0	1	0	1	
	<i>Zelotes anglo</i>	54	0	6	0	0	0	60	0	60	
	<i>Zelotes fratris</i>	0	0	3	4	15	10	18	14	32	
	<i>Zelotes lasalanus</i>	1	0	1	0	0	0	2	0	2	
	<i>Hahnidae</i>	<i>Neoantistea gosiuta</i>	0	0	0	4	0	0	0	4	4
	<i>Linyphiidae</i>	<i>Agneta imm. and females</i>	0	0	3	0	0	0	3	0	3
<i>Aphileta misera</i>		0	0	0	0	4	0	4	0	4	
<i>Ceratinella brunnea</i>		0	0	0	0	1	0	1	0	1	
<i>Grammonota gentilis</i>		0	0	0	0	0	1	0	1	1	

## Appendix.—Continued

Family	Species	Habitat Type								
		PJ		PIPO		MC		Total		
		SFP	BAND	SFP	BAND	SFP	BAND	SFP	BAND	BOTH
	<i>Helophora orinoma</i>	0	0	0	0	0	29	0	29	29
	<i>Lepthyphantes turbatrix</i>	0	0	0	0	2	0	2	0	2
	<i>Mermessus taibo</i>	0	0	2	0	4	2	6	2	8
	<i>Pityohyphantes cristatus</i>	0	0	0	0	1	1	1	1	2
	<i>Spirembolus pallidus</i>	0	0	0	1	0	0	0	1	1
	<i>Wubana drassoides</i>	0	0	0	5	0	3	0	8	8
<i>Lycosidae</i>	<i>Alopecosa kochi</i>	5	11	85	29	135	27	225	67	292
	<i>Hogna sp.</i>	3	0	0	0	0	0	3	0	3
	<i>Hogna carolinensis</i>	0	0	2	0	0	0	2	0	2
	<i>Pardosa montgomeryi</i>	0	0	0	0	6	0	6	0	6
	<i>Pardosa orophila</i>	0	3	8	1	0	0	8	4	12
	<i>Pardosa uncata</i>	0	0	0	0	1	35	1	35	36
	<i>Pardosa yavapa</i>	0	0	47	36	0	6	47	42	89
	<i>Schizocosa mccooki</i>	7	26	0	1	0	0	7	27	34
	<i>Schizocosa saltatrix</i>	0	1	0	0	0	0	0	1	1
	<i>Trochosa terricola</i>	0	0	0	0	0	8	0	8	8
	<i>Varacosa gosiuta</i>	0	1	0	25	0	0	0	26	26
<i>Mimetidae</i>	<i>Mimetus hesperus</i>	1	0	0	0	0	0	1	0	1
<i>Philodromidae</i>	<i>Apollophanes texanus</i>	0	1	0	1	0	0	0	2	2
	<i>Ebo imm.</i>	0	4	0	0	0	0	0	4	4
	<i>Thanatus altimontis</i>	1	0	0	0	0	0	1	0	1
	<i>Thanatus coloradensis</i>	0	4	0	1	0	0	0	5	5
<i>Pholcidae</i>	<i>Psilochorus imitatus</i>	0	3	0	1	0	0	0	4	4
	<i>Psilochorus utahensis</i>	12	0	28	0	0	0	40	0	40
<i>Salticidae</i>	<i>Habronattus geronimo</i>	2	0	0	0	0	0	2	0	2
	<i>Mexigonus arizonensis</i>	0	0	0	1	0	0	0	1	1
	<i>Pellenes imm.</i>	1	0	0	0	0	0	1	0	1
	<i>Phidippus imm.</i>	1	0	0	0	0	0	1	0	1
<i>Theraphosidae</i>	<i>Aphonopelma imm.</i>	1	0	0	0	0	0	1	0	1
<i>Theridiidae</i>	<i>Euryopsis scriptipes</i>	2	1	8	2	0	0	10	3	13
	<i>Latrodectus hesperus</i>	4	8	16	0	0	0	20	8	28
	<i>Steatoda hespera</i>	0	0	0	0	0	2	0	2	2
	<i>Thymoites sclerotis</i>	2	0	1	0	0	0	3	0	3
<i>Thomisidae</i>	<i>Synema sp. probably neomexicanum</i>	3	0	1	0	0	0	4	0	4
	<i>Xysticus apachecus</i>	1	2	13	0	6	0	20	2	22
	<i>Xysticus gulosus</i>	1	0	0	0	0	0	1	0	1
	<i>Xysticus locuples</i>	0	1	0	2	0	1	0	4	4
	<i>Xysticus montanensis</i>	0	0	39	5	1	6	40	11	51
<i>Zorocratidae</i>	<i>Zorocrates karli</i>	0	8	0	0	0	0	0	8	8
Totals	Abundance	178	126	346	182	198	306	722	614	1,336
Totals	Species	33	22	28	24	18	20	54	43	79